Revealing anole diversity in the highlands of the Northern Andes: New and resurrected species of the *Anolis heterodermus* species group

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Abstract

The *Anolis heterodermus* group comprises eight big-headed and short-legged lizard species from the highlands of the northernmost South American Andes. Recent studies revealed unknown lineages within this group that had previously been categorized as a species complex. By widely sampling and applying an integrative taxonomic framework, we (1) assessed the species diversity of the group using a molecular dataset (two mitochondrial and one nuclear markers) along with an inclusive morphological study (scalation, scale configuration and ornamentation, morphometrics, and dewlap and body colour patterns); and (2) we inferred the evolutionary relationships within this species group. Our analyses confirmed the formerly reported differentiation between populations of those high-altitude lizards, and we identified several unknown evolutionary lineages. Our results provided evidence for the existence of nine distinct, independently evolving evolutionary lineages in the *heterodermus* group. As a result, we described two morphologically and genetically highly distinct lineages as species new to science (*A. quimbaya* **sp. nov.** and *A. tequendama* **sp. nov.**). We redescribed *A. heterodermus* and erected as a valid species *Anolis richteri,* a previously described synonym of *A. heterodermus*. A taxonomic key for the identification of species of the *Phenacosaurus* clade was presented. The identification of two additional poorly-known lineages suggested that the diversity of this group of lizards is still unknown; therefore, it is necessary to establish measurements for the group´s conservation, as well as to perform fieldwork and revision of herpetological collections to identify possible hidden diversity within the group.

Keywords

Introduction

The big-headed and short-legged anoles (Dactyloidae) from the highlands of the northernmost South American Andes were earlier grouped under the genus *Phenacosaurus* Barbour, 1920. These lizards were characterized mainly by the presence of heterogeneous flank scalation, prehensile tails, rectangular-shaped ileum processes, and extended toepads from the base of the toe (Barbour 1920; Dunn 1944; Lazell 1969). Later, this genus was recog-

nized as a nested clade within *Anolis* (e.g., Etheridge 1959; Etheridge and de Queiroz 1988). After the evidence of monophyly emerged (Poe 1998), studies started to formally use *Anolis* instead of the formerly named *Phenacosaurus* as a different genus (e.g., Jackman et al. 1999; Poe 2004; Nicholson et al. 2005; Castañeda and de Queiroz 2011, 2013; Nicholson et al. 2012; Poe et al. 2017). Currently, the name *Phenacosaurus* refers to a clade (Castañeda and de Queiroz 2011, 2013) or subclade (Poe et al. 2017) of *Anolis*.

Traditionally, *Phenacosaurus* lizards were grouped in three morphologically-similar groups: the *heterodermus*, *orcesi*, and *neblininus* groups (Williams et al. 1996); but recent evidence indicates that *Phenacosaurus* is a subclade of *Anolis* which includes eight species from the two former groups (*Anolis euskalerriari*, *A. heterodermus*, *A. inderenae*, *A. nicefori*, *A. orcesi*, *A. proboscis*, *A. tetarii*, and *A. vanzolinii*) (Poe et al. 2017). These anoles exhibit from nearly homogeneous to strongly heterogeneous scalation on the flanks, the presence of casqued-heads (i.e., an enlargement of the bones on the top of the skull named as parietal casque or crown, that is less evident in *A. orcesi* and in *A. proboscis*), prehensile tails, and lamellar subdigital scales of all digits extending from the most proximal phalanges, with a distribution restricted to the highlands (> 1800 m) of the Northern Andes (Williams et al.1996; Castañeda and de Queiroz 2011, 2013; Poe et al. 2017). The species with homogeneous or slightly heterogeneous flanks and dorsal scalation (*A. euskalerriari*, *A.nicefori*, *A.orcesi,* and *A. proboscis*) exhibit allopatric distributions and unique characteristics (e.g., *A. proboscis*) that makes them easily distinguishable. However, the remaining species are very difficult to distinguish, and so discerning their taxonomic boundaries becomes a challenge, especially because their populations are sympatrically or parapatrically distributed and exhibit high intra-population phenotypic variation (Lazell 1969).

Lazell (1969) highlighted early attempts to distinguish species within the *heterodermus* group (e.g., *P. richteri* Dunn 1944 and *P. paramoensis* Hellmich 1949), and these failed because of the large overlap of scalation between the species. Consequently, all taxa were synonymized under *A. heterodermus* (formerly *P. heterodermus*) (Lazell 1969) or referred to as an unresolved species clade complex (Williams et al. 1996). A posterior study, using both nuclear and mitochondrial DNA sequences documented a non-correspondence between molecular and geographic distances and inferred *A. heterodermus* to be paraphyletic relative to *A. inderenae* and *A. vanzolinii*, demonstrating that *A. heterodermus* is a clade composed of a complex of sibling species (Castañeda and de Queiroz 2011). This hypothesis was recently confirmed, also revealing that disparate matching between geography and genes in *A. heterodermus* populations occurs also at relatively short geographic distances and documenting at least three independent evolutionary lineages in the Colombian Andes (Vargas-Ramírez and Moreno-Arias 2014). Therefore, they proposed that these cryptic lineages could correspond to distinct species; but they also stated that these

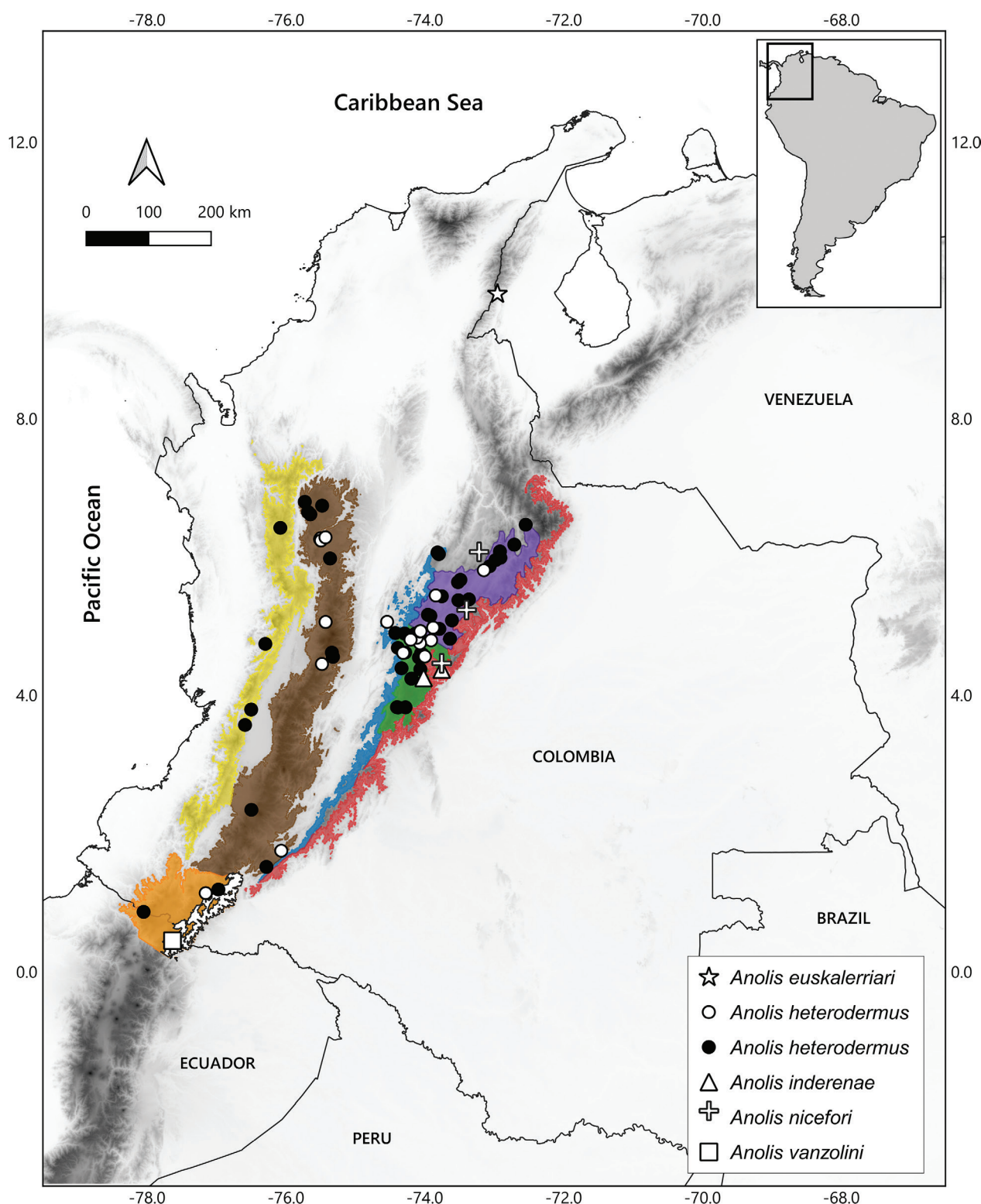findings should be supported with additional lines of evidence.

Considering that these lizards inhabit regions with high human intervention, recognizing their diversity is crucial for delineating effective conservation measures since these anoles are the unique Dactyloidae species inhabiting highlands in the Northern Andes; and they represent a distinctive phylogenetic, morphological, and functional reservoir (Vargas-Ramírez and Moreno-Arias 2014). These anoles represent the twig anole ecomorph (Moreno-Arias and Calderón-Espinosa 2016) with lineages sharing similar and very cold-adaptive ecophysiological traits (Méndez-Galeano et al. 2020), simultaneously exhibiting high variability in their scalation (Lazell 1969) and thermoregulatory behaviours (Méndez-Galeano and Calderón-Espinosa 2017; Méndez-Galeano et al. 2020). Furthermore, some lineages show unique male courtship displays (Beltrán and Barragán-Contreras 2019) indicating a diverse communication strategy across lineages, which could also be affected by the negative demographic responses and even by local extinction propensity documented at high levels of fragmentation and habitat loss (Moreno-Arias and Urbina-Cardona 2013). Lastly, the extinction risk of highland anoles generated by human activities synergically acting with climate change remains virtually unknown. Therefore, focusing on Dactyloidae diversity is a key step towards the evaluation of their threats.

By considerably extending sampling of the *Anolis heterodermus* species group populations throughout the northern Andes and using an integrative taxonomic framework, the goals of this research were to (1) revise the species diversity of the group by combining a molecular dataset (two mitochondrial and one nuclear markers) with an inclusive morphological study (scalation, scale configuration and ornamentation, morphometrics, and dewlap and body colour patterns) and (2) to infer the evolutionary relationships within the species group. As a result of our analyses, we redescribed one species, resurrected another species, and described two genetically and morphologically highly distinct evolutionary lineages as new species to science.

Methods

Molecular sampling

Twenty-five tissue samples for this study were taken from individuals assigned to the *A. heterodermus* species group from 14 localities in the highlands of the northern Andes (Fig. 1; Table S1). The samples were obtained from toe-clippings or leg muscles and stored in 96% ethanol. Remaining tissue samples, and DNA extractions were kept at the **BTBC** Banco de Tejidos de la Biodiversidad, Instituto de Genética, Universidad Nacional de Colombia.

Figure 1. Geographic localities of specimens of the *heterodermus* subgroup (*sensu* Williams et al. 1996), *A. nicefori* and *A. eu-skalerriari* studied across Northern Andes > 1500 m. White symbols correspond to localities with individuals included in both molecular and morphological analyses, and black symbols correspond to localities with individuals included only in morphological analyses. Colored areas indicate the following regions: the Andes before its ramification in the three Cordilleras (A) in orange, The eastern slope of Andes (EA) in white, Western Cordillera (W) in yellow, Central Cordillera (C) in brown, the western slope of Eastern Cordillera (EW) in blue, southern Cundiboyacense plateau and its surrounding mountains (PS) in green, northern Cundiboyacense plateau and its surrounding mountains (PN) in purple and, eastern slope of Eastern Cordillera (EE) in red.

Phylogenetics, phylogeographic, genetic divergence, haplotype network, and species delimitation analyses

A complete molecular dataset comprising sequences of the 25 newly obtained samples, plus the sequences obtained by Vargas-Ramírez and Moreno-Arias (2014) was assembled (Table S1). The phylogeographic differentiation of lizards belonging to different populations of the *Anolis heterodermus* subgroup was evaluated using two independent datasets. These were a 531-bp-long mitochondrial (mtDNA) fragment corresponding to the cytochrome oxidase subunit I (COI) (complete sample set, $N = 93$) and a subsample set including representatives of the COI clades together with sequences of the species *A. euskalerriari* and *A. orcesi*, corresponding to the concatenated partial NADH dehydrogenase subunit II (ND2), the adjacent transfer-RNAs (tRNA-Trp, tRNA-Ala, tRNA-Asn, tRNA-Cys and tRNA-Tyr), and cytochrome oxidase subunit I (COI) (selected sample set, $N = 38$; 1036 bp, 368 bp and 531 bp, respectively). Phylogenetic relationships among representatives of each mitochondrial clade were assessed using a 3694-bp-long alignment comprising the three mitochondrial fragments concatenated with the 1759-bp-long fragment of the nuclear (nDNA) recombination activating gene 1 (RAG1). The data set partitioning and phylogenetic analyses (i.e., Bayesian and Maximum likelihood) were performed following Vargas-Ramírez and Moreno-Arias (2014) and Moreno-Arias et al. (2020). For tree rooting, *Polychrus marmoratus* was used as an outgroup. To assess genetic differences among populations of the *Anolis heterodermus* species group, uncorrected *p*-distances for the ND2 gene were calculated using MEGA 7.0.21 (Kumar et al. 2016). To evaluate the amount of allele sharing between populations, parsimony networks were drawn for the mitochondrial COI and nuclear Rag1 sequences using TCS 1.21 (Clement et al. 2000). Furthermore, the mtDNA data (ND2+tRNA+COI) was used to identify putative species boundaries by employing the non-coalescent species delimitation method mptp. For this, the Bayesian tree based on the mtDNA sequences and the MPTP web server (http://mptp.h-its.org) were used.

Morphology

The total morphology dataset included 158 individuals representing all species of the *heterodermus* subgroup (*sensu* Williams et al. 1996) and covering almost their entire distributional area (Fig. 1; Table S1; Appendix 1). This dataset included individuals from type series of *A. heterodermus*, *A. inderenae, A. vanzolinii* and *A. richteri*; one of the hypothesized synonyms of *A. heterodermus*. The dewlap and body colour pattern datasets included 272 pictures (61 and 211, respectively) from 28 localities including individuals from all the subgroup species (Tables S2, S3). Examined specimens (Appendix 1) came from **EPN** Museum of National Polytechnique School of Ecuador; **ICN** reptile collection of the Natural Sciences Institute of the National University of Colombia;

IAvH Museum of Collection of Biological Resources Research Institute Alexander von Humboldt, Colombia; **MECN** Ecuadorian Museum of Natural Sciences, Ecuador; **MNHN-RA** Muséum National d'Histoire Naturelle, France, **MUAH** Herpetological Museum of Antioquia University, Colombia; **PSO-CZ** Natural History Museum of Nariño University, Colombia; **QCAZ** Zoological Museum of Pontific Catholic University of Ecuador. Other used acronyms correspond to field numbers of specimens pending to be catalogued at **ICN**.

A total of 67 characters were recorded for both morphological analyses and taxa descriptions: ten morphometrics, 17 scale counts, and 40 scale organizations and ornamentations – hence the scalation pattern. Of these characters, 57 corresponded to the ones already proposed by Williams et al. (1995), Poe (2004), and Köhler (2014). The remaining characters were proposed and recorded in this study. The newly proposed characters included three for scale counts (Supplementary informations): 1) the first dorsal scale row where dorsal scales are surrounded by granules, 2) total number of lamellae in the fourth toe, and 3) number of sublabial scales in contact with the infralabials. Additionally, seven characters for scalation pattern were included: 1) dorsal flat scales at a distance of 10% of snout-vent length configured according the three types. Type 1: scales with the same size (1-1-1), type 2: a large scale and small one around half of size (1-0.5) and type 3: a large scale, a second one around half of size and a third one around quarter of size (1-0.5-0.25); 2) nuchal crest, continuous or discontinuous; 3) shape of scales of the nuchal crest whether conic, bulbous or flat; 4) dorsal crest, continuous or discontinuous; 5) dorsal crest size extending to first quarter of the body, to the middle of the body, or to the tail; 6) casque head (crown) "V" or "U" shaped; and 7) a continuous row of enlarged sublabial scales reaching the mouth's commissure or a line below the first canthal scale.

