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Eight in one: morphological and molecular analyses reveal cryptic diversity in Amazonian alopoglossid lizards (Squamata: Gymnophthalmoidea)

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Among the currently recognized species of *Alopoglossus*, the Amazonian *Alopoglossus angulatus* has the widest distribution. We here analyse variation in scutellation and morphometrics of *A. angulatus* by examining 785 specimens of *Alopoglossus*. We also analyse intra- and interspecific genetic structure and differentiation using two mitochondrial (*Cytb* and *ND4*) and two nuclear (*SNCAIP* and *PRLR*) genes from 97 samples. Both morphological and molecular analyses are based on specimens and samples from Brazil, Colombia, Ecuador, French Guiana, Guyana, Peru and Suriname. Our results reveal *A. angulatus* as a monophyletic group composed of eight independently evolved lineages: *A. angulatus s.s.* plus three revalidated species plus two newly described species plus two putative species. We provide descriptions of all taxa, except for the putative species, including the first description of the neotype of *A. angulatus* and redescriptions of resurrected junior synonyms. Illustrations, diagnoses and geographical distribution maps are provided. Gene and species trees are also provided. The two new taxa recognized in this paper, along with the revalidation of three taxa, increase the total number of known species of *Alopoglossus* from nine to 14.

ADDITIONAL KEYWORDS: cryptic species – molecular phylogeny – new taxa – Reptilia – South America – species redescription – taxonomic revision – tropical.

INTRODUCTION

The Neotropical lizard genus *Alopoglossus* Boulenger (1885) includes nine known species [*Alopoglossus angulatus* (Linnaeus, 1758), *Alopoglossus atriventris* Duellman (1973), *Alopoglossus buckleyi* (O'Shaughnessy, 1881), *Alopoglossus copii* Boulenger (1885), *Alopoglossus embera* Peloso & Morales (2017), *Alopoglossus festae* Peracca (1904), *Alopoglossus lehmanni* Ayala & Harris (1984), *Alopoglossus meloi* Ribeiro-Júnior (2018) and *Alopoglossus viridiceps* Torres-Carvajal & Lobos (2014)] and is distinguished from all gymnophthalmoid genera, except *Ptychoglossus* Boulenger (1890), by the following

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combination of characters: an open Meckel's groove, a tubular frontal bone and oblique plicae on the surface of the tongue (Harris, 1985; Goicoechea *et al.*, 2016). From *Ptychoglossus* (in parentheses), they differ in having keeled scales on the forelimbs (smooth forelimb scales) and rhomboid, laterally imbricating dorsal scales (parallel-sided dorsal scales) (Harris, 1994). Widespread across the Amazon Basin and adjacent areas, *A. angulatus* has the widest distribution of all species of *Alopoglossus* (Köhler *et al.*, 2012; Ribeiro-Júnior & Amaral, 2017).

Alopoglossus angulatus was described by Linnaeus (1758) as *Lacerta angulata* based on a single specimen collected by Rolander in 'America'. More than a century later, Cope (1876) described *Lepidosoma carinicaudatum* based on a single specimen from Marañon, collected during the Prof. Orton Expedition to Ecuador, Peru and Brazil. In 1881, O'Shaughnessy formalized the rehabilitation of *Lepidosoma carinicaudatum* to the genus *Leposoma* Spix (1825). Subsequently, the genus *Alopoglossus* was described by Boulenger (1885) to accommodate both the new species described by him, *Alopoglossus copii* and *Alopoglossus carinicaudatus* (= *Leposoma carinicaudatum* Cope, 1876). In 1924, Ruthven described *Alopoglossus amazonius* based on one specimen from Villa Murtinho, Matto Grosso, Brazil. Brongersma (1946) described *Alopoglossus copii surinamensis* from the 'forest on the Lucie River, Suriname'. *Alopoglossus andeanus* was described by Ruibal (1952) based on a single specimen from La Pampa, Puno, Peru; also, the author placed *A. amazonius* in the synonymy of *A. carinicaudatus*. In 1973, Hoogmoed resurrected *Lacerta angulata*, as *Alopoglossus angulatus*, and placed *A. carinicaudatus* in its synonymy. Hoogmoed (1973) also restricted the type locality of *A. angulatus* to Brown's Mountain [Brownsberg], Suriname, by neotype selection. Ávila-Pires (1995) published a detailed description of *A. angulatus* from Brazilian Amazonia. Köhler *et al.* (2012) studied the variation in scutellation and morphometrics of *Alopoglossus* spp., with an emphasis on Ecuadorian and Peruvian specimens, and placed *A. andeanus* in synonymy of *A. angulatus*. Ribeiro-Júnior (2018) described *A. meloi* in a revision of *A. angulatus* specimens broadly distributed in the Amazon Basin and redefined the nomenclature of some diagnostic characters of Alopoglossidae.

The first phylogenetic analysis of species-level relationships in *Alopoglossus* was the study by Pellegrino *et al.* (2001). Based on genetic data from three mitochondrial and two nuclear genes, the authors erected the subfamily Alopoglossinae, consisting solely of *Alopoglossus*. Castoe *et al.* (2004) increased sampling and re-analysed data of Pellegrino *et al.* (2001), proposing the inclusion of *Ptychoglossus* in Alopoglossinae. The close relationship between these two genera had already been suggested by Harris (1994) based on morphological similarities. Recently, Goicoechea *et al.* (2016) presented trees rejecting the monophyly of Gymnophthalmidae as traditionally circumscribed (e.g. Pellegrino *et al.*, 2001; Castoe *et al.*, 2004). Instead, *Alopoglossus* and *Ptychoglossus* form a clade sister to a much larger clade composed of Teiidae and the remaining gymnophthalmids. To preserve the family names Gymnophthalmidae and Teiidae, Goicoechea *et al.* (2016) erected Alopoglossidae to family status, including only *Alopoglossus* and *Ptychoglossus*. To date, Alopoglossidae includes two genera and 24 species.

Despite some recent studies (e.g. Köhler *et al.*, 2012; Torres-Carvajal & Lobos, 2014; Ribeiro-Júnior & Amaral, 2017; Ribeiro-Júnior, 2018), the taxonomy of *A. angulatus* requires further resolution based on denser geographical sampling and integrative taxonomy approaches. Here, we present the results of a major revision of the widespread *A. angulatus*, in which we account for morphological and molecular variation to survey the distinctiveness and intraspecific structure. We include the description of two new species, resurrection of three species (with redescription of the holotypes), the first redescription of the neotype of *A. angulatus* and the recognition of two differentiated lineages as putative species, with a key to the species of *Alopoglossus*.

MATERIAL AND METHODS

SAMPLING

We selected 315 vouchers from 199 different localities (Fig. 1) and 58 tissue samples to assess the phenotypic and genetic structure of *A. angulatus*. Information on the specimens included in the morphological and molecular analyses is provided in the species descriptions and the Supporting Information (Table S1 and Referred Specimens).

MOLECULAR DATA COLLECTION AND PREPARATION

We took a molecular approach to investigate the degree of phylogenetic differentiation and the population structure and to identify possible species limits. The molecular dataset consisted of two mitochondrial protein-coding genes [mtDNA; cytochrome *b* (*Cytb*) and NADH dehydrogenase subunit 4 (*ND4*)] and two protein-coding nuclear genes [nuDNA; the synuclein alpha interacting protein gene (*SNCAIP*) and the prolactin receptor gene (*PRLR*)]. Details on laboratory procedures and amplification protocols can be found in the Supporting Information (Amplification Protocol

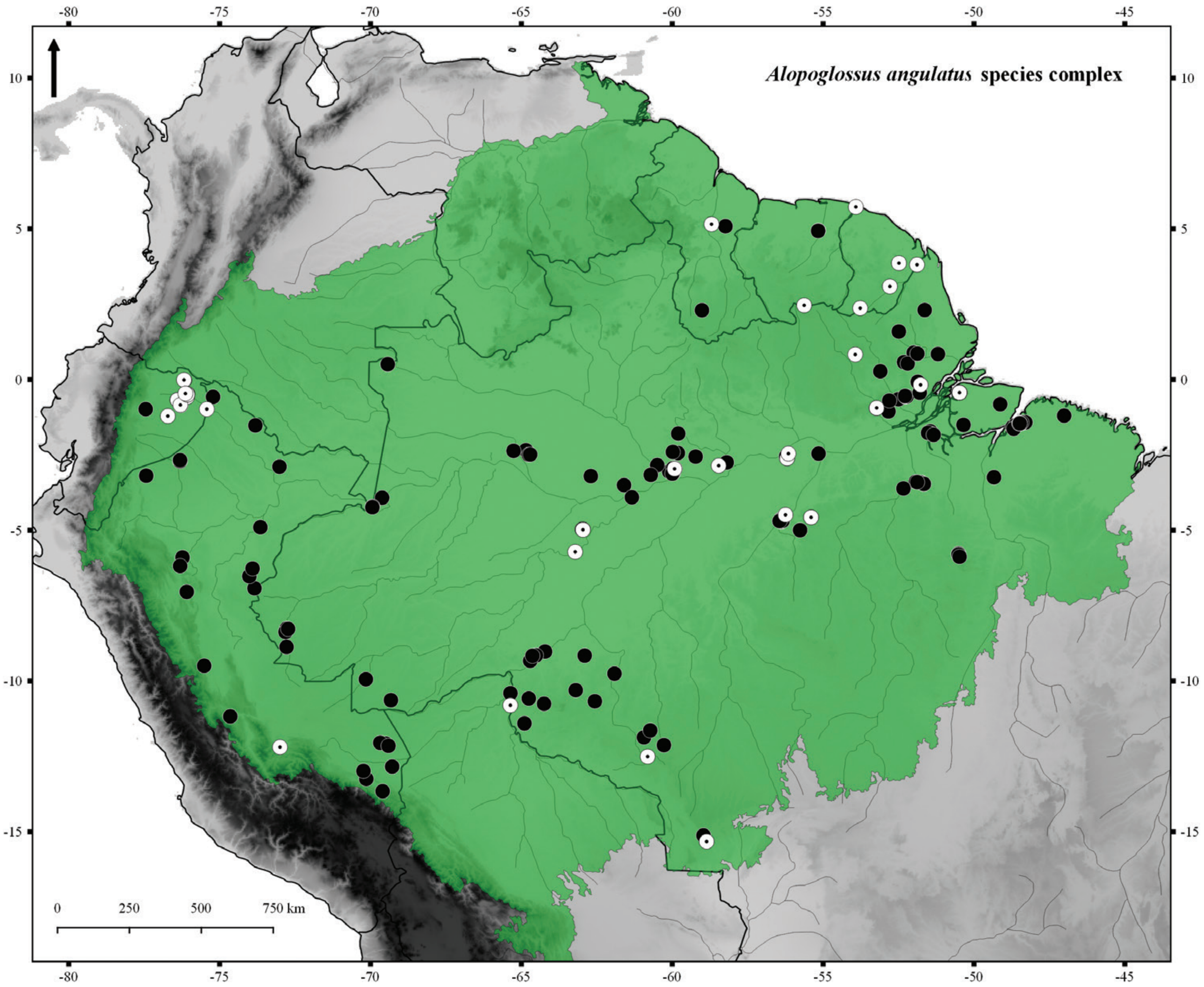

Figure 1. Distribution of the sampling localities: specimens included in the morphological (black dots) and molecular analyses (white dots).

and Table S2). Purified PCR products were sequenced using the Big Dye Terminator sequencing kit (Applied Biosystems, Waltham, MA, USA) in an automated sequencer ABI 3130 XL (Applied Biosystems, Waltham, MA, USA) at the Laboratório Temático de Biologia Molecular (LTBM) at the Instituto Nacional de Pesquisas da Amazônia (INPA). The QCAZ samples were amplified at the Laboratorio Molecular at the Museo de Zoología de la Pontificia Universidad Católica del Ecuador (QCAZ) and sequenced by Macrogen Inc. Sequences were deposited in GenBank (Supporting Information, Data Availability).