Morphometrics data were first size corrected to avoid allometric effects. To do that, we regressed all nine variables against snout-vent length and extracted the standardized residuals. Posteriorly with the standardized dataset plus snout-vent length data, we applied a MANOVA with sex as a factor to detect sexually dimorphic variables and discarded them for posterior analyses. With the size and sex corrected for this dataset, we identified morphometrics groups with a k-means analysis, making groupings from $K = 3$ to $K = 12$. To choose the best grouping we used the maximum average value of cohesion from a silhouette analysis. Such analysis corresponds to a graphical method used to validate the consistency of groups of data using cohesion as a measure, ranking from -1 to +1, indicating how similar an object is to its own group compared to other clusters, if high object values are well-matched with their own group. Therefore, the group is consistent and statistically valid (Rousseeuw 1987). The former analyses were conducted using the functions kmeans of the R package kmeansstep (Towers 2019) and the silhouette analysis using the R package cluster (Maechler et al. 2019) on the R statistical software (R Core Team 2018). Finally, we described morphometrical variation by

means of a PCA using the correlation matrix, extracting components with an eigenvalue > 1, and plotting the best grouping according to individual scores at each component varimax rotated.

A similar procedure of data transformation and grouping was implemented for the other two datasets. For scale count, the procedure was the same except for the size correction. For the scalation pattern, we first transformed all multistate variables to binary ones, and the sex correction was tested with a X^2 independent test. Second, we conducted a grouping analysis with the function kmodes of the R package klaR (Weihs et al. 2005). To describe scalation pattern variation a CATPCA was conducted instead of a PCA. Principal components and correspondence analysis were conducted uisng SPSS 22 (IBM 2013).

Dewlap configuration and body pattern

We categorized the dewlap configuration (colour and pattern) and the body pattern of individuals belonging to each morphological group defined by the pattern scales analysis from photographs taken in the field and representing at least the same localities of individuals analysed for morphology and molecular analyses (Tables S1–S3). To avoid a subjective classification, all procedures were performed by only one investigator (IB). Because the photos were taken in the field with different light exposures, we did not use a standard colour reference chart for dewlap colour classification. Instead, the classification was performed according to the colour categories seen by the researcher. Body pattern categorization included several measurements: the body pattern (longitudinal, multicolour, solid, spotted, and banded), body coloration and the presence/absence of a coloured tail patch, a rostral line, and a flank line (see Fig. S1 for descriptions of pattern categories and the other body traits).

Prior to analyses, we tested for differences between males and females in both dewlap configurations and body patterns. Since we did not find strong evidence of sexual dimorphism in these traits (Fisher's exact test dewlap: $p = 0.19$, body pattern: $p = 0.15$), we analysed all individuals together. We analysed the dewlap configuration and body pattern independently because in many cases, we did not have the information available for the same individual. Moreover, signals located in different body regions are likely to be influenced by different ecological pressures. For instance, coloration and other patterns in "concealed" body parts (e.g., dewlap), might be driven by sexual selection, while those in "exposed" body parts (e.g., dorsum), might be constrained by natural selection (Stuart-Fox and Ord 2004).

First, we tested if *heterodermus* populations shared similar dewlap configurations and body patterns, using a multiple correspondence analysis (MCA) using the R packages FactoMineR (Husson et al. 2020) and factoextra (Kassambara and Mundt 2020) on R statistical software. Missing values were handled using the R package missMDA (Husson and Josse 2020). Then, we tested for

differences in dewlap and body pattern only between the *heterodermus* subgroups using a Fisher's exact test. The Bonferroni correction for multiple pairwise comparisons was performed using the R package RVAideMemoire (Hervé 2020). Although spectrophotometric measurements would most objectively identify animal coloration (Endler 1990), it was not possible to obtain this information. Therefore, our approach was preliminary and was mostly focused on detecting differences between populations relative to a human observer, without inferring the biological significance of such differences.
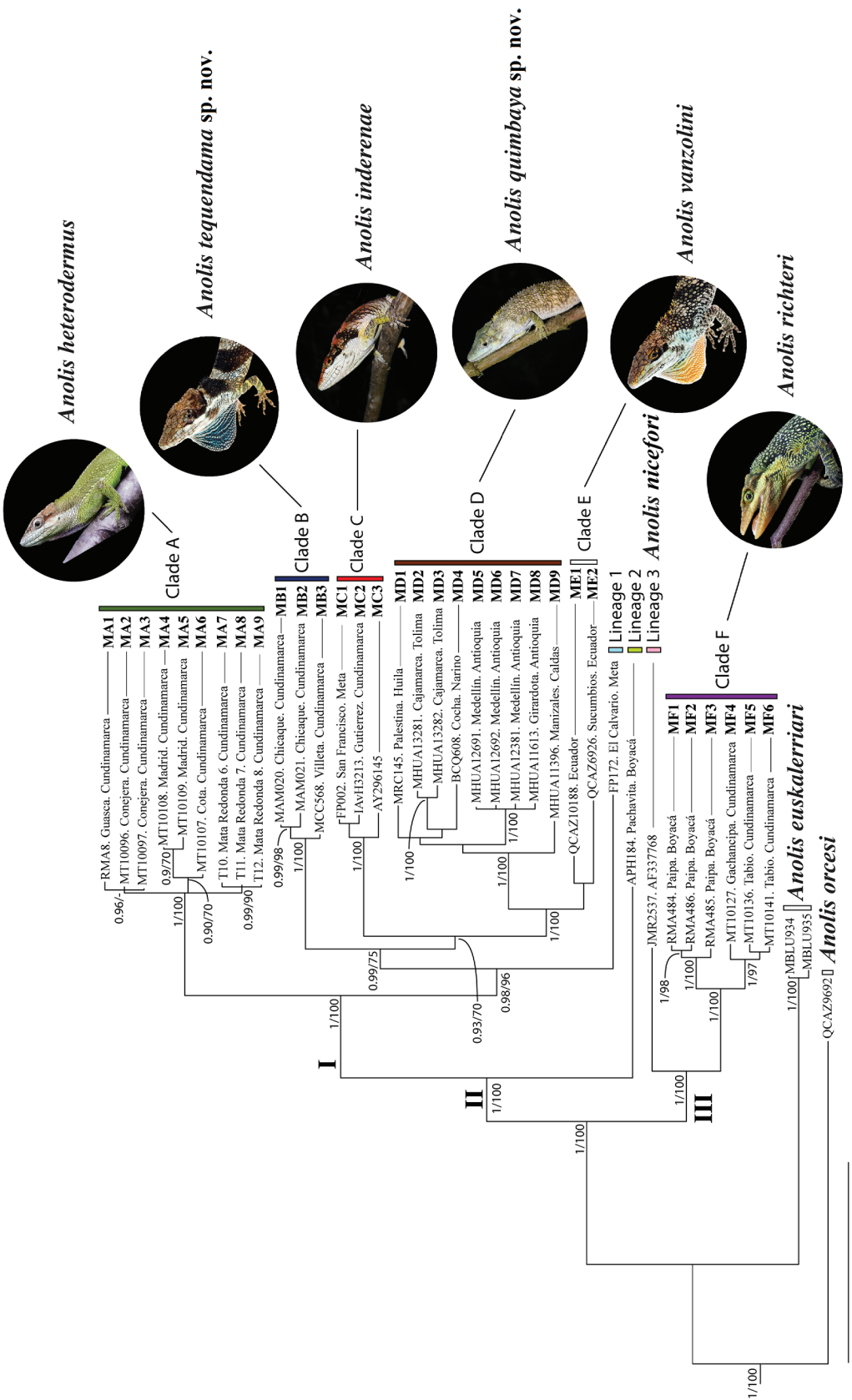
Results

Phylogenetic, phylogeographic, genetic divergence, haplotype networks, and species delimitation analyses
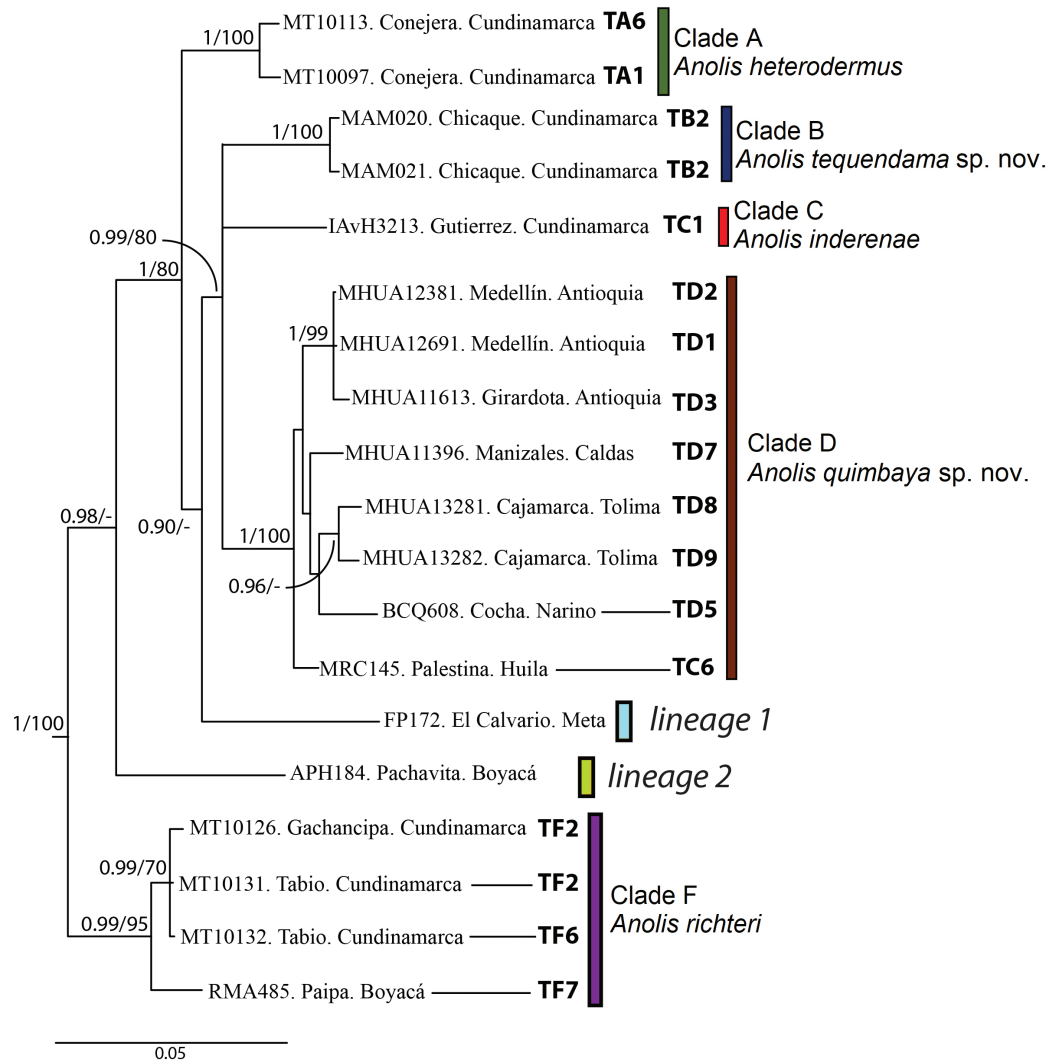
The COI dataset represented 30 different haplotypes (Fig. S2; Table S1) and the concatenated mtDNA dataset represented 35 different haplotypes (Fig. 2; Table S1). Figures 2 and 3 refer to phylogenetic analyses and figure 4 to a parsimony network analysis. The phylogenetic analyses of the COI data set revealed the same clades and independent lineages and a similar branching pattern to the concatenated mtDNA dataset. Since the resulting mtDNA (ND2+COI) tree was better supported, we focused on this one for describing the relationships between haplotypes. Both phylogenetic methods positioned the haplotypes into nine weakly to robustly supported clades and independent lineages (Clades A to F and Lineages 1–3; Fig. 2). Furthermore, these clades and lineages are grouped into two robustly supported major clades (I and III) and one lineage (II).

The first major clade included five strongly supported sister subclades and one lineage (Clades A to E and Lineage 1; Fig. 2). The maximally supported subclade A (identified by Vargas-Ramírez and Moreno-Arias (2014) as subgroup A) included individuals from Cundinamarca department in the middle eastern Andean cordillera (Haplotypes MA1-MA9 in Fig. 2; Table S1). Furthermore, clade A was composed of three weakly to robustly supported genetic groups from Guasca-Conejera, Madrid-Cota and Matarredonda sites in Cundinamarca department. This clade had maximum support as a sister of the clade (B, C, (D + E)) + Lineage 1) (Fig. 2).

The successive sister clades B, C, D and E comprised individuals from Cundinamarca, Meta, Antioquia Caldas, Huila, Tolima and Nariño departments in Colombia, and Sucumbíos in Ecuador (Haplotypes MB1-MB3, MC1-MC3, MD1-MD9 and ME1-ME2. Fig. 2). Clades B, C and D appeared robustly supported. Lineage 1 was found in the Meta department (Fig. 2). Furthermore, clade D corresponded to subgroup B identified by Vargas-Ramírez and Moreno-Arias (2014) and clades C and E corresponded to the already recognized species *A. inderenae* and *A. vanzolinii* respectively (Fig. 2).

Figure 2. Bayesian tree for mitochondrial haplotypes of the *heterodermus* subgroup (*sensu* Williams et al. 1996). Each individual haplotype bears the letter M meaning mtD-NA, followed by a letter for the respective clade and a number. Major clades and major lineages are identified by roman numbers I, III, and II, respectively. Support values are Bayesian posterior probabilities and thorough ML bootstrap values. Values not shown for nodes with < 0.75 posterior probabilities and < 50% bootstrap support. Colour code as in Figure 1. Outgroup *Polychrus marmoratus* removed for clarity. Inset photos: **Clade A** *Anolis heterodermus*, Male, Cerro de la Conejera, Bogotá D. C, Photo RMA; **Clade B** *Anolis heterodermus*, Male, Supatá, Cundinamarca, Photo José Vieira; **Clade C** *A. inderenae*, Male, Gutiérrez, Cundinamarca Photo: RMA; **Clade D** *Anolis heterodermus*, Female, Dapa-Yumbo, Valle del Cauca, Photo: Wilmar Bolívar; **Clade E** *A. vanzolinii*, Female, La Bonita, Sucumbios, Ecuador, photo: José Vieira; **Clade F** *A. heterodermus*, Male, Gachancipá, Cundinamarca, photo MVR.

Figure 3. Bayesian tree for the complete genetic evidence data set (mtDNA + nDNA) of the *heterodermus* subgroup (*sensu* Williams et al. 1996). Clades/lineages are indicated on the right. Support values are Bayesian posterior probabilities and ML bootstrap values. Values not shown for nodes with < 0.75 posterior probabilities and < 50% bootstrap support. Colour code as in Figure 1. Outgroup *Polychrus marmoratus* removed for clarity.

The major lineage II corresponded to lineage 2 from Pachavita, Boyacá. This clade was revealed as the sister of major clade I with maximum support. The major clade III included Lineage 3, which corresponded to the recognized species *A. nicefori* as sister taxon of the maximally supported Clade F (identified by Vargas-Ramírez and Moreno-Arias (2014) as subgroup C). This clade showed a strong phylogeographical structure with two robustly supported reciprocally monophyletic subclades from Boyacá and Cundinamarca departments (Fig. 2). Finally, *A. euskalerriari* and *A. orcesi* were revealed as successive sister taxa of the *Anolis heterodermus* species group. For the combined evidence (mtDNA+nDNA) of selected samples of the *Anolis heterodermus* species group (Table S1), the analyses also resulted in a branching pattern similar to the mtDNA tree, albeit with different support of the nodes (Fig. 3). However, in this tree, clades B, C and D were revealed as a polytomy.