We verified and edited sequences using Geneious v.6.1.8 (Biomatters) and aligned them with AliView v.1.17.1 (Larsson, 2014). For nuDNA, the gametic phase of heterozygous individuals was resolved with PHASE v.2.1.1 (Stephens *et al.*, 2001), using the online platform seqPHASE (Flot, 2010) to generate input files. The optimal partitioning strategy and evolutionary substitution models were selected based on the Bayesian information criterion (BIC) and the corrected Akaike information criterion (AICc) with PartitionFinder v.2.0 (Lanfear *et al.*, 2016).

PHYLOGENETIC RELATIONSHIPS AND POPULATION STRUCTURE

For phylogenetic inferences, we used a total of 58 *A. angulatus* samples broadly distributed across Amazonia. To confirm the phylogenetic positioning within the genus, we included samples of the congeneric *A. atriventris* (*N* = 20, amplified to all genes), and *ND4* sequences of *A. buckleyi* (*N* = 3), *A. copii* (*N* = 1), *A. festae* (*N* = 8) and *A. viridiceps* (*N* = 6). Other species of the genus (*A. embera*, *A. lehmanni* and *A. meloi*) were not included in our phylogenetic approach owing to the lack of available sequences in GenBank. One sample of *Arthrosaura reticulata* (O'Shaughnessy, 1881) was used as the outgroup.

To evaluate phylogenetic relationships, we inferred gene trees based on concatenated mtDNA, whereas nuDNA genes were treated separately, and on the concatenated full dataset. Maximum likelihood gene trees were estimated with RAxML v.8.2.0 (Stamatakis, 2014) through 100 replicates using the GTRGAMMA model. Topologies based on Bayesian inference were generated with MrBayes v.3.2.5 (Ronquist *et al.*, 2012) through four runs of ten million generations sampled every 100 generations, with a burn-in of 10%. Convergence of analyses was verified in TRACER v.1.6.0 (Rambaut *et al.*, 2013). We estimated genetic distances between mtDNA haploclades with MEGA v.7.0.25 (Kumar *et al.*, 2016) using uncorrected and corrected distances based in the Tamura–Kumar model (Tamura & Kumar, 2002) and 500 bootstrap replicates to assess standard errors.

Population structure [i.e. number of populations (k) and individual assignments] was investigated with the software BAPS v.6.0 (Corander & Tang, 2007) using concatenated mtDNA and independent nuDNA genes, but excluding external group and GenBank sequences. The mixture approach was initially used to test a maximum value of $k = 10$ populations. The results were submitted to the admixture analysis, implemented using 100 iterations to estimate admixture coefficients and 20 iterations to estimate such coefficients for 200 reference individuals from each population.

SPECIES DELIMITATION AND SPECIES TREE

We performed a species delimitation analysis by implementing the multispecies coalescent model in BPP v.3.1 (Yang, 2015). Candidate species were defined a priori, considering the phylogeographical haploclades recovered by the mtDNA gene trees for the *A. angulatus* species complex and *A. atriventris*. To validate these hypothetical species, we used the analytical option 'A11' to jointly delimitate species and estimate species trees while testing different scenarios of divergence times (tau prior = 2/300 recent divergences or 2/3000 old divergences) and historical effective population sizes (theta prior = 2/300 small population size or 2/3000 large population size). Each combination was submitted to the three species model priors implemented by BPP to increase the reliability of the proposed delimitations. We implemented 150 000 generation runs and discarded the initial 50 000 generations.

Finally, to account for potential gene tree uncertainties attributable to coalescent processes, we inferred a species tree with BEAST v.1.8.6 (Drummond *et al.*, 2012) using the StarBeast approach (Heled & Drummond, 2010) and considering the Yule speciation model. Species assignment and topology were established based on the results from the species delimitation analysis. Divergence times were estimated using an uncorrelated relaxed clock based on a prior with normal distribution for the mtDNA (mean = 0.0065, SD = 0.0025 for the ucld. mean parameter). This setting represents a nucleotide substitution rate of 0.65%/Myr determined to Asian agamids and is widely used on squamate phylogenies (Macey *et al.*, 1998; Werneck *et al.*, 2012). For nuclear markers, we used priors with gamma distribution for the parameter ucld.mean and exponential for the parameter ucld.stdev with a mean of 0.5, as suggested by Werneck *et al.* (2012). We ran 50 million generations, with samples taken every 5000 generations. Stationarity was evaluated with TRACER v.1.6.0 (Rambaut *et al.*, 2013), and a maximum clade credibility tree (MCC) was summarized with Tree Annotator v.1.8.6 (Drummond *et al.*, 2012), discarding 10% of the initial trees.

MORPHOLOGICAL DATA COLLECTION AND ANALYSIS

As part of a broad-scope study on the taxonomy of the genus, we examined 785 specimens of *Alopoglossus* (315 specimens of *A. angulatus* and 470 specimens of other species in the genus) from Brazil, Colombia, Ecuador, French Guiana, Guyana, Peru and Suriname (see type series in the main text and Supporting Information, Referred Specimens), deposited in the following herpetological collections: Museu Paraense Emílio Goeldi, Belém, Brazil (MPEG); Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil (MZUSP); Museu de História Natural Capão da Imbuia, Curitiba, Brazil (MHNCI); Instituto de Pesquisas Científicas e Tecnológicas do Estado do Amapá, Macapá, Brazil (IEPA); Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil (INPA-H); Universidade de Brasília, Brasília, Brazil (CHUNB); Museo de Zoología de la Pontificia Universidad Católica del Ecuador, Quito, Ecuador (QCAZ); Centro de Ornitología y Biodiversidad, Lima, Peru (CORDIBI); the Academy of Natural Sciences of Drexel University, Philadelphia, USA (ANSP); the American Museum of Natural History, New York, NY, USA (AMNH); the Museum of Comparative Zoology, Cambridge, MA, USA (MCZ); the National Museum of Natural History, Washington, DC, USA (USNM); the University of Michigan Museum of Zoology, Ann Arbor, MI, USA (UMMZ); and the Naturalis Biodiversity Center, Leiden, The Netherlands (RMNH). Museum acronyms follow Sabaj-Perez (2016), except for the following: Department of Ecology, National Amazon Research Institute, Manaus, Brazil (APL); Laboratory of Amphibians and Reptiles, Federal University of Rio Grande do Norte, Natal, Brazil (AAGARDA); and Paulo Bührnheim Zoological Collection, Federal University of Amazonas, Manaus, Brazil (CZPB-RP). The species descriptions are based on 315 specimens previously identified as *A. angulatus*, and the comparison with other species in the genus is based on 470 specimens of *A. atriventris*, *A. buckleyi*, *A. copii*, *A. festae*, *A. meloi* and literature.