The parsimony network analyses for the 32 COI mtD-NA haplotypes resulted in clusters matching the clades of the phylogenetic 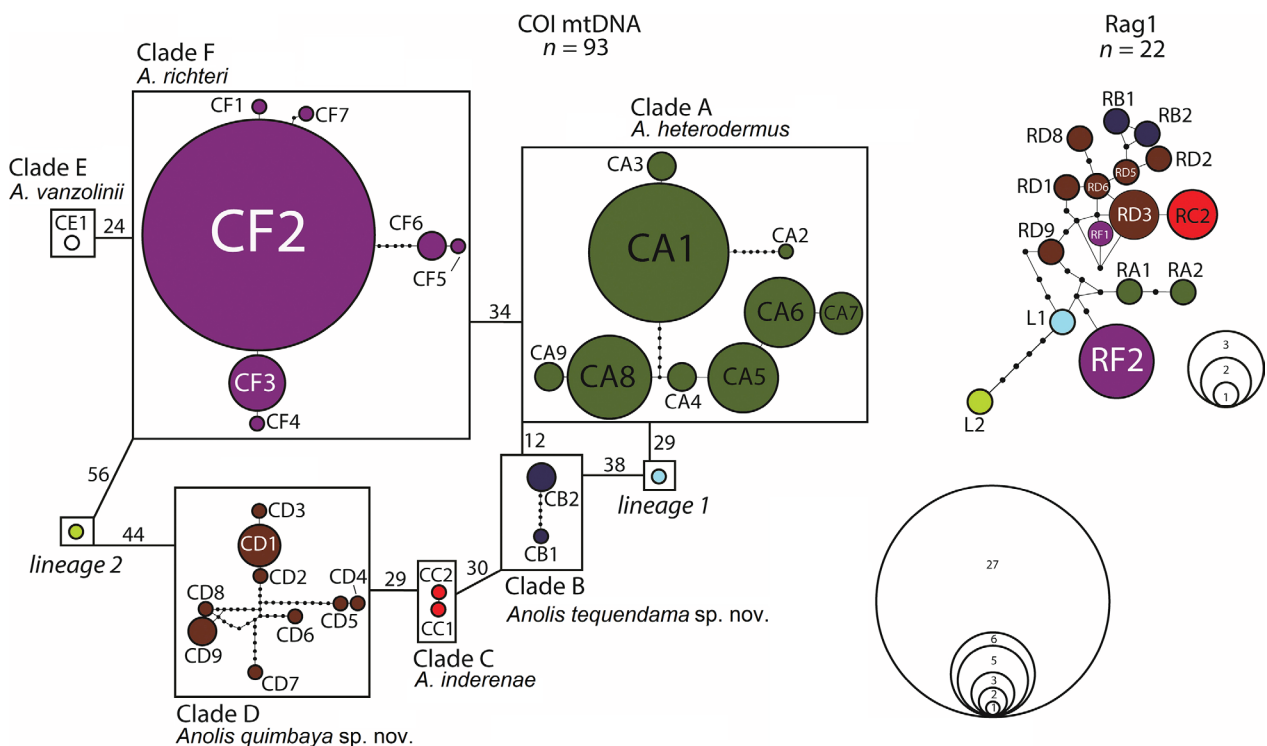analyses (Fig. 4). Those clusters were not connected using 90%-95% connection probability thresholds. The maximum number of mutational steps within each cluster ranged from 1 (between haplotypes CA1-CA3, CA4-CA5, CA6-CA7, CA6-CA7 and CA8-CA9 in Clade A; CC1-CC2 in Clade C; CD1-CD2 and CD3, CD4-CD5, CD8-CD9 in Clade D; CF1-CF2, CF2-CF7, CF3-CF4, CF5-CF6 in clade F) to 17 (between haplotypes CD4-CD8 in Clade D). Fixed differences between individual clades and lineages ranged from 12 between Clade A and Clade B and 56 between Clade F and Lineage 2. Network analyses of Rag1 sequences revealed 16 haplotypes (Fig. 4); all of them were private to each mtDNA clade and lineage. Two private haplotypes corresponded to Clades A (RA1, RA2), B (RB1, RB2), C (CC1, CC2) and F (RF1, RF2) and seven haplotypes were private for Clade D (RD1, RD2, RD3, RD5, RD6, RD8, RD9). Additionally, one private haplotype was revealed for each, Clade C (RC2), Lineage 1 (L1), and Lineage 2 (L2) (Fig. 4).

Within the *heterodermus* group, the mean uncorrected *p*-distances based on ND2 between clades (and lineages)

Table 1. Evolutionary divergence percentage based on the uncorrected *p*-distances (lower diagonal) and standard error (upper diagonal) over sequence pairs between assessed clades and lineages. In diagonal uncorrected *p*-distances (standard error) within lineages or species. ric: *A. richteri* (Clade F); het: *A. heterodermus* (Clade A); teq: *Anolis tequendama* **sp. nov.** (Clade B); ind: *A. inderenae* (Clade C); van: *A. vanzolinii* (Clade E); qui: *Anolis quimbaya* **sp. nov.** (Clade D). Species that do not belong to *heterodermus* group eus: *A. euskalerriari*, orc: *A. orcesi*, and pro: *A. proboscis*. In brackets number of individuals.

Lineage or species	ric [7]	Lineage 3 [2]	Lineage 1 [1]	Lineage 2 [1]	het [11]	teq [3]	ind [1]	van [1]	qui [9]	eus [2]	orc [1]	pro [1]
ric	3.5 (0.003)	0.006	0.008	0.008	0.008	0.011	0.007	0.010	0.009	0.009	0.013	0.015
Lineage 3	6.9	0.5 (0.002)	0.008	0.008	0.007	0.010	0.007	0.009	0.010	0.010	0.011	0.013
Lineage 1	9.3	9.9	—	0.008	0.007	0.009	0.007	0.007	0.008	0.009	0.012	0.013
Lineage 2	8.3	8.4	9.1	—	0.007	0.010	0.008	0.010	0.010	0.010	0.012	0.013
het	7.5	9.0	6.3	8.3	0.7 (0.002)	0.009	0.007	0.007	0.007	0.010	0.012	0.013
teq	10.1	11.7	7.9	9.6	6.8	0.6 (0.002)	0.009	0.008	0.008	0.012	0.013	0.013
ind	8.2	9.9	7.7	8.9	6.9	6.9	—	0.007	0.007	0.010	0.011	0.012
van	10.0	11.1	6.8	9.3	6.0	5.5	5.5	—	0.006	0.011	0.011	0.012
qui	8.8	11.2	8.1	9.7	6.5	6.4	6.3	3.8	1.3 (0.003)	0.011	0.013	0.012
eus	12.1	12.9	14.2	13.7	13.3	14.8	14.0	15.0	14.4	0.1 (0.001)	0.013	0.013
orc	15.8	15.6	17.6	15.4	16.4	17.1	17.0	16.0	17.5	16.2	—	0.012
pro	22.1	19.4	21.4	20.4	20.4	19.8	21.6	19.6	19.6	19.2	20.4	—

Figure 4. Parsimony networks for mitochondrial (left) and nuclear (right) haplotypes of the *heterodermus* subgroup (*sensu* Williams et al. 1996), based on alignments of 1092 bp of mtDNA and 1057 bp of the intron 1 of the nuclear R35 gene (n = number of individuals). Colour code as in Figs. 1 and 2. Circle size reflects haplotype frequency; missing haplotypes are represented by small black circles. Each line connecting haplotypes corresponds to one mutational step. Mitochondrial haplotypes or haplotype clusters shown in boxes remain unconnected under the 90%–95% thresholds. Numbers next to lines linking clusters indicate minimum fixed differences between clusters. Connection limit for nuclear haplotypes is 95%. The colours of haplotypes correspond to respective mitochondrial haplotypes. For abbreviations, see Figure 2.

ranged from 3.8 % between Clade E vs. Clade D to 11.7% between Clade B and Lineage 3 (Table 1). Uncorrected *p*-distances between the *heterodermus* group vs. *A. euskalerriari* and *A. orcesi* ranged from 12.1% to 17.6% (Table 1). The mptp species delimitation method favoured nine distinct species and were congruent with the clades and lineages also revealed by the phylogeographic and phylogenetic analyses (Figs 2, 3, and 4). Two species corresponded to Clades A and B from Cundinamarca and two species more matched Clades C and E, the already recognized species *A. inderenae* and *A. vanzolinii*. Additionally, three species matched with Lineages 1, 2, and the species *A. nicefori,* and two more species matched Clades D and F.

Morphology

Based on morphometrics, five groups were detected with an acceptable cohesion (average silhouette width: 0.32). Variations in morphometrics (excluding the sexually dimorphic variables head width $F = 23.7$, $p = 0.001$; head length $F = 8.2$, $p = 0.005$; tail length $F = 3.9$, $p = 0.049$; and toe length $F = 0.7$, $p = 0.031$) were explained by the three first principal components (63 %). Each component associated respectively with the femoral length, fourth toe width, and snout-vent length (Fig. S3A). Lizards from groups 1 and 5 were short-legged, those of group 2 were medium-legged, while those of groups 3 and 4 were long-legged (Fig. S3A). Lizards from groups 1 and 3 exhibited thinner toes than the others from the remaining groups (Fig. S3A). Mean body sizes of groups 3 (73.4 mm), 5 (72.6 mm) and 1 (72.1 mm) were larger than those of groups 2 (69.5 mm) and 4 (67.8 mm) (Fig. S3A).

According to scale counts, five groups were also detected (mean silhouette width: 0.22). Variation in count scales was explained by the six principal components (69 %) (excluding the sexually dimorphic variables: number of lamellae in the second and third phalanges of the fourth toe $F = 8.2$, $p = 0.004$; the total number of lamellae in the fourth toe $F = 5.4$, $p = 0.025$; and number of loreal rows $F = 4.3$, $p = 0.041$). The first three components accounted for 45% of the variance, and they associated with the number of the first dorsal row surrounded by granules, number of supralabials (Fig. S3B), and scales on the top of the head. The first whole dorsal row-surrounded by granules was the fifth row for lizards of groups 5 (Inter Quartile Range [IQR] = 4–6) and 3 (IQR = 4–5). For lizards of groups 1 and 2, it was the fourth row (IQR = 3–4), and for those of the group 4, it was the third row (IQR = 3–3) (Fig. S3B). Lizards of the Group 1 had ten supralabials (IQR = 9–10). Those of groups 2 and 5 had nine supralabials (IQR = 8–10 and IQR = 8–9), and lizards from groups 3 and 4 had eight supralabials (IQR = 8–9) (Fig. S3B).

The analysis of the scalation pattern revealed seven groups (average silhouette width: 0.33). Variation in scalation pattern (excluding thirteen sexually dimorphic variables) was explained by the eleven principal components 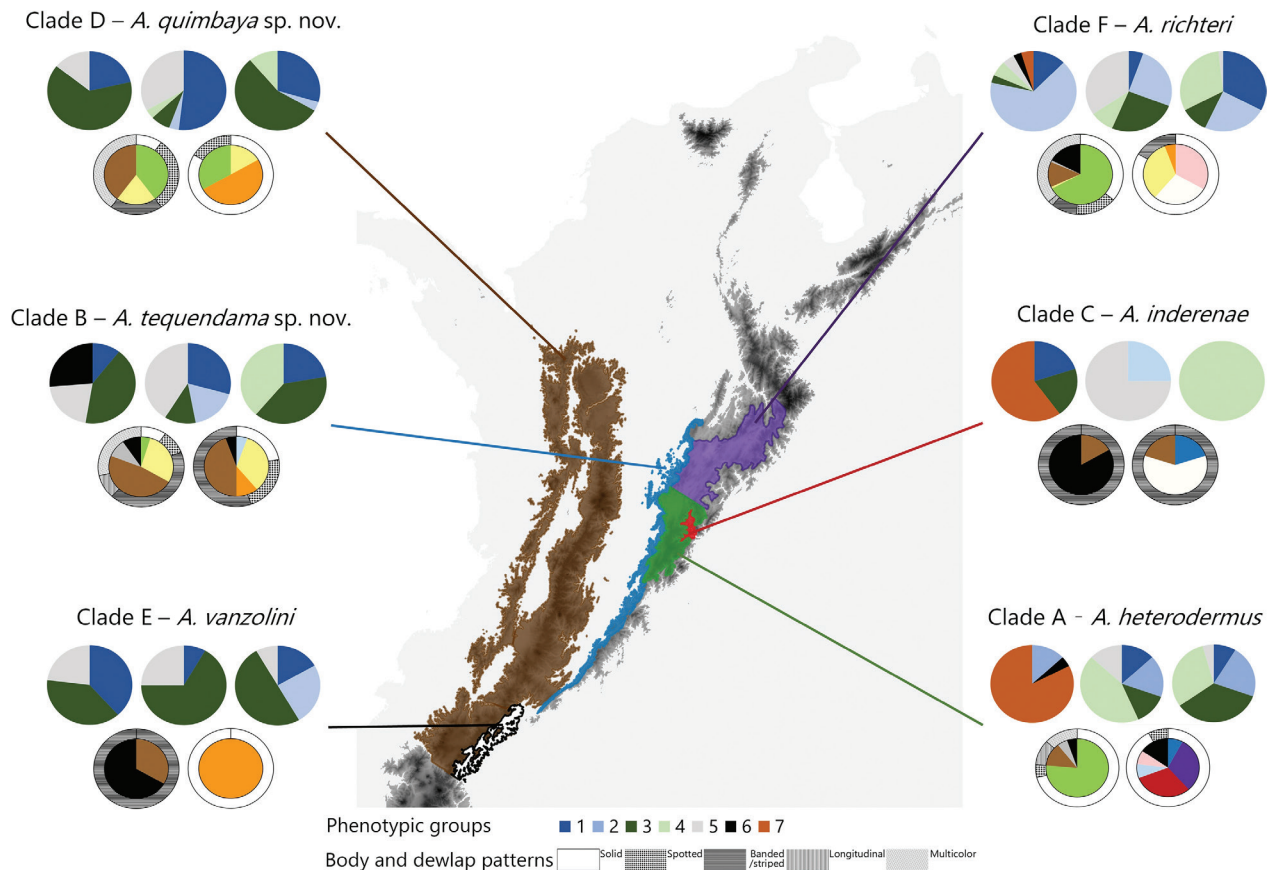(75%) with the first three components accounting for 34% of the variance (Fig. S3C). The variance in the first component was associated with scalation patterns in sublabial scales, mid-nuchal and middorsal crests, and crown shape. The second principal component was associated with the scalation patterns of middorsal and caudal crests, dorsal, and mental scales; and the third principal component was associated with the scalation pattern of the circumnasal (Fig. S3C). Lizards from groups 2, 7, and 4 exhibited a sublabial row contacting infralabials to the first canthal or reaching to the mouth commissure, continuous nuchal crest, and U-shaped crown, (Fig. S3C) compared to the remaining lizard groups whose sublabial row did not reach the first canthal; their nuchal crest was discontinuous, and their crown was V-shaped (Fig. S3C).

Dewlap configuration and body pattern

The great diversity in dewlap pattern and colour differences observed in lizards was marginally captured by the analysis, but we identified some patterns. The first two dimensions of the MCA explained only 21% of the variation in dewlap configuration. Nonetheless, the analysis showed that lizards belonging to a specific morphological group shared similar dewlap configurations (Fig. S4A). Associations among morphological groups and dewlap features were particularly true for major dewlap colour ($F = 78.7$, $p < 0.01$) but marginally true for the dewlap pattern ($F = 1.6$, $p = 0.07$).

An orange dewlap was present in 75% of the lizards from group 1 (the remaining 25 % had whitish dewlaps) and in a unique lizard from group 6. Most of group 2 lizards (94%) had dewlaps that were yellow-white or pink and most of group 3 lizards (90 %) had dewlaps that were yellow-brown or orange. Lizards of group 5 showed both blackish green and green dewlaps in the same proportion. Dewlaps of lizards from group 7 were highly variable; however, dewlaps blue, purple, or red-coloured were only seen in that group; and those colours were exhibited by 64% of the lizards. Other lizard dewlaps belonging to group 7 were blackish (12%), whitish (12%), pink (6%) or brown (6%) (Fig. S4A). Dewlaps with a solid pattern were seen mostly in groups 1 (83%), 2 (75%), and 7 (71%). Lizards belonging to group 3 were highly variable: 40% showed striped dewlap pattern, 35% solid, and 25% were spotted, while lizards of group 5, showed both solid and striped dewlaps in the same proportion. A unique lizard of group 6 showed a striped dewlap (Fig. S4A). Although there was no significant evidence of sexual dichromatism in the dewlap in these *Anolis* groups, males from group 3 showed solid and spotted dewlaps that were brown with some light-coloured scales. In contrast, females more often had yellow or orange dewlaps with black or brown stripes.