Measurements were taken with digital callipers (± 0.1 mm); scale counts and other morphological characters were observed using a stereomicroscope. The measurements (abbreviations in parentheses) are as follows: axilla–groin length (AGL), from the anterior margin of the hindlimb to the posterior margin of the forelimb; forelimb length (FL); head depth (HD) at the highest point dorsoventrally; head length (HL) from the anterior margin of tympanic aperture to the tip of snout; hindlimb length (HLL); head width (HW) at the widest point; neck length (NL), from the posterior margin of the tympanic aperture to the anterior margin of the forelimb; shank length (ShL); snout–vent length (SVL), from the border of cloaca to the tip of snout; tail length (TL). Abbreviations used to indicate sex are as follows: m, male; f, female; j, juvenile.

The nomenclature of scale characters follows Ribeiro-Júnior (2018). The meristic characters are as follows (abbreviations in parentheses): dorsal scales (D), counted from the parietals posteriorly to the insertion of hindlimbs; ventrals (V), counted between the interbrachial and preanal shields; scale rows around the midbody (Mb); scale rows around the tail, immediately posterior to the cloaca; supraoculars (So); suboculars (Sbo); postoculars (Po); superciliaries (Sc); palpebrals (Pal), on lower eyelid; loreal; frenocular; supralabials (Sl); infralabials (Il); scales on sides of neck (Neck), in transverse rows; pairs of chin shields (Pairs); granular scales between the pairs of chin shields (BtwP); gulars (G), counted between the interbrachial and mental plates; femoral pores (Pores); lamellae under fourth finger (F); lamellae under fourth toe (T).

We applied univariate and multivariate statistics to test for morphological distinctness between the *A. angulatus* species groups recognized by the molecular analyses. Measurement and scalation characters were first analysed using univariate, non-parametric tests: the Kruskal–Wallis test to compare the medians of each character between the species delimitated by BPP, and the Mann–Whitney post hoc test to compare medians between pairs of groups (significance was assessed with Bonferroni correction for multiple comparisons). In addition, we performed multivariate linear discriminant analyses (LDAs) to examine the degree of separation between the species delimitated by BPP. Three LDAs for meristic data were performed: (1) including all individuals (males and females, excluding pores); (2) including only males (including pores); and (3) including only females (pores are absent). Body measurements used in all analyses were divided by SVL, and only individuals ≥ 40 mm SVL were included (sexually mature length for *Alopoglossus*; Vitt *et al.*, 2007); males and females were analysed jointly because no detectable sexual size dimorphism exists in adults of *Alopoglossus* (Vitt *et al.*, 2007). All statistical analyses were calculated using PAST v.3.26 software (Hammer *et al.*, 2001).

Coloration in life is based on photographs of specimens in life (when available, or in satisfactory quality), and coloration in preservative is based on type material. Variations in coloration in preservative were obtained based on specimens deposited in the herpetological collections cited above.

Distribution maps are based on specimens examined and localities sampled for DNA (for a general view of records, see Fig. 1; maps are in the Supporting Information). All georeferences are in geographical coordinate system and WGS 1984 datum. The distribution map was created using QGis Las Palmas (v.2.18.3; http://www.qgis.org/es/site/).

The general description format of species follows Ribeiro-Júnior *et al.* (2016), considering the standardization of the nomenclature of alopoglossid and gymnophthalmid morphological characters suggested by Ribeiro-Júnior (2018).

RESULTS

MOLECULAR ANALYSES

The mtDNA gene tree recovered the monophyly of *Alopoglossus* and indicated that individuals initially identified as *A. angulatus* corresponded to different phylogeographical lineages (hereafter, the *A. angulatus* species complex; Fig. 2). The phylogenetic organization of congeneric species exhibited *A. atriventris* positioned as sister clade to the *A. angulatus* species complex, *A. buckleyi* placed as sister of the clade containing *A. atriventris* and *A. angulatus* species complex, and *A. viridiceps* and *A. festae* externally positioned as sister taxa with high support values. The positioning of *A. copii* was uncertain.

Within the *A. angulatus* complex, a deep split separated a clade broadly distributed in eastern Amazonia ('East'; pink clade in Fig. 2) from the other lineages. A second split placed samples from Ecuador, which formed a well-supported clade ('Ecuador'; red clade in Fig. 2), as sister to five possible distinct

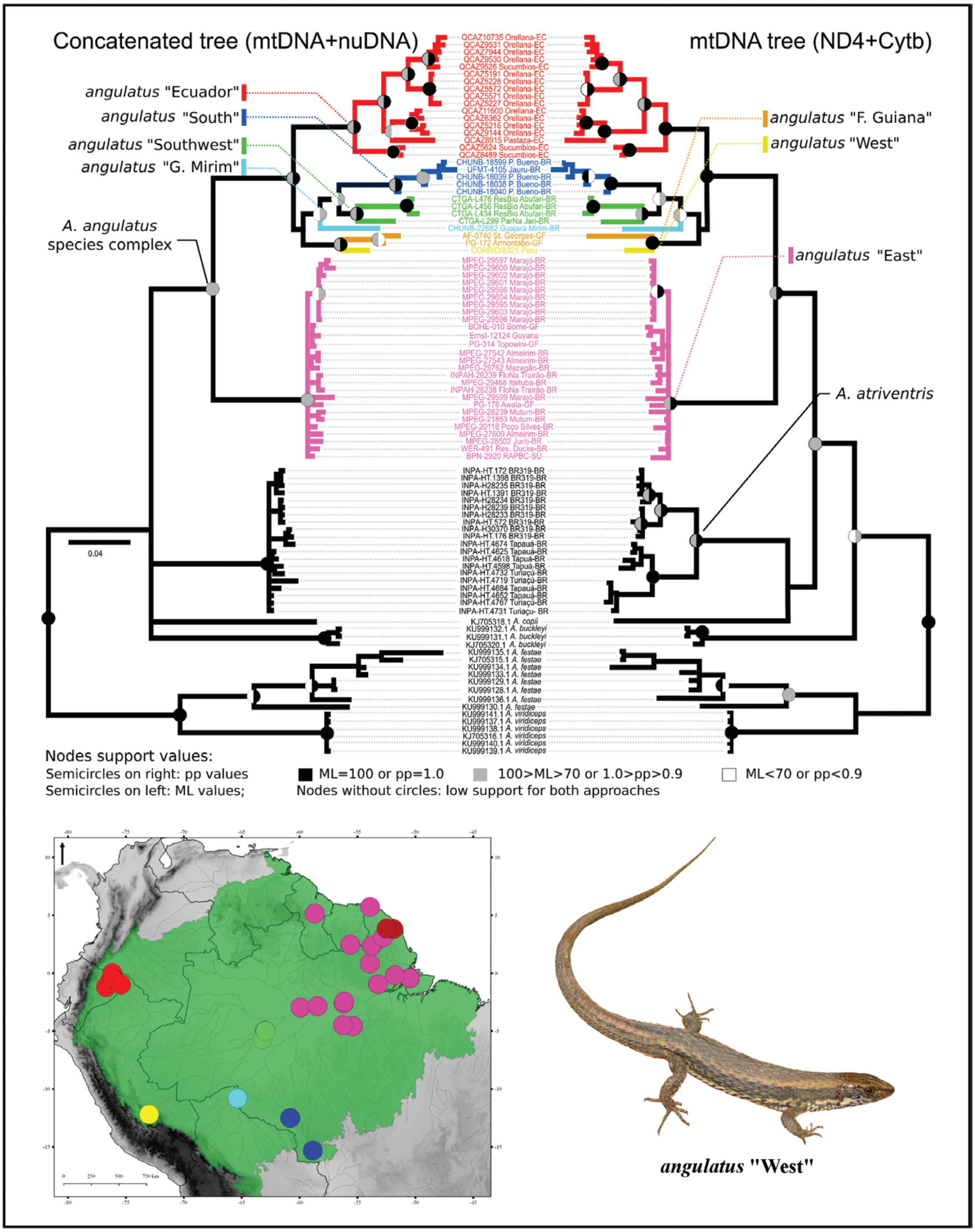

Figure 2. Mitochondrial (mtDNA) and concatenated (mtDNA + nuDNA) gene trees of five *Alopoglossus* species plus the *Alopoglossus angulatus* species complex. Branch colours represent the different delimited lineages. Posterior probability (pp) and bootstraps values (ML) are indicated by colours in the nodes.

evolutionary units with moderate to high support values. These putative species were identified as distributed to the south ('South'; blue clade) and south-west of the Amazonia ('Southwest'; green clade), Guajará-Mirim ('G. Mirim'; light blue branch), Peru ('West'; yellow branch) and French Guiana ('F. Guiana';

orange branch) (Fig. 2). The south and southwest lineages were recovered as sister clades, with the sample from Guajará-Mirim being their next sister taxon. Individuals from French Guiana were closely related to the sample from Peru, but the phylogenetic position of this clade was poorly supported.

Nuclear genes recovered an overall similar pattern to that obtained with the mtDNA dataset, although with less resolution between recovered lineages and some instances where *A. atriventris* samples grouped with lineages of the *A. angulatus* species complex, rendering it paraphyletic. The *SNCAIP* gene tree (Supporting Information, Fig. S1) recovered the 'Southwest', 'F. Guiana' and 'South' clades, but without the complete differentiation between samples of 'South' and 'G. Mirim'. Resolution of this marker was less informative to determine the phylogenetic positioning of eastern samples. Despite samples of *A. atriventris* grouping with high support, their placement was uncertain, being poorly supported as a sister group of the major clade containing 'South', 'G. Mirim', 'Southwest' and 'F. Guiana' samples. Regarding the *PRLR* gene tree (Supporting Information, Fig. S2), although the Ecuadorian and *A. atriventris* clades were recovered with high support, some samples attributed to these clades by the mtDNA were positioned externally to them. 'South' and 'Southwest' clades also showed this pattern. Samples of the 'East' clade grouped together with low support.

The concatenated gene tree recovered the same topology of mtDNA to the *A. angulatus* species complex (Fig. 2). Regarding the congeneric species, the phylogenetic positions of *A. atriventris*, *A. buckleyi* and *A. copii* were uncertain, while *A. festae* and *A. viridiceps* were externally positioned as sister taxa with high support values.

The corrected genetic distances between mtDNA phylogroups ranged from 5.8% (SD = 1.1%, comparison among 'West' and 'F. Guiana' clades) to 15.8% (SD = 1.5%, genetic difference between 'F. Guiana' and 'East' clades); values of uncorrected distance varyied from 5.2% (SD = 0.9%) to 14.2% (SD = 1.1%) for the same relationships (Supporting Information, Table S3).

Population structure analyses presented congruent patterns between nuclear and mitochondrial markers. For the mtDNA, four distinct populations with signals of genetic admixture were identified (Supporting Information, Fig. S3). These clusters generally distinguished the putative species of Ecuador, individuals from eastern Amazonia and *A. atriventris*, while grouping the differentiated lineages of *A. angulatus* 'West' and 'F. Guiana' with organisms of the 'South', 'Southwest' and 'G. Mirim'. The structuring pattern for *PRLR* reflected the four populations found by mtDNA, but also suggested an admixture scenario between individuals from eastern Amazonia and the putative species of Ecuador (Supporting Information, Fig. S3). In contrast, three clusters ('East' individuals, *A. atriventris* and 'South-southwest' individuals plus putative species from F. Guiana) were identified with no evidence of mixture for *SNCAIP* (Supporting Information, Fig. S3). However, it is worth mentioning that we were not able to amplify *SNCAIP* sequences from Ecuadorian samples.