The variation in body patterns found in *Anolis* lizards was again only marginally captured by our analysis (Fig. S4B). The first two dimensions of the MCA explained 25% of the variation in body pattern configuration. Importantly, the presence of the coloured tail patch and

Figure 5. Phenotypic diversity and geographic distribution of *heterodermus* subgroup species from DNA analyses. The first row of pie charts from left to right indicates the frequency of each scalation pattern, morphometrics, and scalation count groups. The second row of pie charts indicates the frequency of the main colour (those described in the methods) and pattern of the body (left) and dewlap (right). Geographic regions and colours in the map indicate an estimated range of each species: brown (northern Andes before its ramification in the three "Cordilleras", Western and Central "Cordilleras"), white (eastern slope of Northern Andes), blue (western slope of Eastern "Cordillera"), green (southern "Cundiboyacense" plateau and its surrounding mountains), purple (northern "Cundiboyacense" Plateau and its surrounding mountains), red (eastern slope of Eastern "Cordillera").

the rostral line did not significantly contribute to the explained variance. Associations among morphological groups and body features was only true for the body pattern ($F = 83.6$, $p < 0.01$) and main colour ($F = 77.1$, $p < 0.01$). All body patterns were observed in groups 2, 3, 5 and 7 but in different proportions. Lizards of groups 2 and 7 were mostly solid-coloured (36 % and 63 %, respectively) and multi-coloured (37% and 12%, respectively). In group 3 lizards with banded body patterns (42%) and multi-coloured (32%) were more frequent, while group 5 grouped mainly multi-coloured lizards (36%) and banded (27%) and spotted (18%) body patterns. All lizards of group 1 showed banded bodies and a unique lizard belonging to group 6 exhibited a solid body pattern (Fig. S4B).

Main body colour types were observed in lizard groups 2, 3, 5 and 7. Lizards of group 2 were mostly green (67%) and black (17%), and in group 3 they were mostly brown (68 %) and yellow (21 %). In group 5 lizards were yellow (36 %) and brown, green, and grey (18% each). In group 7, lizards were mostly green (67%), black and brown (14% each one). The main colour of the body in lizards belonging to group 1 was brownish-black and a unique lizard of group 6 had a brown body colour (Fig. S4B).

The scalation pattern grouping was highly congruent with the remaining groupings based on the other morphological facets and geography. The correspondence of scalation patterned groups (explained by the inertia value as result of the sum of inertia value of the two first dimensions) with morphometric groups scored 93% ($X^2 = 51.1$, $p = 0.001$), while scale count groupings scored 81% ($X^2 = 45.6$, $p = 0.005$) and the inertia scored 81% with geography ($X^2 = 219.0$, $p < 0.01$). Also, phenotypic diversity in morphology, scalation, and distribution pattern was associated with the clades revealed by the DNA molecular analyses (Fig. 5). Based on this integrative evidence, we confirmed the formerly reported differentiation between the northernmost South American populations of high-altitude anoles and identified previously unknown lineages (Fig. 5). Furthermore, we offered integrative evidence for the existence of nine distinct evolutionary lineages of lizards within the *heterodermus* group. Four of these lineages corresponded to already recognized species (*A. heterodermus* – Clade A; *A. inderenae* – Clade C; *A. nicefori*-Lineage 3, and *A. vanzolinii* – Clade E). However, no names were available for Clades B, D and F. Consequently, we describe 1) Clades B and D (*Anolis tequendama* **sp. nov**. and *A. quimbaya* **sp. nov**, respective-

Table 2. Morphometrics of *heterodermus* subgroup species in mm. N = number of individuals. Traits = SVL snout-vent length, HL head length, HW head width, FL femoral length, TL tail length, TOEL length of the longest toe, TOEW width of the longest toe, LST number of lamellae under the second and third phalange of the largest toe, LTOT total number of lamellae under largest toe, OH otic height, IP length of interparietal scale, IP2 length of the second interparietal scale. In parenthesis Standard Deviation. Traits ratio relative to SVL in brackets.

Species	Sex	N	SVL	HL	HW	FL	LT	TOEL	TOEW	LST	LTOT	OH	IP	IP2
A. heterodermus	♂	17	71.1 (5.1)	21.0 (1.9) [0.3]	11.3 (1.5) [0.2]	14.6 (1.9) [0.2]	95.0 (9.2) [1.3]	8.6 (1.2) [0.10]	1.8 (0.4) [0.03]	19.5 (1.7)	28.6 (2.1)	1.1 (0.3)	2.6 (0.3)	1.4 (0.4)
	♀	7	65.9 (5.0)	19.2 (1.4) [0.3]	9.8 (0.5) [0.2]	13.1 (1.7) [0.2]	87.5 (17.0) [1.3]	8.1 (1.4) [0.10]	1.6 (0.1) [0.02]	19.0 (1.3)	28.3 (3.3)	1.0 (0.3)	2.5 (0.5)	1.5 (0.4)
A. richteri	♂	25	73.4 (8.4)	22.2 (2.4) [0.3]	11.3 (1.5) [0.1]	14.8 (1.7) [0.2]	107.0 (12.6) [1.5]	9.2 (1.4) [0.10]	1.7 (0.3) [0.02]	21.1 (1.9)	31.0 (2.1)	1.1 (0.3)	2.6 (0.6)	1.8 (0.6)
	♀	31	69.4 (7.4)	20.2 (1.9) [0.3]	10.0 (1.1) [0.1]	14.0 (1.5) [0.2]	96.3 (12.8) [1.4]	8.4 (0.9) [0.10]	1.6 (0.4) [0.02]	19.8 (1.7)	29.3 (2.1)	1.0 (0.3)	2.2 (0.4)	1.5 (0.3)
A. quimbaya **sp. nov.**	♂	11	73.0 (6.7)	22.2 (2.2) [0.3]	11.0 (1.0) [0.1]	12.8 (2.1) [0.2]	88.8 (7.5) [1.2]	9.5 (1.0) [0.10]	1.7 (0.2) [0.02]	21.8 (1.5)	32.7 (2.2)	1.1 (0.2)	2.8 (0.5)	2.1 (0.5)
	♀	14	73.6 (3.6)	21.7 (1.1) [0.3]	10.9 (0.8) [0.1]	12.6 (1.6) [0.2]	86.2 (5.9) [1.2]	9.5 (0.8) [0.10]	1.7 (0.2) [0.02]	20.6 (0.9)	31.8 (1.6)	1.1 (0.2)	2.8 (0.6)	2.0 (0.5)
A. tequendama **sp. nov.**	♂	7	65.7 (7.4)	19.3 (2.6) [0.3]	9.1 (1.1) [0.1]	12.0 (1.3) [0.2]	80.3 (13.7) [1.2]	8.3 (1.4) [0.13]	1.3 (0.2) [0.02]	19.4 (1.1)	29.0 (2.1)	1.0 (0.2)	2.7 (0.2)	1.8 (0.4)
	♀	8	67.8 (5.0)	20.0 (2.4) [0.3]	9.6 (1.0) [0.1]	12.5 (1.7) [0.2]	80.2 (9.3) [1.2]	7.5 (2.4) [0.11]	1.4 (0.3) [0.02]	19.0 (1.1)	28.4 (1.6)	1.1 (0.2)	2.7 (0.4)	1.5 (0.4)
A. inderenae	♂	3	91.9 (9.6)	28.1 (3.7) [0.3]	14.4 (2.1) [0.2]	18.8 (2.8) [0.2]	157 (1.4) [1.7]	14.0 (2.3) [0.15]	2.4 (0.4) [0.03]	23.3 (1.5)	34.3 (1.5)	1.1 (0.4)	3.7 (0.4)	2.5 (0.3)
	♀	2	107.5 (9.8)	30.8 (3.0) [0.3]	15.0 (0.1) [0.1]	21.5 (3.0) [0.2]	152.7 (8.1) [1.4]	13.9 (1.6) [0.13]	2.7 (0.1) [0.03]	23.0 (2.8)	34.0 (2.8)	1.5 (0.3)	3.4 (0.2)	2.6 (0.2)
A. vanzolinii	♂	8	86.1 (16.0)	27.0 (5.5) [0.3]	13.5 (2.8) [0.2]	17.4 (4.7) [0.2]	112.2 (21.3) [1.3]	12.7 (2.8) [0.15]	2.0 (0.4) [0.02]	24.3 (1.4)	37.0 (3.0)	1.3 (0.4)	1.9 (0.5)	2.0 (0.7)
	♀	4	85.0 (18.3)	26.3 (5.3) [0.3]	12.7 (2.0) [0.1]	16.6 (2.1) [0.2]	111.9 (21.1) [1.3]	12.9 (2.5) [0.15]	2.0 (0.4) [0.02]	24.2 (0.8)	36.6 (2.2)	1.4 (0.4)	1.7 (0.5)	1.5 (0.4)

ly) as species new to science; 2) we resurrect *A. richteri* (Clade F) as a full species that was a previous synonym of *A. heterodermus,* and 3) we re-describe *A. heterodermus sensu stricto* (see taxonomic accounts). Furthermore, we considered lineages 1 and 2 as candidate species while more morphological and molecular data can be acquired. Table 2 shows the traits of each recognized species.

Species accounts

Anolis heterodermus Duméril, 1851 (redescription)

Phenacosaurus paramoensis Hellmich, 1949, p. 105 [ZSM 118/1937].

Lectotype. MNHN-RA 1664. Adult male. From "Nouvelle Grenade" (Colombia), restricted to the vicinity of Bogotá city, Cundinamarca department, Colombia.

Paralectotypes. MNHN-RA 6798 (adult female), 1664A, 1664B, 6798A (males). All paralectotypes bear the same locality data of lectotype.

Diagnosis. *Anolis heterodermus* shares short limbs, a large, casqued head, a prehensile tail without caudal autotomy, and lamellar subdigital scales of all digits extending from the most proximal phalanges with the other species of the *Phenacosaurus* clade. *Anolis heterodermus* differs from *A. proboscis*, *A. orcesi*, *A. euskalerriari* and *A. nicefori* by the presence of granular scales surrounding dorsal heterogeneous flat scales. From *A. richteri*, *A. tequendama* **sp. nov.**, *A. tetarii*, *A. vanzolinii*, *A. inderenae* and *A. quimbaya* **sp. nov.**, by the presence of a unicoloured purple, red, or black dewlap and a U-shaped crown. *Anolis heterodermus* further differs from *A. richteri*, *A. tequendama* **sp. nov.**, *A. tetarii*, *A. vanzolinii*, and *A. quimbaya* **sp. nov.**, by the presence of a continuous row of enlarged sublabials reaching the mouth commissure; from *A. vanzolinii*, *A. tequendama* **sp. nov.** and *A. quimbaya* **sp. nov.** by a continuous nuchal crest; and from *A. vanzolinii* by < 24 expanded lamellae under second and third phalange of fourth toe and < 35 lamellae in total fourth toe.

External description of lectotype. Snout-vent length = 75.1 mm; head length = 22.4 mm; head width = 11.6 mm; femoral length = 13.4 mm; ear height = 1.6 mm; tail length = 88.8 mm; fourth toe length = 7.4 mm. Dorsal head and supraocular disc scales smooth; frontal depression present; dorsal surface of rostral scale smooth, not notched; three scales across the snout between second canthals; supraorbital semicircles distinct, separated by one scale; no scales separate interparietal and supraorbital semicircles; U-shaped crown; supraocular disc one to three enlarged scales, scales along the medial edge of the supraocular disc broken by larger scales that contact the supraorbital semicircles; one or two elongated supraciliary scales, followed by a series of small scales; two loreal

rows; eight total loreals; circumnasal scale does not contact sulcus between rostral and first supralabial, one scale from the naris to the rostral; preoccipital present; nine supralabials to center of eye; eleven infralabials to center of eye; four postrostrals excluding first supralabials; mental scale does not extend posterolaterally along with the lateral limits of the rostral with posterior border in a straight line transverse to head; six sublabials enlarged in contact with infralabials; a row of enlarged sublabials reaching the mouth commissure present, row of enlarged sublabials beyond posteriorly to a line just below the first canthal present; dewlap present, reaching posterior to axillae; rows of single scales on dewlap; tubelike axillary pocket absent; enlarged postcloacal scales. Nuchal and caudal crests present; nuchal crest continuous. Dorsal crest to base of tail; dorsal crest continuous; one enlarged middorsal row; dorsal scales heterogeneous and smooth; three rows of scales between middorsal crest and the beginning of dorsal flat scales surrounded entirely by granules; size of the flat dorsal scales in HW 1–0.5–0.25; five longitudinal dorsal scales in the fifth scale row in 10% of SVL. Ventral scales smooth, slightly overlapped, and rounded apices, in transverse rows; eleven longitudinal ventral scales in 10% of SVL. Supradigitals smooth; toepads expanded and overlap the first phalanx; twenty expanded lamellae under second and third phalanges of fourth toe; tail crest with a single row of scales.

Paralectotypes variation. Snout-vent length = 49.4–69.0 mm ($N = 4$, mean = 64.9 mm, SD = 9.5 mm); head length = 15.9–21.8 mm; head width = 7.8–11.5 mm; femoral length = 9.1–12.1 mm; ear height = 1.4–1.7 mm; tail length = 68.5–100.1 mm; fourth toe length = 6.0–7.3 mm. Dorsal head and supraocular disc scales smooth or rough and smooth, respectively; frontal depression present; dorsal surface of rostral scale smooth, not notched; 3–4 scales across the snout between second canthals; supraorbital semicircles distinct, separated by 0–1 scales; 0–1 scales separate interparietal and supraorbital semicircles; U-shaped crown; supraocular disc one to three enlarged scales, scales along the medial edge of the supraocular disc broken by larger scales that contact the supraorbital semicircles or continuous without larger scales in contact with supraorbital semicircles; one or two elongated supraciliary scales, followed by a series of small scales; 1–2 loreal rows; 5–6 total loreals; circumnasal scale does not contact sulcus between rostral and first supralabial, 0–1 scale from the naris to the rostral; preoccipital present or absent; 9–10 supralabials to center of eye; 9–10 infralabials to center of eye; four postrostrals excluding first supralabials; mental scale extends or does not posterolaterally along with the lateral limits of the rostral with posterior border in a straight line transverse to head; five sublabials enlarged in contact with infralabials; a row of enlarged sublabials reaching the mouth commissure present, row of enlarged sublabials beyond posteriorly to a line just below the first canthal present; dewlap present, reaching posterior to axillae; rows of single scales on dewlap; tubelike axillary pocket absent; enlarged postcloacal scales absent in female, present in males. Nuchal

and caudal crests present; nuchal crest continuous. Dorsal crest to base of tail; dorsal crest continuous; one enlarged middorsal row; dorsal scales heterogeneous and smooth; 2–3 rows of scales between middorsal crest and the beginning of dorsal flat scales surrounded entirely by granules; size of the flat dorsal scales in HW 1–0.5–0.25; five longitudinal dorsal scales in the fifth scale row in 10% of SVL. Ventral scales smooth, slightly overlapped and rounded apices, in transverse rows; 10–13 longitudinal ventral scales in 10% of SVL. Supradigitals smooth or multikeeled; toepads expanded and overlap the first phalanx; 16–21 expanded lamellae under second and third phalanges of fourth toe; tail crest with a single row of scales.

Colour in life. Body green or light brown dorsally, lighter ventrally; dorsal surfaces of the body, limbs, and tail with abundant white, black or sometimes blue scales, single or in groups forming disorderly spots; transversal bands absent (Fig. 6A); white or yellow-green line running from the supralabials through the tympanum until the forelimbs; a patch of blue or red scales on the tail base; unicoloured (solid) dewlap that can be purple, red, or black; no difference in dewlap colour between males and females (Fig. 6A).