Species delimitation analysis pointed to different possibilities related to distinct historical scenarios (Supporting Information, Table S4). When testing sizes of small populations, the most likely number of species delimited was eight, designating each one of the mitochondrial haploclades of *A. angulatus* species complex and *A. atriventris* as species. Scenarios of large population sizes and recent divergence times exhibited higher probability to three delimited species, collapsing the clades of 'F. Guiana', 'Ecuador', 'G. Mirim', 'South', 'Southwest' and 'West' as a single species. Finally, simulations considering large populations and old divergences suggested four species, with lineages of 'F. Guiana', 'West', 'South', 'Southwest' and 'G. Mirim' proposed as one species.

The species tree exhibited the initial diversification of the *A. angulatus* species complex and *A. atriventris* dating from the Miocene [posterior probability (pp) = 1.0; 95% highest posterior density (HPD) = 17–6 Mya; Fig. 3]. The divergence between 'East' and *A. atriventris* was dated at Plio-Pleistocene (pp = 1.0; 95% HPD = 3–1 Mya), with this clade being sister to the remaining species. The putative Ecuadorian species diverged from the poorly supported group containing 'F. Guiana', 'West', 'South', 'Southwest' and 'G. Mirim' at ~10 Mya (pp = 0.97; 95% HPD = 14–5 Mya). Species of the 'West' grouped with 'F. Guiana', diverging at 3 Mya (pp = 0.97; 95% HPD = 6–0 Mya). The 'South' species

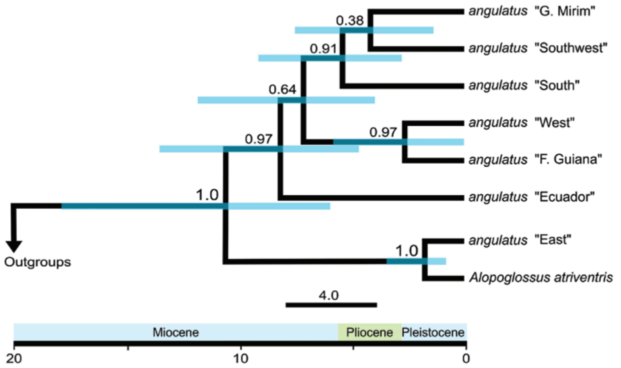

Figure 3. Species tree and divergence times inferred under a coalescent model with *BEAST for the lineages delimitated by BPP. Node values correspond to posterior probabilities, and blue bars represent the 95% highest posterior density (HPD) intervals of divergence times (in millions of years).

diverged at the Mio-Pliocene interval (pp = 0.91; 95% HPD = 9–2 Mya) from 'G. Mirim' and 'Southwest', with this last group being poorly supported.

STATISTICAL ANALYSES OF MORPHOLOGICAL DATA

Univariate and multivariate statistical analyses revealed variable degrees of morphological divergence in morphometrics and scalation features among the species delimited by molecular analyses (all groups were included, except '*A. angulatus* Southwest' and '*A. angulatus* F. Guiana' owing to absence of morphological data; '*A. angulatus* Westermost', not present in molecular analyses, was included in statistical analyses because qualitative characters supported the recognition of it as a separate morphological group; see comments below).

Comparisons of measurements using the Kruskal–Wallis test (H) revealed no significant differences on median values between groups only for neck length (H = 1.717, d.f. = 5, P = 0.8867), whereas all other variables differed significantly between groups (axilla–groin length, H = 30.2, d.f. = 5, P = 0.0134; head depth, H = 18.28, d.f. = 5, P = 0.0026; head width, H = 19.17, d.f. = 5, P = 0.0017; head length, H = 18.28, d.f. = 5, P = 0. 0026; forelimb length, H = 24.34, d.f. = 5, P = 0.0001; hindlimb length, H = 24.02, d.f. = 5, P = 0.0002; shank length, H = 32.84, d.f. = 5, P = 0.004). All scalation characters analysed using the Kruskal–Wallis test showed significant differences between groups (dorsals, H = 64.4, d.f. = 5, P < 0.0001; ventrals, H = 37.7, d.f. = 5, P = 0.0004; midbody, H = 30.13, d.f. = 5, P = 0.0139; postoculars, H = 70.82, d.f. = 5, P < 0.0001; palpebrals, H = 86.32, d.f. = 5, P < 0.0001; scales in transverse rows on sides of neck, H = 223.7, d.f. = 5, P < 0.0001; granular scales between the pairs of chin shields, H = 75.02, d.f. = 5, P < 0.0001; gulars, H = 13.43, d.f. = 5, P = 0.0196; femoral pores in males, H = 22.81, d.f. = 5, P = 0.0003; lamellae under fourth finger, H = 18.69, d.f. = 5, P = 0.0021; lamellae under fourth toe, H = 38.3, d.f. = 5, P < 0.0001). The number of scales around the tail, supraoculars, suboculars, superciliaries, loreals, frenoculars, supralabials, infralabials and pairs of chin shields were not included in the Kruskal–Wallis test (variance ≤ 3).

Mann–Whitney pairwise comparisons of measurements showed significant differences in axilla–groin length, head width, forelimb length, hindlimb length and shank length between at least one pair of groups per measurement; Mann–Whitney pairwise comparisons of scalation characters revealed significant differences between at least one pair of groups in all characters, except the number of gular scales (results are summarized in the Supporting Information, Tables S5 and S6; Figs S4–S6). The number of specimens per group, variation (minimum and maximum), median and standard deviation values of all measurements and scalation characters are presented in the Taxonomy section, below.

In the LDA using measurements, the first three functions explained 92.72% of the total variance in the eight characters (49.48, 28.48 and 14.76%, respectively). The first and second functions almost completely separated the '*A. angulatus* South' group from '*A. angulatus* East' (but separated it from all others), and the first and third functions completely separated the '*A. angulatus* South' group from all other groups (Fig. 4A–C). The most important characters in the first function were head width and shank length; in the second function they were head length and head depth, and in the third function head depth and head length (summarized data in Supporting Information, Table S7).