Habitat, ecology, and behaviour. *Anolis heterodermus* inhabits scrublands, forests, and "páramos" in the Colombian Andes. This species preferentially uses small branches and very narrow surfaces such as twigs and exhibits very slow movements, consistently with their twig anole ecomorph. The species occurs at high altitudes; therefore, it experiences a wide range of temperatures ranging between 5°C and 25°C in some localities. Recent studies have shown that this species has a higher degree of thermoconformism compared to similar species inhabiting lower elevations at highlands (i.e., *Anolis richteri* and *Anolis tequendama* **sp. nov.**), but it shares similar ecophysiological traits such as preferences, locomotor optimum, and minimum and maximum temperatures. Northern populations of *A. heterodermus* have been found in sympatry with southern populations of *A. richteri*. Their sexual and aggressive behaviour includes a repertoire of dewlap extensions, sagittal body expansions and head-bobbing frequencies. However, this species has a relatively less complex and elaborated display compared to *A. richteri*.

Geographic distribution. *Anolis heterodermus* is a Colombian endemic lizard inhabiting mainly the southern plateaus of the department of Cundinamarca and the surrounding hills, as well as the eastern slope of the Eastern Cordillera in the Cundinamarca department (Fig. 8). Altitudinal range is approximately between 2500 m and 3600 m.

Remarks. *Anolis heterodermus* was described by syntypes from "Nouvelle Grenade" (currently Colombia, Panamá, Venezuela and Ecuador). However, Lazell (1969) designated the *A. heterodermus* syntype MNHN-R
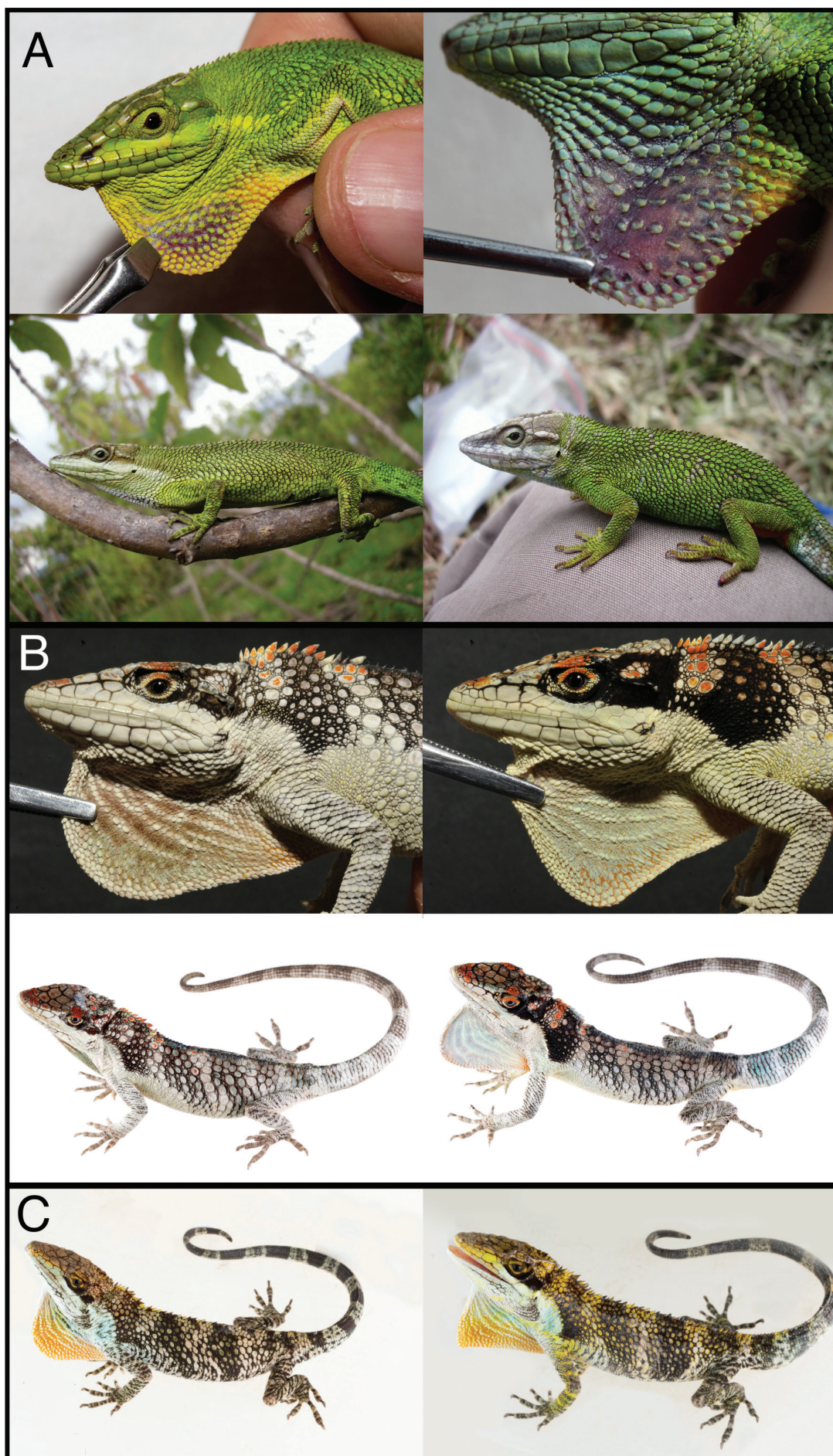
Figure 6. Dewlap and body of female (left) and male (right) of *A. heterodermus* (**A**), *A. inderenae* (**B**), and *A. vanzolinii* (**C**).

1664 as lectotype, leaving the other type specimens as paralectotypes; redefined *Anolis richteri* as a synonym of *A. heterodermus* and restricted the *A. heterodermus* type locality to the vicinity of Bogotá, Colombia. Although *A. heterodermus* type material corresponds to the geographic distribution of only one evolutionary lineage (Clade A), the original description could be attributed to most of the *A. heterodermus* species group or other evolutionary lineages, which makes it impossible to recognize or distinguish this biological entity. Additionally, in his revision, Lazell (1969) recognized as *A. heterodermus* individuals from different localities, most of them corresponding to the geographic distribution of different evolutionary lineages described here as distinct species, including *A. richteri*, re-erected now as a valid species. After the description of *A. inderenae*, *A. vanzolinii* and *A. tetarii*, the *A. heterodermus*' original description and the revision of Lazell (1969) maintained most of the cryptic diversity of *A. heterodermus* species group under the nominal species *A. heterodermus*.

Anolis quimbaya sp. nov.

https://zoobank.org/F2F613C1-227C-45B4-9EFF-8830B56A5B21

Anolis heterodermus Castañeda and de Queiroz (2011) p. 796 table 1. [ICN 11265];
Anolis heterodermus Castañeda and de Queiroz (2013) supplementary material. [ICN 10610];
Dactyloa heteroderma Prates et al. (2015) p. 264 [MHUA-R 11265]

Holotype. MHUA-R 12691. Adult male with dewlap present, enlarged postanal scales. From Santa Elena, Medellin municipality, Antioquia department, Colombia (6.2688°N –75.4992°W, 2400 m), collected by Juan Manuel Daza in May 2014.
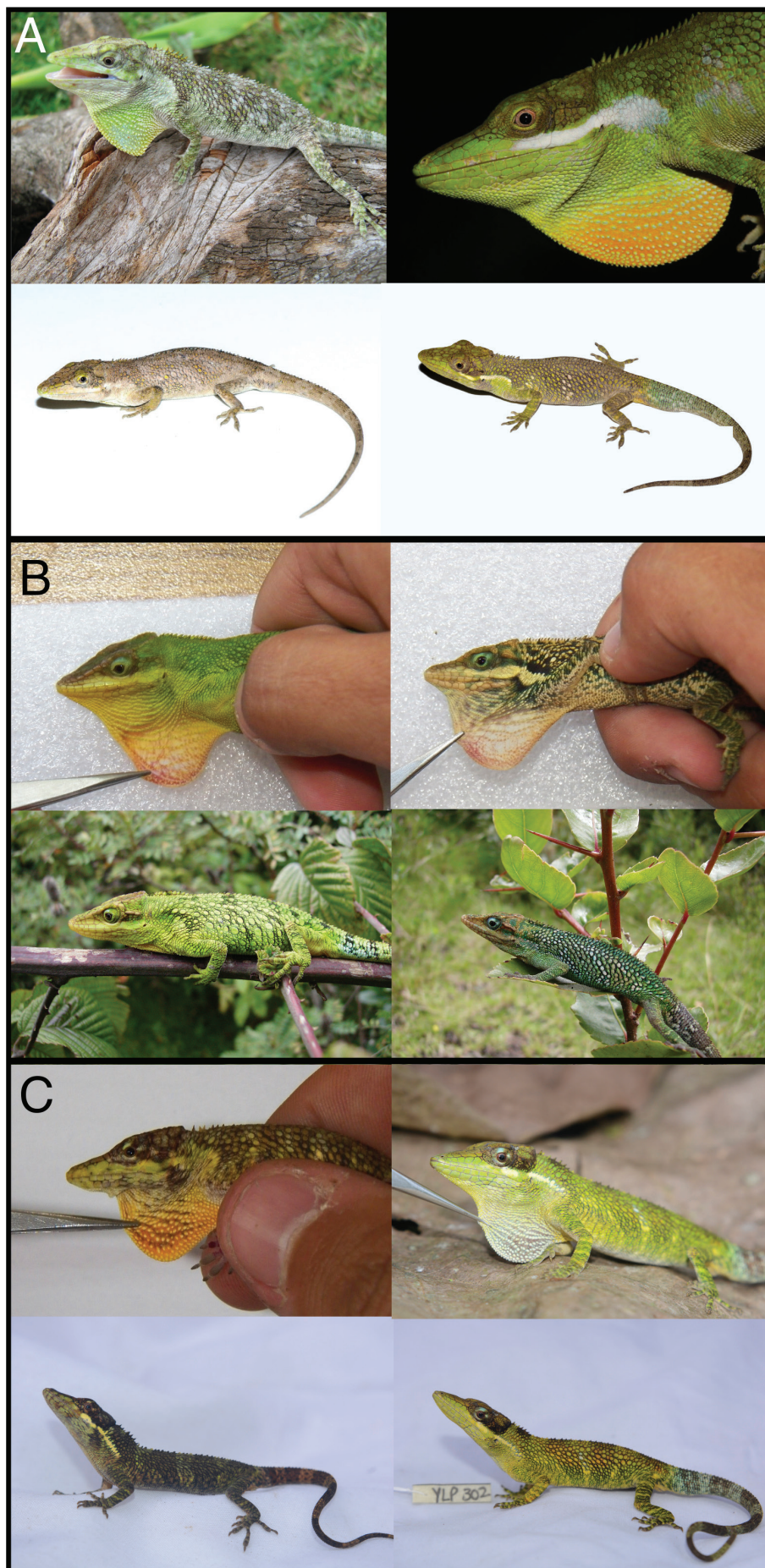
Paratypes. MHUA-R 11265 (an adult female, 6.25545°N –75.50733°W, 2450 m), MHUA-R 12381 (an adult female, 6.236388°N –75.49442°W, 2600 m) from the same locality data of holotype, collected by Luz Mery Martínez in 2005 and Alejandro Suárez in 2011. MHUA-R 11060 (an adult male, 6.796086°N –75.72757°W, 3000 m) collected by M. Castaño in 2003, MHUA-R 11730 (an adult female, 6.648611°N –75.68056°W, 3000 m), MHUA-R 12524 (adult female, 6.61599°N –75.64796°W, 2900 m) from Belmira municipality, Antioquia department, Colombia collected by Carlos Ortiz in 2012. MHUA-R 11613 (adult female) from Girardota municipality, Antioquia department, Colombia (6.28192°N –75.42962°W, 2350 m), collected by Juan Pablo Hurtado in 2007. MHUA-R 10938 (adult male) from La Union municipality, Antioquia department, Colombia (5.977075°N –75.3641°W, 2450 m), collected by A. M, Higuita in 2003. MHUA-R 10505 (adult male) from Santa Rosa de Osos municipality, Antioquia department, Colombia (6.74081°N –75.4783°W, 2700 m), collected by Ángela Ortega in 2001.

Diagnosis. *Anolis quimbaya* **sp. nov.** shares short limbs, a large, casqued head, a prehensile tail without caudal autotomy, and lamellar subdigital scales of all digits extending from the most proximal phalanges with the other species of the *Phenacosaurus* clade. *Anolis quimbaya* **sp. nov.** differs from *A. proboscis*, *A. orcesi*, *A. euskalerriari* and *A. nicefori* by the presence of granular scales surrounding dorsal heterogeneous flat scales. *Anolis quimbaya* **sp. nov.** further differs from *A. heterodermus*, *A. richteri*, *A. tetarii*, *A. inderenae,* and *A. tequendama* **sp. nov.** by an orange or green dewlap (*A. vanzolinii* orange only) from *A. inderenae*, *A. heterodermus*, *A. richteri* and *A. tetarii* by the presence of a discontinuous nuchal crest; from *A. heterodermus* and *A. inderenae* by the presence of a continuous row of enlarged sublabials that do not reach the mouth commissure; from *A. heterodermus* by a V-shaped crown. From *A. vanzolinii* by < 24 expanded lamellae under second and third phalange of fourth toe and < 35 lamella in total fourth toe, maximum snout-vent length 87 mm (110 mm), femoral length/snout-vent length ratio 0.17 (0.20), tail length/snout-vent ratio 1.19 (1.31), fourth toe length/snout-vent length ratio 0.13 (0.15) and sexual dimorphism in dewlap pattern.

Etymology. The specific epithet is used as a noun in apposition. The name refers to the extinct indigenous ethnic group called the Quimbaya who inhabited the central cordillera of Colombia, where the species is mainly distributed. "Los Quimbaya" in Spanish is also a noun to refer to the indigenous people belonging to the Kimbaya nation, to the people who previously spoke the Kimbaya dialect and the archaeological period when those people lived.

Common name. Quimbaya anole [English]. Anolis quimbaya [Spanish]

External description of holotype. Snout to vent length 72.5 mm; head length 22.5 mm; head width 11.2 mm; femoral length 12.2 mm; ear height 1.0 mm; tail length 88.0 mm; fourth toe length 10.2 mm, fourth toe width 1.8 mm. Dorsal head and supraocular disc scales smooth and rough, respectively; frontal depression present; dorsal surface of rostral scale smooth, not notched; three scales across the snout between second canthals; supraorbital semicircles distinct, in contact; no scales separate interparietal and supraorbital semicircles; V-shaped crown; supraocular disc one to three enlarged scales, scales along the medial edge of the supraocular disc broken by larger scales that contact the supraorbital semicircles; one or two elongated supraciliary scales, followed by a series of small scales; two loreal rows; eight total loreals; circumnasal scale no contacts sulcus between rostral and first supralabial, one scale from the naris to the rostral; preoccipital absent; nine supralabials to center of eye; nine infralabials to center of eye; four postrostrals excluding first supralabials; four postmentals excluding first infralabials; mental partially divided posteriorly, extends posterolaterally along with the lateral limits of the rostral, with posterior border in a straight line transverse

Figure 7. Dewlap and body of female (left) and male (right) of *A. quimbaya* **sp. nov.** (**A**), *A. richteri* (**B**) and *A. tequendama* **sp. nov.** (**C**).

to head; three enlarged sublabials in contact with infralabials; a row of enlarged sublabials reaching the mouth commissure absent, a row of enlarged sublabials beyond posteriorly to a line just below the first canthal absent; dewlap present, reaching posterior to axillae; rows of single scales on dewlap; tubelike axillary pocket absent; enlarged postcloacal scales. Nuchal and caudal crests present; nuchal crest discontinuous. Dorsal crest to base of tail; dorsal crest discontinuous; one enlarged middorsal row; dorsal scales heterogeneous and smooth; four rows of scales between middorsal crest and the beginning of dorsal flat scales surrounded entirely by granules; size of the flat dorsal scales in HW 1–0.5–0.25; six longitudinal dorsal scales in the fifth scale row occupying 10% of SVL. Ventral scales smooth, slightly overlapped and rounded apices, in transverse rows; twelve longitudinal ventral scales in 10% of SVL. Supradigitals smooth or multikeeled; toepads expanded and overlap the first phalanx; twenty-one expanded lamellae under second and third phalanges of fourth toe; tail crest with a single row of scales.