In the LDA using scalation characters and including all individuals (males and females), the first two functions explained 92.51% of the total variance in the 16 characters (85.71 and 6.8%, respectively). The groups '*A. angulatus* East' and '*A. angulatus* South' were completely separated from all others, and '*A. angulatus* Ecuador' was partly separated from '*A. angulatus* West', '*A. angulatus* G. Mirim' and '*A. angulatus* Westernmost' (Fig. 4D–F). The most important character in the first function was the number of transverse rows of scales on the sides of neck, and in the second function the rows of scales around the midbody (summarized data in Supporting Information, Table S8).

In the LDA using scalation characters considering only males, the first two functions explained 91.49% of the total variance in the 17 characters (79.49 and 12%, respectively), and they completely separated '*A. angulatus* South' and '*A. angulatus* East' from all others, and almost completely separated '*A. angulatus* Ecuador' from '*A. angulatus* West' and '*A. angulatus* G. Mirim' (Supporting Information, Fig. S7). The most important character in the first function was the number of transverse rows of scales on the sides of the neck, and in the second function the rows of scales around the midbody (summarized data in Supporting Information, Table S9). The first two functions explained 90.67% of the total variance in the 16 characters in the LDA using scalation characters considering only females (84.06 and 6.61%, respectively). They completely separated '*A. angulatus* South' and '*A. angulatus* East' from all other groups, and '*A. angulatus* Ecuador' from all groups (Supporting Information, Fig. S7), with the number of transverse rows of scales on the sides of the neck being most important character in the first function, and number of superciliaries being most important in the second function (summarized data in Supporting Information, Table S10).

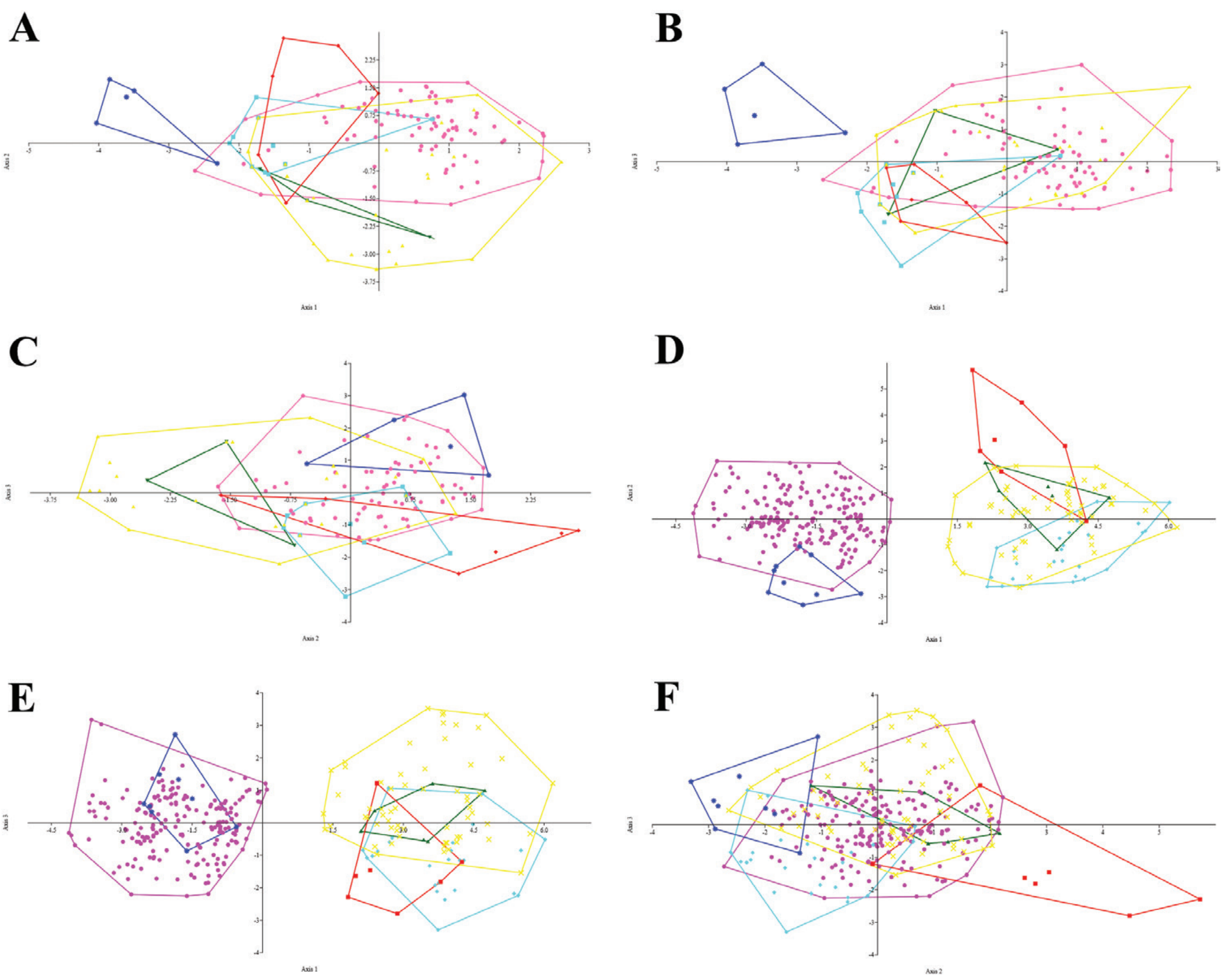

Figure 4. Discriminant analysis of measurements (A–C; only adult specimens included) and scalation characters (D–F; all specimens included) between specimens of the *Alopoglossus angulatus* groups recognized by molecular analyses. Colours used in linear discriminant analyses are the same as those used in molecular trees: pink, '*A. angulatus* East'; light blue, '*A. angulatus* G. Mirim'; dark blue, '*A. angulatus* South'; yellow, '*A. angulatus* West'; red, '*A. angulatus* Ecuador'; green, '*A. angulatus* Westernmost' (included here, but not represented in the molecular analyses).