Paratypes variation. Snout to vent length 61.2–79.5 mm (*N* = 8, mean = 72.1 mm, SD = 5.9 mm); head length 19.4–79.9 mm; head width 9.4–12.9 mm; femoral length 10.0–12.7 mm; ear height 0.8–1.3 mm; tail length 75.0–92.0 mm; fourth toe length 8.1–10.7 mm; fourth toe width 1.3–2.0 mm. Dorsal head and supraocular disc scales smooth or rough; frontal depression present; dorsal surface of rostral scale smooth, not notched; 3–7 scales across the snout between second canthals; supraorbital semicircles distinct, in contact; 0–1 scales separate interparietal and supraorbital semicircles; shape of the crown "V"; supraocular disc one to three enlarged scales, scales along the medial edge of the supraocular disc broken by larger scales that contact the supraorbital semicircles or continuous without larger scales in contact with supraorbital semicircles; one or two elongated supraciliary scales, followed by a series of small scales; 1–2 loreal rows; 3–11 total loreals; circumnasal scale contacts or not the sulcus between rostral and first supralabial, 0–1 scales from the naris to the rostral; preoccipital present or absent; 7–9 supralabials to center of eye; 6–9 infralabials to center of eye; four 3–4 postrostrals excluding first supralabials; 2–5 postmentals excluding first infralabials; mental completely or partially divided posteriorly, extends or not posterolaterally along with the lateral limits of the rostral, with posterior border in a straight line transverse to head; 4–5 sublabials enlarged in contact with infralabials; a row of enlarged sublabials reaching the mouth commissure absent, row of enlarged sublabials beyond posteriorly to a line just below the first canthal absent; dewlap present, reaching or not posterior to axillae; rows of single scales on dewlap; tubelike axillary pocket absent; enlarged postcloacal scales absent in females, present in males. Nuchal and caudal crests present; nuchal crest discontinuous. Dorsal crest to base of tail; dorsal crest discontinuous; one enlarged middorsal row; dorsal scales heterogeneous and smooth; 2–5 rows of scales between middorsal crest and the beginning of dorsal flat scales surrounded entirely

by granules; size of the flat dorsal scales in HW 1–1–1, 1–0.5 or 1–0.5–0.25; 4–7 longitudinal dorsal scales in the fifth scale row in 10% of SVL. Ventral scales smooth, slightly overlapped, and rounded apices, in transverse rows; 10–15 longitudinal ventral scales in 10% of SVL. Supradigitals smooth or multikeeled; toepads expanded and overlap the first phalanx; 20–24 expanded lamellae under second and third phalanges of fourth toe; tail crest with a single row of scales.

Colour in life. Body brown or green dorsally, lighter ventrally; transversal brown or yellow bands present in many individuals; dorsal surfaces of body, limbs, and tail with abundant white, brown and yellow scales, single or in groups forming disorderly spots (Fig. 7A); white or yellowish line running from the supralabials through the tympanum to the forelimbs; a patch of blue or red scales in the tail base is infrequent; unicoloured (solid) or spotted dewlaps that can be orange (males) or greenish (females) (Fig. 7A).

Habitat, ecology, and behaviour. *Anolis quimbaya* **sp. nov.** inhabits scrublands, forests, cloud forests, and "páramos" in the Colombian Andes. This species preferentially uses small branches and narrow surfaces such as twigs and exhibits very slow movements, consistently with their twig anole ecomorph. As well as *Anolis tequendama* **sp. nov.**, *A. quimbaya* **sp. nov.** usually has a smaller body size compared to *A. heterodermus* and *A. richteri*. Furthermore, it is the lesser-studied species compared with *Anolis heterodermus*, *A. richteri*, and *A. tequendama* **sp. nov.** in terms of its thermal biology, as well as sexual and aggressive behaviour, thus these traits have not yet been analyzed in detail.

Geographic distribution. *Anolis quimbaya* **sp. nov.** is a widely distributed lizard from the northern and western slope of the Andes in Ecuador to the Western and Central Cordilleras of Colombia (Fig. 8). Altitudinal range is approximately between 1800 and 3100 m.

Anolis richteri (Dunn, 1944) revalidated
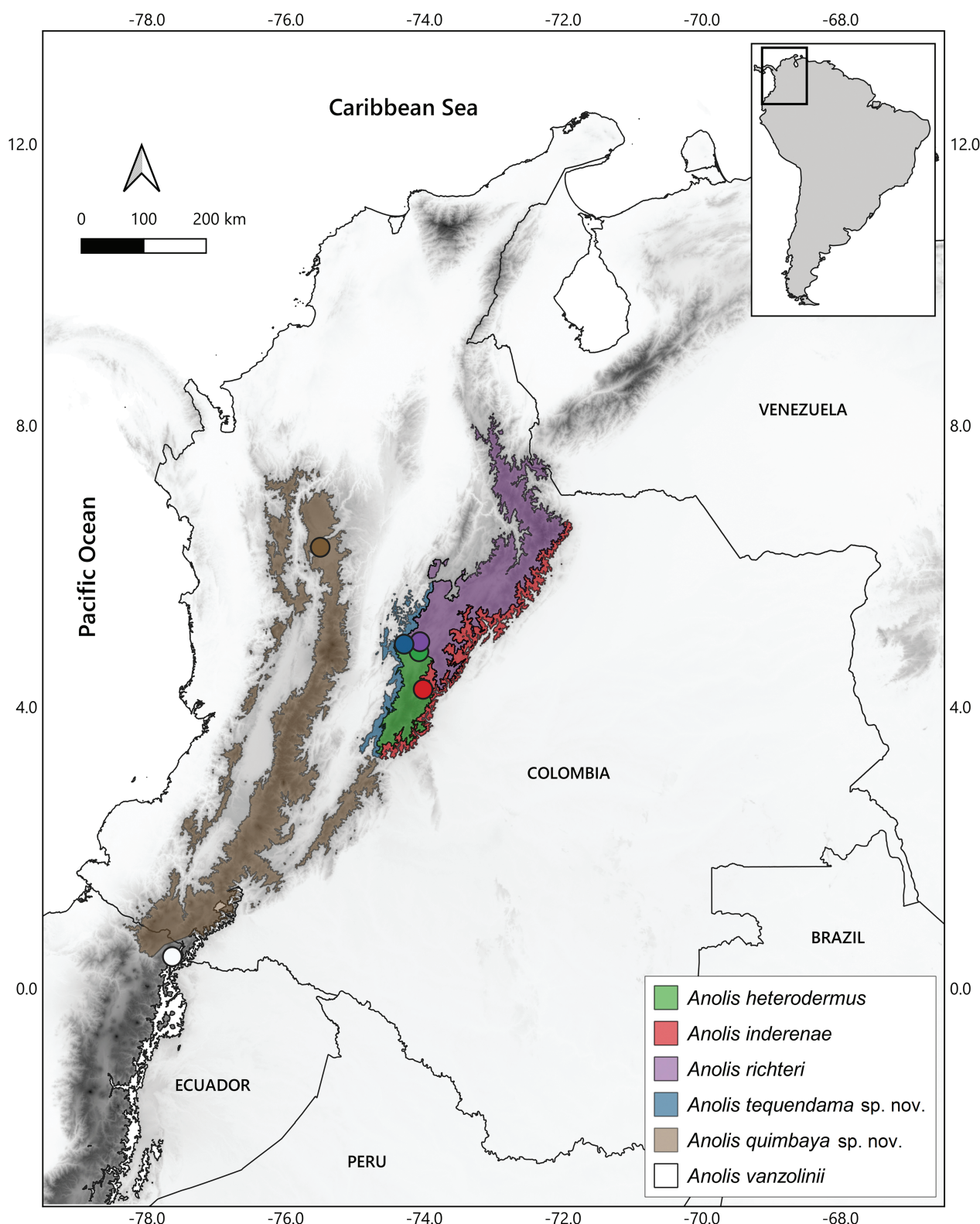
Phenacosaurus richteri Dunn, 1944
Anolis heterodermus Castañeda and de Queiroz (2013), supplementary material. [ICN 5974, 5975]

Holotype. ICN 5974. Adult male, dewlap present, enlarged postanal scales. From Tabio, Cundinamarca department, Colombia (4.9167°N –75.1000°W, 2645 m), collected by Friedrich Medem.

Paratypes. ICN 5975 (adult female), 5976, 5977 (juvenile males). All paratypes have the same locality and collector data as the holotype.

Diagnosis. *Anolis richteri* shares short limbs, a large head, a casqued-head, a prehensile tail without caudal autotomy, and lamellar subdigital scales of all digits ex-

Figure 8. Geographic distribution of *heterodermus* subgroup species. Circles correspond to the type localities of each species.

tending from the most proximal phalanges with the other species of the *Phenacosaurus* clade. *Anolis richteri* differs from *A. proboscis*, *A. orcesi*, *A. euskalerriari*, and *A. nicefori* by its strongly heterogeneous dorsal scalation (slightly heterogeneous in *A. nicefori*) and by the presence of granular scales surrounding dorsal heterogeneous flat scales. *Anolis richteri* further differs from *A. heterodermus*, *A. vanzolinii*, *A. tetarii*, *A. tequendama* **sp. nov.**

and *A. quimbaya* **sp. nov.** by unicoloured white/cream or pink coloured male dewlap, sometimes with visible blood irrigations, from *A. vanzolinii*, *A. tequendama* **sp. nov.** and *A. quimbaya* **sp. nov.** by a continuous nuchal crest, from *A. heterodermus* and *A. inderenae* by the presence of a continuous row of enlarged sublabials that do not reach the mouth commissure, from *A. heterodermus* by a V-shaped crown; and from *A. vanzolinii* by < 24 expand-

ed lamellae under second and third phalange of fourth toe and < 35 lamellae in total fourth toe.

External description of holotype. Snout-vent length = 73.9 mm; head length = 22.2 mm; head width = 12.2 mm; femoral length = 13.7 mm; ear height = 1.1 mm; tail length = 119 mm; fourth toe length = 9.2 mm. Dorsal head and supraocular disc scales rough and smooth, respectively; frontal depression present; dorsal surface of rostral scale smooth, not notched; four scales across the snout between second canthals; supraorbital semicircles distinct, in contact; one scale separate interparietal and supraorbital semicircles; V-shaped crown; supraocular disc one to three enlarged scales; scales along the medial edge of the supraocular disc broken by larger scales that contact the supraorbital semicircles; one or two elongated supraciliary scales, followed by a series of small scales; one loreal row; seven total loreals; circumnasal scale does not contact sulcus between rostral and first supralabial, one scale from the naris to the rostral; preoccipital present; eight supralabials to center of eye; seven infralabials to center of eye; four postrostrals excluding first supralabials; four postmentals excluding first infralabials; mental completely divided posteriorly, extends posterolaterally along with the lateral limits of the rostral, with posterior border in a straight line transverse to head; six sublabials enlarged in contact with infralabials; a row of enlarged sublabials reaching the mouth commissure absent, row of enlarged sublabials beyond posteriorly to a line just below the first canthal absent; dewlap present, not reaching posterior to axillae; rows of single scales on dewlap; tubelike axillary pocket absent; enlarged postcloacal scales. Nuchal and caudal crests present; nuchal crest continuous. Dorsal crest to base of tail; dorsal crest continuous; one enlarged middorsal row; dorsal scales heterogeneous and smooth; two rows of scales between middorsal crest and the beginning of dorsal flat scales surrounded entirely by granules; size of the flat dorsal scales in HW 1–0.5–0.25; five longitudinal dorsal scales in the fifth scale row in 10% of SVL. Ventral scales smooth, slightly overlapping and rounded apices, in transverse rows; twelve longitudinal ventral scales in 10% of SVL. Supradigitals smooth; toepads expanded and overlap the first phalanx; twenty expanded lamellae under second and third phalanges of fourth toe; tail crest with a single row of scales.

Paratype variation. Snout-vent length = 40.0–69.7 mm (N = 3, mean = 58.9 mm, SD = 15.7 mm); head length = 13.2–20.1 mm; head width (HW) = 6.4–10.8 mm; femoral length = 7.8–13.1 mm; ear height = 0.6–1.0 mm; tail length = 54.5–90.9 mm; fourth toe length = 5.4–9.2 mm. Dorsal head and supraocular disc scales smooth; frontal depression present or absent; dorsal surface of rostral scale smooth, not notched; 4–5 scales across the snout between second canthals; supraorbital semicircles distinct, separated by 0–1 scales; 0–1 scales separate interparietal and supraorbital semicircles; V-shaped crown; supraocular disc one to three enlarged scales; scales along the medial edge of the supraocular disc broken by larger scales that contact the supraorbital semicircles; one or two elongated

supraciliary scales, followed by a series of small scales; 1–2 loreal rows; seven total loreals; circumnasal scale no contact with sulcus between rostral and first supralabial, one scale from the naris to the rostral; preoccipital present or absent; 7–8 supralabials to center of the eye; 8–10 infralabials to center of the eye; four postrostrals excluding first supralabials; 5–6 postmentals excluding first infralabials; mental completely or partially divided posteriorly, extends posterolaterally along with the lateral limits of the rostral, with posterior border in a straight line transverse to head; 5–6 sublabials enlarged in contact with infralabials; a row of enlarged sublabials reaching the mouth commissure absent, row of enlarged sublabials beyond posteriorly to a line just below the first canthal present or absent; dewlap present, reaching or not posterior to axillae; rows of single scales on dewlap; tubelike axillary pocket absent; enlarged postcloacal scales absent in female, present in males. Nuchal and caudal crests present; nuchal crest continuous. Dorsal crest to base of tail; dorsal crest continuous; one enlarged middorsal row; dorsal scales heterogeneous and smooth; 2–3 rows of scales between middorsal crest and the beginning of dorsal flat scales surrounded entirely by granules; size of the flat dorsal scales in HW 1–0.5–0.25; five longitudinal dorsal scales in the fifth scale row in 10% of SVL. Ventral scales smooth, slightly overlapped and rounded apices, in transverse rows; 11–13 longitudinal ventral scales in 10% of SVL. Supradigitals smooth; toepads expanded and overlap the first phalanx; 21–22 expanded lamellae under second and third phalanges of fourth toe; tail crest with a single row of scales.

Colour in life. Body green, black, or brown dorsally, lighter ventrally; dorsal surfaces of body, limbs, and tail with abundant white, black, and yellow scales, single or in groups forming disorderly spots; transversal bands present but not frequent (Fig. 7B); white or green-yellow line running from the supralabials through the tympanum to the forelimbs; a patch of blue or red scales in the tail base; unicoloured (solid) dewlap that can be yellow in females, and pink or white/cream in both sexes (Fig. 7B).

Habitat, ecology, and behaviour. *Anolis richteri* inhabits scrublands, forests, and "páramos" in the Colombian Andes. This species preferentially uses small branches and very narrow surfaces such as twigs and exhibits very slow movements, consistently with their twig anole ecomorph. This species occurs at relatively lower altitudes compared to *A. heterodermus* and relatively higher altitudes compared to *A. tequendama* **sp. nov.** and has an active thermoregulation strategy compared to both species. Southern populations of *A. richteri* have been found in sympatry with northern populations of *A. heterodermus*. Their sexual and aggressive behaviour includes a wide repertoire of dewlap extensions, sagittal body expansions and head-bobbing frequency. The courtship display is more elaborate than *A. heterodermus*.

Geographic distribution. *Anolis richteri* is a Colombia endemic lizard inhabiting mainly the northern *plateau* of

Cundinamarca and Boyacá departments and its surrounding hills as well as hills of the southernmost Santander department (Fig. 8). Altitudinal range is approximately between 2500 and 3500 m.

Remarks. Despite the fact that Dunn (1944) assigned a holotype for *A. richteri*, he did not indicate the museum numbers of the specimens used for the type series. Posteriorly, Medem (1965) documented the specimens belonging to the series of *Anolis richteri* (holotype MCZ 69120 and paratypes MCZ 69121, 69122 and 69123), also indicating that the three specimens come from the same locality and suggesting that the remaining specimens, from other localities, used by Dunn could be *A. richteri* as well. The series was posteriorly returned to Colombia and currently is catalogued with museum numbers ICN 5974 (Holotype), ICN 5975, ICN 5976, and ICN 5977 (Paratypes). Since a series was explicitly assigned it is not necessary to declare a new taxonomic act (e.g., assignment of lectotype and paralectotypes) but re-erect *A. richteri* as valid species as Dunn (1944) originally documented and our integrative lines of evidence revealed. In addition, because both Dunn (1944) and Lazell (1969) described and synonymized the species based on evidence including samples of several lineages, a redescription of the name-bearing types of *A. richteri* is necessary.

Anolis tequendama sp. nov.

https://zoobank.org/2B827F96-8720-4715-88A9-43C9AB9A4CB5

Anolis heterodermus Castañeda and de Queiroz (2013) supplementary
    material. [ICN 10609]

Holotype. ICN 4548. Adult male with everted hemipenis, dewlap present, enlarged postanal scales. From the *Vereda* Sabaneta, San Francisco municipality, Cundinamarca department, Colombia (4.891173°N –74.289925°W, 2850 m), collected by Henry Zuñiga and Jane R. Rodríguez in 1981.

Paratypes. ICN 4546 and 4547 adult male and female, respectively from the same locality data of the holotype, collected by Jose Vicente Rueda in 1981. ICN 5734 adult female from Cueva Grande hill From the Vereda Sabaneta, San Francisco municipality, Cundinamarca department, Colombia, collected by Henry Zúñiga in 1981. ICN-1499 adult male from the Vereda de Fute, Las Mercedes, Bojacá municipality, Cundinamarca department, Colombia (4.616388°N –74.281944°W, 2600 m), collected by J. Hernandez-Camacho in 1962. ICN 5765 (adult female) from Laguna de Pedro Palo, Tena municipality, Cundinamarca department, Colombia (4.683888°N –74.387222°W, 2050 m), collected by Oscar Pinto in 1981. ICN 9688 (adult female) from Barro Colorado, La Agüadita, Fusagasugá municipality, Cundinamarca department, Colombia (4.388888°N –74.334444°W, 1800 m), collected by D. Rivera in 1990. ICN 10609 (adult male) from Granjas del

Padre Luna, Alban municipality, Cundinamarca department, Colombia (4.899133°N –74.424122°W, 2090 m), collected by John D. Lynch in 1985.

Diagnosis. *Anolis tequendama* **sp. nov.** shares short limbs, a large casqued head, a prehensile tail without caudal autotomy, and lamellar subdigital scales of all digits extending from the most proximal phalanges with the other species of the *Phenacosaurus* clade. *Anolis tequendama* **sp. nov.** differs from *A. proboscis*, *A. orcesi*, *A. euskalerriari* and *A. nicefori*, by its strongly heterogeneous dorsal scalation. *Anolis tequendama* **sp. nov.** differs from *A. nicefori* by the presence of granular scales surrounding dorsal heterogeneous flat scales. *A. tequendama* **sp. nov.** differs from *A. heterodermus*, *A. richteri*, *A. tetarii*, *A. inderenae*, *A. vanzolinii* and *A. quimbaya* **sp. nov.** by a male dewlap colour uniformly brown or brown bluish. *Anolis tequendama* **sp. nov.** further differs from *A. inderenae*, *A. heterodermus*, *A. richteri* and *A. tetarii* by the presence of a discontinuous nuchal crest, from *A. heterodermus* and *A. inderenae* by the presence of a continuous row of enlarged sublabials that do not reach the mouth commissure; from *A. heterodermus* by a V-shaped crown; and from *A. vanzolinii* by < 24 expanded lamellae under second and third phalange of fourth toe and < 35 lamellae in total fourth toe.

Etymology. The specific epithet is used as a noun in apposition. The name refers to the Tequendama Falls, a popular waterfall near Bogotá that is part of the Bogotá River and has cosmological importance for the Muisca indigenous people; inhabitants of the Bogotá Plateau. In the Muisca language (called "*Muysccubun*"), Tequendama means "he who precipitates downward", referring to the waterfall.

Common name. Tequendama anole [English]. Anolis tequendama [Spanish]

External description of holotype. Snout-vent length = 76.8 mm; head length = 23.4 mm; head width = 11.3 mm; femoral length = 14.6 mm; ear height = 1.2 mm; tail length = 97.1 mm; fourth toe length = 10.3 mm. Dorsal head and supraocular disc scales either rough; frontal depression present; dorsal surface of rostral scale smooth, not notched; five scales across the snout between second canthals; supraorbital semicircles distinct, in contact; no scales separate interparietal and supraorbital semicircles; V-shaped crown; supraocular disc one to three enlarged scales, scales along the medial edge of the supraocular disc broken by larger scales that contact the supraorbital semicircles; one or two elongated supraciliary scales, followed by a series of small scales; two loreal rows; seven total loreals; circumnasal scale no contacts sulcus between rostral and first supralabials, one scale from the naris to the rostral; preoccipital absent; nine supralabials to center of eye; ten infralabials to center of eye; four postrostrals excluding first supralabials; five postmentals excluding first infralabials; mental completely divided posteriorly, extends posterolaterally along with the lateral limits of the rostral, with posterior border in a straight

line transverse to head; five sublabials enlarged in contact with infralabials; a row of enlarged sublabials reaching the mouth commissure absent, row of enlarged sublabials beyond posteriorly to a line just below the first canthal absent; dewlap present, not reaching posterior to axillae; rows of single scales on dewlap; tubelike axillary pocket absent; enlarged postcloacal scales. Nuchal and caudal crests present; nuchal crest discontinuous. Dorsal crest to base of tail; dorsal crest discontinuous; one enlarged middorsal row; dorsal scales heterogeneous and smooth; three rows of scales between middorsal crest and the beginning of dorsal flat scales surrounded entirely by granules; size of the flat dorsal scales in HW 1–1–1; six longitudinal dorsal scales in the fifth scale row in 10% of SVL. Ventral scales smooth, slightly overlapped, and rounded apices, in transverse rows; thirteen longitudinal ventral scales in 10% of SVL. Supradigitals smooth; toepads expanded and overlap the first phalanx; twenty expanded lamellae under second and third phalanges of fourth toe; tail crest with a single row of scales.

Paratypes variation. Snout-vent length = 61.3–79.9 mm (*N* = 7, mean = 66.8 mm, SD = 9.2 mm) ; head length = 19.4–24.3 mm; head width = 9.4–12.9 mm; femoral length = 10.0–12.7 mm; ear height = 0.8–1.3 mm; tail length = 75.0–92.0 mm; fourth toe length = 8.1–10.7 mm. Dorsal head and supraocular disc scales rough or smooth; frontal depression present or absent; dorsal surface of rostral scale smooth, not notched; 3–5 scales across the snout between second canthals; supraorbital semicircles distinct, in contact; 0–1 scales separate interparietal and supraorbital semicircles; V-shaped crown; supraocular disc one to three enlarged scales, scales along the medial edge of the supraocular disc broken by larger scales that contact the supraorbital semicircles; one or two elongated supraciliary scales, followed by a series of small scales; 1–2 loreal rows; 4–9 total loreals; circumnasal scale contacts or not the sulcus between rostral and first supralabials, one scale from the naris to the rostral; preoccipital present or absent; 7–11 supralabials to center of eye; 7–11 infralabials to center of eye; 4–5 postrostrals excluding first supralabials; 2–5 postmentals excluding first infralabials; mental completely or partially divided posteriorly, extends or not posterolaterally along with the lateral limits of the rostral, with posterior border in a straight line transverse to head; 5–6 sublabials enlarged in contact with infralabials; a row of enlarged sublabials reaching the mouth commissure absent, row of enlarged sublabials beyond posteriorly to a line just below the first canthal absent; dewlap present, reaching or not posterior to axillae; rows of single scales on dewlap; tubelike axillary pocket absent; enlarged postcloacal scales absent in females, present in males. Nuchal and caudal crests

present; nuchal crest discontinuous. Dorsal crest to midbody or to base of tail; dorsal crest discontinuous; 0–1 enlarged middorsal row; dorsal scales heterogeneous and smooth; 2–4 rows of scales between middorsal crest and the beginning of dorsal flat scales surrounded entirely by granules; size of the flat dorsal scales in HW 1–1–1, 1–0.5 and 1–0.5–0.25; 5–8 longitudinal dorsal scales in the fifth scale row in 10% of SVL. Ventral scales smooth, slightly overlapped and rounded apices, in transverse rows; 11–16 longitudinal ventral scales in 10% of SVL. Supradigitals smooth; toepads expanded and overlap the first phalanx; 18–21 expanded lamellae under second and third phalanges of fourth toe; tail crest with a single row of scales.

Colour in life. Body dorsally brown or yellow, lighter ventrally; transversal black, brown, or blue bands present in most individuals; dorsal surfaces of the body, limbs, and tail with abundant blue, brown and yellow scales, single or in groups forming disorderly spots (Fig. 7C); white or yellowish line running from the supralabials through the tympanum to the forelimbs; a patch of blue or red scales in the tail base; males commonly show unicoloured (solid) or spotted dewlaps which can be brown with some light coloured scales; females more often show striped dewlaps which are usually yellow with black or brown stripes (Fig. 7C). Although all *heterodermus* subgroup species change their body colour when stressed due to intense manipulation, the colour change in *A. tequendama* **sp. nov.** is particularly notorious and often includes changes in dewlap colour.

Habitat, ecology, and behaviour. *Anolis tequendama* **sp. nov.** inhabits scrublands, forests, and cloud forests in the Colombian Andes. This species preferentially uses small branches and narrow surfaces such as twigs and exhibits very slow movements, consistently with their twig anole ecomorph. This species occurs at lower altitudes and generally has a smaller body size compared to *A. heterodermus* and *A. richteri*. It has an active thermoregulation strategy compared to *A. heterodermus* but similar to *A. richteri*. The sexual and aggressive behaviour of this species have not been studied in detail but research in this area seems promising given their wide variation in body and dewlap colour.

Geographic distribution. *Anolis tequendama* is a Colombia endemic lizard inhabiting the northwestern slope of the Eastern Cordillera in Cundinamarca department (Probably also in Boyacá department and in the north and southeast and northernmost parts of Tolima and Huila departments respectively) (Fig. 8). Altitudinal range is approximately between 1900 and 2600 m.

Taxonomic key for the 11 *Anolis* species of the *Phenacosaurus* clade

(Images of characters in Supplementary informations and Figs 6–7, Fig. S1)

1. Homogeneous dorsal scalation..**2**
   – Heterogeneous dorsal scalation..**4**
2. Rounded or granular flank scales **3**
   – Hexagonal-like flank scales...*Anolis euskalerriari*
3. Supraorbital semicircles separated by one or two scales, interparietal separated from supraorbital semicircles by two scales, males with an elongated, thick nasal extension with serrate borders and ascendant projected, homogeneous grey-greenish dewlap colour.. *Anolis proboscis*
   – Supraorbital semicircles in contact, interparietal in contact with supraorbital semicircles, males without nasal extension, homogeneous yellow or orange dewlap colour ....*Anolis orcesi*
4. Heterogeneous flank scalation without granules surrounded flat scales ....*Anolis nicefori*
   – Heterogeneous flank scalation with some flat scales surrounded entirely by granules..........................**5**
5. Nuchal crest discontinuous **9**
   – Nuchal crest continuous or rarely discontinuous **6**
6. Row of enlarged sublabials reach the mouth commissure **7**
   – Row of enlarged sublabials do not reach the mouth commissure **8**
7. Crown "V"-shaped, male dewlap bicoloured, dewlap colour white/cream with brown or orange stripes ....
   .... *Anolis inderenae*
   – Crown "U"-shaped, unicoloured dewlap, dewlap colour purple, red or black ....*Anolis heterodermus*
8. Male dewlap white/cream or pink coloured, sometimes with visible blood irrigations ....*Anolis richteri*
   – Male dewlap yellow coloured, without visible blood irrigations...*Anolis tetarii*
9. Male dewlap colour uniformly brown or brown-bluish..*Anolis tequendama* **sp. nov.**
   – Male dewlap colour orange or green...**10**
10. < 24 expanded lamellae under second and third phalange of fourth toe, < 35 lamella in total, dorsal scales arranged in any type, male dewlap orange, female dewlap greenish..*Anolis quimbaya* **sp. nov.**
    – ≥ 24 expanded lamellae under second and third phalange of fourth toe, ≥ 35 lamella in total, type 1 dorsal scales never arranged in type 1 pattern, dewlap orange in both sexes ....*Anolis vanzolinii*

Discussion

Our study confirmed the formerly reported differentiation among populations of high-altitude *Phenacosaurus* anoles lizards from the northern Andes and the identification of several unknown evolutionary lineages. Our analyses also showed consistent genetic differentiation of those lineages revealed by both mitochondrial and nuclear gene pools, as well as morphological and geographical differences, providing evidence for the existence of nine distinct evolutionary lineages within the *heterodermus* group. These results increase the diversity of this highland anole group to ten species (counting *A. tetarii*, not included in this study).

Our phylogenetic analyses revealed nine reciprocally monophyletic groups and lineages corresponding to the haplo-groups revealed by the mtDNA haplotype network analyses that presented unique nDNA haplotypes (in the network, Lineage 3 and *A. vanzolinii* were not included) (Fig. 4). Furthermore, almost all uncorrected *p*-distances of the mitochondrial ND2 genes between the analyzed populations fell within the genetic differentiation values observed between other distinct congeneric *Anolis* species (> 8 %) (Glor et al. 2001; Glor et al. 2005), including closely related *Anolis* species (> 5 %) (D´Angiolella et al. 2011; Gartner et al. 2013). The genetic distance of 3.8% in ND2 between *A. vanzolinii* and *A. quimbaya* **sp. nov**. could be interpreted in several ways. This low genetic distance value of differentiation would suggest a different diversification *tempo* between *Phenacosaurus* anoles compared to the lowland anoles for the ND2 gene, or a more recent divergence between both species. Alternatively, it could suggest that genetic distance corresponds to intraspecific differentiation.

The last possibility is challenging compared to the remaining lines of evidence. Despite the wide overlapping in several phenotypic characters, *A. quimbaya* **sp. nov.** and *A. vanzolinii* differ strongly and significantly in body size ($F = 14.3$, $p = 0.001$), head length ($F = 6$, $p = 0.019$), femoral length ($F = 8.8$, $p = 0.005$), tail length ($F = 5.3$, $p = 0.028$), toe length ($F = 16.7$, $p > 0.01$), and in the numbers of lamellae under fourth toe in total ($F = 39.2$, $p > 0.01$) and in the second and third phalanges ($F = 53.8$, $p > 0.01$). Therefore *A. quimbaya* **sp. nov.** is a smaller anole with shorter head, legs, tail, and fewer subdigital lamellae than *A. vanzolinii*; one of the widely known giant twig anoles (Williams et al. 1996a, 1996b). Scale configuration was also different between both species with four or less sublabials in contact with infralabials in *A. quimbaya* **sp. nov.** (82 % of individuals) and five or more in *A. vanzolinii* (83 % of individuals). Furthermore, other molecular lines of evidence support morphometric differentiation, revealing that the genetic differences be-

tween both lineages correspond to interspecific differentiation; both lineages exhibit high genetic distance values for the COI (> 5 %), each lineage is recognized as an independent haplogroup separated by at least 124 mutational steps in the mtDNA haplotype network and showing exclusive nuclear haplotypes in the nuclear haplotype network (Fig. 4).

Even with the weak support for the differences between *A. vanzolinii* vs. *A. quimbaya* **sp. nov.** concerning their body and dewlap colour patterns, mainly due to the small sample size for the first one (i.e., only three photos), some exclusive patterns were detected. Irrespective of the high variation in dorsal coloration in *A. quimbaya* **sp. nov.** across its wide distribution, no individuals have black colouration, the main colour detected in *A. vanzolinii*. Additionally, although in both species striped-pattern body was detected, in *A. quimbaya* **sp. nov.** the most common pattern was unicoloured. Dimorphism in dewlap colouration was also detected in *A. quimbaya* **sp. nov.** while both sexes in *A. vanzolinii* were entirely orange. Therefore, matching with the above evidence and the distributional data available, we here confirm that previous lizards identified as *A. heterodermus* found in Putumayo, Colombia (Mueses 2006) and Ecuador (Torres-Carvajal 2010) correspond to *A. vanzolinii* and *A. quimbaya* **sp. nov.**, respectively.

Previous morphological studies already documented the high morphological variation within the *heterodermus* group (Dunn 1944; Lazell 1969), and molecular data provided robust evidence about the species complex status of the group (Williams et al. 1996; Castañeda and de Queiroz 2011; Vargas-Ramírez and Moreno-Arias 2014; Poe et al. 2017). Furthermore, morphological evidence did not support the *heterodermus* subgroup based on the degree of flank scale heterogeneity (Williams et al. 1996), since *A. nicefori* and other similar linages with weak heterogeneous scalation flanks (Lineages 1 and 2), were paraphyletic. However, we found a considerable morphological variation of several phenotypic attributes distributed throughout the lineages with some values matching more frequently specific lineages. Under the proposed phylogenetic framework, we identified conservative attributes between clades such as long legs and wide toes (*A. richteri*, *A. inderenae*, *A. heterodermus*) and short legs and narrow toes (the remaining species), low number of middorsal rows and a high number of supralabials (*A. richteri* and *A. inderenae*) and high middorsal and a low number of supralabials (the remaining species), and a green body colour (*A. richteri*, *A. heterodermus*) or green brownish colour (remaining species). Instead, scalation patterns and dewlap attributes were less conservative with continuous nuchal crest (*A. richteri*, *A. inderenae*, *A. heterodermus*), sublabials in contact with infralabials beyond the first canthal (*A. inderenae*, *A. heterodermus*) and a U-shaped crown (*A. heterodermus*). A non-conservative attribute was the dewlap configuration (Fig. 5).

Colour variation is a distinctive trait in anoles (Nicholson et al. 2007) and particularly in the *heterodermus* clade (Torres-Carvajal et al. 2010; Beltrán 2019). However, due to the complexity of this trait, few attempts have been

made to identify relevant features that have the potential to distinguish subgroups (Beltrán 2019). Here, we describe some of the multiple features that compose the dewlap and body colour patterns in a practical and relatively simple way, to investigate differences between the *heterodermus* species complex in a multivariate space. Our analysis showed that lizards belonging to a specific morphological group shared similar dewlap patterns and colours. This evidence supports the importance of dewlap configuration in mediating species recognition and complex signalling during courtship and agonistic encounters (Stuart-Fox and Ord 2004). However, the results were less clear regarding the body colour patterns because there was considerable overlap in body configurations among groups.

Although variation in body configurations in our dataset was significant and most of it was not captured by our analysis, we still lack solid explanations for the origin and evolution of the diversity of body colour patterns in this group. A plausible explanation is that the variation in exposed body parts such as the dorsum is constrained by natural selection, most commonly in the form of predation. This will reduce the differences among individuals, making it difficult to separate groups within the species complex. Nonetheless, we observed some patterns that are worth exploring in future studies. For instance, *A. inderenae* and *A. vanzolinii* showed fewer body colour and diversity patterns compared to the other species. It would be relevant to examine if this low diversity is associated with their large size or habitat heterogeneity, since habitat use, agonistic and interspecific interactions are factors already known to affect behavioural displays (Dufour et al. 2018), therefore, selecting certain body patterns over others. However, it is important to mention that our analyses did not consider differences in colour and patterns from an animal's perspective (e.g., using visual models), and so we lack spectral information that is not captured by standard digital cameras such as ultraviolet wavelengths (Stuart-Fox and Ord 2004). Therefore, making accurate inferences on the significance of these colour differences in the ecology and behaviour of these lizards was not possible (Stevens et al. 2007). Nonetheless, our analyses build on an integrative perspective of taxonomy aimed at identifying traits that can be helpful for researchers to identify the group of interest in the field or in a museum collection.

Biogeography

Current distributions and phylogenetic history of the species of the *heterodermus* group have been associated with climatic and geological processes. According to a preliminary proposal based on a single rate of molecular evolution (Fig. 3 in Vargas-Ramírez and Moreno-Arias 2014), diversification of the species complex started with the separation of *A. euskalerriari* around 10.5 mya, with subsequent splits as follow: A) between *A. richteri* and remaining species (7 mya), B) *A. heterodermus* and remaining species (4.2 mya), C) *A. inderenae* and *A. vanzolinii* (3.2 mya), and D) *A. vanzolinii* and *A. quimbaya* **sp. nov.** (2.3

mya). Divergence of *A. tequendama* **sp. nov.** could have occurred between 4.2 to 3.2 mya (Split E). Most of the divergence events closely match intense orogenic activity in the northern Andes from the Middle Miocene (~ 12 mya) to the early Pliocene (~ 4.5 mya). During this time, the Ecuadorian Andes and the Eastern Cordillera uplifted independently but interconnected with mid-elevation hills which after reaching elevations above 2000 m, changed climatic conditions and increased precipitation on the flanks of the cordilleras (Hoorn et al. 2010). A similar estimation was recently documented using paleo-elevationary reconstructions, indicating that the northern Andes uplifted from the early Miocene to the mid-Pliocene (Boschman 2021). Around 10 mya (when split A probably occurred) the domain Perijá range and Santander Massif already reached 2000 m elevation (Boschman 2021). After that, around 7 mya in the Eastern Cordillera domain, elevations predominated between 1600–2100 m, and later, around 4 mya, the Eastern Cordillera was dominated by elevations over 2100 m on the plateau of the Cundinamarca-Boyacá departments and elevations around 3000 m in the southernmost and northernmost parts (current Sumapaz and Cocuy "páramos") (Boschman 2021). During this time splits B and E could have occurred due to the formation of new habitats (i.e., "páramos", Andean and sub-Andean forests), as product of climatic and geological changes (Hoorn et al. 2010, Boschman 2021). The remaining splits (C and D) could be associated with the increase of elevation of the Garzón Massiff domain above 2000 m and the interconnection of this domain with the Central Cordillera, and the former with the Western Cordillera during the last 3 mya (Boschman 2021).

Conclusion

The utilisation of an integrative taxonomic framework allowed us to describe two species new to science: *A. quimbaya* **sp. nov.** and *A. tequendama* **sp. nov.**, redescribe *A. heterodermus* and erect as a valid species *A. richteri*, a previous synonym of *A. heterodermus*. The identification of those lineages, including the two poorly-know lineages 1 and 2 suggests that the diversity of high-altitude lizards of the *heterodermus* group remains underestimated. The Middle Miocene to Pleistocene period of significant orogenic and climatic events in northern South America that have shaped the group´s evolutionary history may have produced higher diversity than previously existed and that we are now beginning to understand. Since this group of lizards inhabits the threatened Andean montane tropical region (Etter 1993) that is typically characterised by high human population densities and extreme transformation rates, the recognition of its diversity aimed at establishing protective measurements is an urgent priority (see Vargas Ramírez and Moreno-Arias 2014). Fieldwork and careful revision of herpetological collections aimed at increasing knowledge of Lineages 1 and 2, as well as identifying hidden diversity is also urgently needed.

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Appendix 1

Specimens examined:

Anolis heterodermus. COLOMBIA — **Cundinamarca** • 1 ♂; Bogotá, cerro de Monserrate; ICN 7291• 1 ♂; Laguna de los Colorados, Páramo de Sumapaz; MAM-065 • 1 ♂; Altamira salida a Villavicencio; ICN 4184 • 1 ♀; Vereda Las Águilas, PNN Sumapaz, cerca al Batallón de alta montaña No. 1; IAvH 8810 • 2 ♂♂; same collection data as for preceding; IAvH 88/13 • 2 ♂♂; Vereda Santa Rosa, PNN Sumapaz, Locality 20, Base militar Santa Rosa; IAvH 88/15 • 2 ♀♀; Cajicá, carretera Cajicá-Tabio; ICN 5959/69 • 1 ♂; Choachí, páramo de Cruz Verde, Km 12 carretera Bogotá-Choachí; ICN 2384 • 1 ♂; Parque Ecológico Matarredonda; Miguel Méndez Galeano leg.; MAM 017 • 1 ♀; same collection data as for preceding; Miguel Méndez Galeano leg.; MAM 018 • 1 ♂; Tenjo, Cerro de Juaica; ICN 13138. — **Meta** • 2 ♂♂; Cubarral, páramo de Sumapaz; ICN 10598/99) • 1 ♂; Vereda Pedregal, Laguna Patio Bonito; ICN 8049 • 2 ♂♂; ICN 10011/12.

Anolis inderenae. COLOMBIA — **Cundinamarca** • 1 ♀; Gutiérrez, Vereda El Carmen; Holotype: IAvH 3213 • 1 ♀; same collection data as for preceding; Paratype: IAvH 2999 • 2 ♂♂; same collection data as for preceding; Paratypes: IAvH 3381/3744. — **Meta** • 1 ♂; El Calvario, corregimiento de San Francisco; Felipe Parra leg.; FP 002.

Anolis quimbaya sp. nov. COLOMBIA — **Antioquia** • 1 ♂; Urrao, vereda el Chuscal, quebrada La Nevera; ICN 10610. — **Caldas** • 1 ♀; Manizales, Natural Reserve Rio Blanco; MHUA-R 11396. — **Cauca** • 2 ♂♂; Puracé, Coconuco, Hacienda Pisochago; IAvH 3218/19. — **Nariño** • 2 ♀♀; Chachagüí, corregimiento de Hato Viejo, Vereda Palmas Altas; PSO-CZ 554/557 • 1 ♀; Pasto, corregimiento de Morasurco, Vereda Josefina, Reserva El Morar; PSO-CZ 555 • 1 ♂; same collection data as the preceding; PSO-CZ 556. —**Tolima** • 1 ♀; Cajamarca; MHUA-R 13284 • 1 ♀; Ibagué, termales El Rancho, alto río Combeima; IAvH 3219 • 1 ♀; Las Juntas; ICN 4185. — **Valle del Cauca** • 1 ♂; El Cairo; MHUA-R 12859 • 1 ♀; La Cumbre; corregimiento de Bitaco, Vereda Chicoral, Alto Bitaco, finca Monte Bello; IAvH 4920 • 1 ♂; San Antonio; torre de la TV; ICN 4186. ECUADOR — **Carchi** • 3 ♀♀; Bajo Chilma; QCAZ 8721/55/56 • 1 ♂; same collection data as for preceding; QCAZ 8754.

Anolis richteri. COLOMBIA — **Boyacá** • 1 ♂; Belén; ICN 2161• Cerinza, Vereda Toba; 1 ♂; DMB 281 • Duitama, 1 ♀; Km 6 carretera Duitama-Charalá; Pedro Ruiz leg.; PR 5056 • 1 ♂; same collection data as for preceding; Pedro Ruiz leg.; PR 5057 • 1 ♂; Páramo La Rusia; ICN TP 168 • 1 ♂; Guacamayas; Vereda Alisal, finca El Trompetal; ICN TP 147 • 1 ♀; same collection data as the preceding ; ICN TP 191 • 2 ♀♀; Paipa, Reserva Municipal Ranchería; IAvH 7580/81 • 1 ♀; Tutazá, Vereda Tobal; DMB 302 • 1 ♀; Ventaquemada; ICN 7285 • 1 ♀; Villa de Leiva, área urbana, puente de la quebrada San Agustín; IAvH 7706 • 1 ♀; SFF Iguaque; ICN 7293. — **Cundinamarca** • 13 ♀♀; Cajicá, carretera Cajicá-Tabio; ICN 5954/58/59/70/81, ICN 5992 to 5994, ICN 6247/49, ICN 6337 to 6339 • 12 ♂♂; same collection data as the preceding; ICN 5953/57/80/82/95, ICN 6244/45/48/56, ICN 6337 to 6339 • 2 ♀♀; Fúquene, Laguna de Fúquene, cerca al puerto; ICN TP 159/162 • 3 ♂; Gachancipá; MAM 051, ICN TP 133/162 • 3 ♀♀; same collection data as the preceding; MAM 052-053, ICN TP 174 • 1 ♂; Gachetá; ICN TP 143 • 1 ♀; Guatavita, Vereda Carbonera Baja; ICN 12729 • 1 ♀;

Tabio, finca El Recodo; MAM 016 • 4 ♂♂; Tausa, Represa del Neusa; ICN 2308, ICN 2197, ICN 5955/56 • 2 ♀♀; same collection data as the preceding; ICN 2817/4478 • 1 ♂; Vereda Chorrillo; ICN 2203. — **Santander** • 2 ♀♀; El Peñón, carretera entre El Peñón y la casa de espeleología; IAvH 8354/55 • 1 ♂; sector Las Cruces, carretera hacia la caverna el Caracol; IAvH 8346 • 1 ♂; Vereda Jabonera, bosque del Acueducto; IAvH 8347 • ICN 10507/08.

Anolis tequendama **sp. nov.** COLOMBIA — **Cundinamarca** • 2 ♀♀; Alban, Granjas del Padre Luna; María Cristina Ardila leg.; MC 11229/52 • 3 ♂♂; San Antonio de Tequendama, Parque Natural Chicaque; Miguel Méndez Galeano leg.; MAM 019/21/22 • 2 ♀♀; same collection data as the preceding; Miguel Méndez Galeano leg.; MAM 020/24 • 1 ♂;

Villeta, Vereda La Esmeralda; Miller Castañeda leg.; MCC 568 • 1 ♀; same collection data as the preceding; Miller Castañeda leg.; MCC 573.

Anolis vanzolinii. COLOMBIA — **Putumayo** • 2 ♂♂; Colón; ICN 10597 • 1 ♂; Colón, Natural Reserve El Recuerdo; ICN 10594 • 1 ♂; Santiago, Vereda Vijinchoy; ICN 10595 • 1 ♀; same collection data as the preceding; ICN 10596. ECUADOR — **Sucumbíos** • 1 ♀; Santa Bárbara; QCAZ 9051 • 1 ♀; sector La Bretania, en la Y hacia El Playón–El Carmelo-Santa Bárbara; QCAZ 6926 • 1 ♂♂ La Bonita; Holotype; MECN 1573 • 2 ♂♂; same collection data as the preceding; Paratypes; EPN 9823/24, 2 ♂♂; same collection data as the preceding; QCAZ 10189/91• 1 ♀; same collection data as for preceding; QCAZ 13533.

Supplementary material 1

Supplementary informations

Authors: Moreno-Arias RA, Méndez-Galeano MA, Beltrán I, Vargas-Ramírez M (2023)
Data type: .pdf
Explanation notes: Relevant characters to the identification of species of the heterodermus group
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Link: https://doi.org/10.3897/vz.73.e94265.suppl1

Supplementary material 2

Table S1

Authors: Moreno-Arias RA, Méndez-Galeano MA, Beltrán I, Vargas-Ramírez M (2023)
Data type: .pdf
Explanation notes: Samples used in this study and GenBank accession numbers.
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Link: https://doi.org/10.3897/vz.73.e94265.suppl2

Supplementary material 3

Table S2

Authors: Moreno-Arias RA, Méndez-Galeano MA, Beltrán I, Vargas-Ramírez M (2023)
Data type: .pdf
Explanation notes: Animal photographs, associated details and body measurements used in this study.
Copyright notice: This dataset is made available under the Open Database License (http://opendatacommons.org/licenses/odbl/1.0). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.
Link: https://doi.org/10.3897/vz.73.e94265.suppl3

Supplementary material 4

Table S3

Authors: Moreno-Arias RA, Méndez-Galeano MA, Beltrán I, Vargas-Ramírez M (2023)
Data type: .pdf
Explanation notes: Animal photographs, associated details and dewlap measurements used in this study.
Link: https://doi.org/10.3897/vz.73.e94265.suppl4

Supplementary material 5

Figure S1

Authors: Moreno-Arias RA, Méndez-Galeano MA, Beltrán I, Vargas-Ramírez M (2023)
Data type: .jpg
Explanation notes: Body patterns of the heterodermus species group.
Link: https://doi.org/10.3897/vz.73.e94265.suppl5

Supplementary material 6

Figure S2

Authors: Moreno-Arias RA, Méndez-Galeano MA, Beltrán I, Vargas-Ramírez M (2023)
Data type: .jpg
Explanation notes: Bayesian tree for COI haplotypes of the *heterodermus* subgroup.
Link: https://doi.org/10.3897/vz.73.e94265.suppl6

Supplementary material 7

Figure S3

Authors: Moreno-Arias RA, Méndez-Galeano MA, Beltrán I, Vargas-Ramírez M (2023)
Data type: .jpg
Explanation notes: Morphological variation of the *heterodermus* subgroup.
Link: https://doi.org/10.3897/vz.73.e94265.suppl7

Supplementary material 8

Figure S4

Authors: Moreno-Arias RA, Méndez-Galeano MA, Beltrán I, Vargas-Ramírez M (2023)
Data type: .jpg
Explanation notes: Body and dewlap pattern variation of the *heterodermus* subgroup.
Link: https://doi.org/10.3897/vz.73.e94265.suppl8