In all LDAs, '*A. angulatus* West', '*A. angulatus* G. Mirim' and '*A. angulatus* Westernmost' were overlapped, but clear qualitative differences could distinguish specimens among these three groups ('*A. angulatus* West' has only three pairs of chin shields; '*A. angulatus* G. Mirim' has four pairs of chin shields; '*A. angulatus* Westernmost' has an enlarged pair of pregular scales; this character supported our recognition of it as a separated group in statistical analyses, because it was not present in the molecular analyses).

The several cryptic species existing under the name *A. angulatus* recognized by the analyses of molecular and morphological datasets indicated the need for reformulations towards a more informative taxonomic system for the genus *Alopoglossus*. Morphological qualitative evidence remained crucial in descriptions and precise diagnoses, and this is presented below.

TAXONOMIC STATUS OF THE POPULATIONS OF *ALOPOGLOSSUS* PREVIOUSLY REFERRED TO *A. ANGULATUS*

We provided the first description of the neotype of *A. angulatus* and compared it with specimens of the *A. angulatus* species complex to define *A. angulatus s.s.* and its morphological variation. Comparisons between *A. angulatus s.s.* and other individuals of *A. angulatus* species complex were then made, and five distinct groups of individuals were recognized among specimens in the western and southern portion of Amazonia. They are not conspecific with *A. angulatus s.s.* or any previously recognized congener, and have unique meristic and qualitative characters. Therefore, we here present six species among the examined material based on the shape of neck scales (similar in shape to dorsals, non-granular, keeled and imbricate; at least posterior ones phylloid) and on the overall congruence with lineages identified and species delimited based on the molecular data and coalescent-based analysis. Of these, two represent new species and three are resurrections of junior synonyms + *A. angulatus s.s.* Based on the consensus between morphological and molecular evidence (de Queiroz, 2007), we provide standardized descriptions for these six species, their respective distributions, a summary of selected characters of scutellation and morphometrics, and an updated identification key to all species in the genus *Alopoglossus*. The 'Southwest' and 'French Guiana' lineages, recognized by molecular analyses as putative new species, will be treated elsewhere.

TAXONOMY

REPTILIA: SQUAMATA

GYMNOPHTHALMOIDEA FITZINGER, 1826

ALOPOGLOSSIDAE GOICOECHEA *ET AL.*, 2016

ALOPOGLOSSUS BOULENGER, 1885

ALOPOGLOSSUS ANGULATUS (LINNAEUS, 1758)

[FIGS 2–4 (*A. ANGULATUS* 'EAST'); FIGS 5, 6, 7A; TABLES 1 AND 2]

Lacerta angulata Linnaeus (1758: 204).
Agama angulata Daudin (1802: 389).
Alopoglossus carinicaudatus Ruthven (1924: 3, part); Ruibal (1952: 508, part); Cunha (1961: 123, part); Peters & Donoso-Barros (1970: 15, part).
Alopoglossus copii surinamensis Brongersma (1946: 231).
Alopoglossus angulatus Hoogmoed (1973: 216); Ávila-Pires (1995: 307, part); Köhler *et al.* (2012: 176, part); Ribeiro-Júnior (2018: 29, his fig. 3B, 32, part).
Neotype: RMNH 15200, female, Suriname, Brown's Mountain [Brownsberg] (4°56′N, 55°10′W), 20 August 1961, Marinus Hoogmoed. Neotype selected by Hoogmoed (1973: 223), because the original holotype, from 'America', seems to be lost (Figs 5, 6).

Material examined: Two hundred (*N* = 200) referred specimens for morphological analyses and 21 samples for molecular analyses from Brazil, French Guiana, Guyana and Suriname (see Supporting Information; Appendix S2, Table S1).

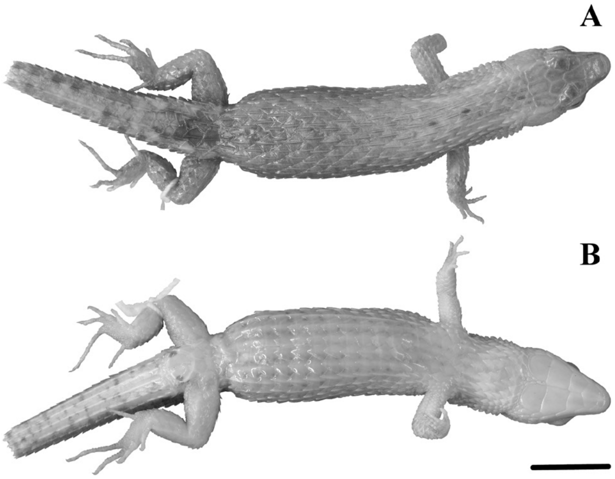

Figure 5. Dorsal (A) and ventral (B) views of the neotype of *Alopoglossus angulatus* (RMNH 15200). Scale bar: 10 mm.

Diagnosis

Alopoglossus angulatus is distinguished from all other species of *Alopoglossus* by the combination of the following characters: (1) scales on sides of neck non-granular, keeled, imbricate (at least medial and posterior ones phylloid), in six to nine transverse rows; (2) three pairs of chin shields; (3) third pair of chin shields with rounded posterior margins, in direct contact with gulars or separated from them by a row of small scales; (4) absence of a pair of medial enlarged pregular scales; (5) scales on gular region subequal in size, but varying in shape: lateral ones strongly keeled, pointed, phylloid; anterior, medial and posterior ones varying from smooth to feebly keeled, phylloid; anteriormost transverse row with scales varying from smooth to feebly keeled, almost rounded posteriorly and varying from similar in size to slightly smaller than those in the proceeding rows; (6) ventral scales feebly keeled, mucronate, imbricate, with bluntly pointed posterior margins; (7) total number of femoral pores in males 20–29.

Comparisons with other species

Alopoglossus angulatus differs from *A. atriventris*, *A. buckleyi*, *A. copii*, *A. embera*, *A. festae*, *A. lehmanni* and *A. viridiceps* (in parentheses) in having scales on sides of neck similar in shape to dorsals, non-granular, keeled, imbricate (granular in *A. atriventris* and *A. buckleyi*; mostly granular in *A. embera*, *A. festae*, *A. lehmanni* and *A. viridiceps*; conical with apparent

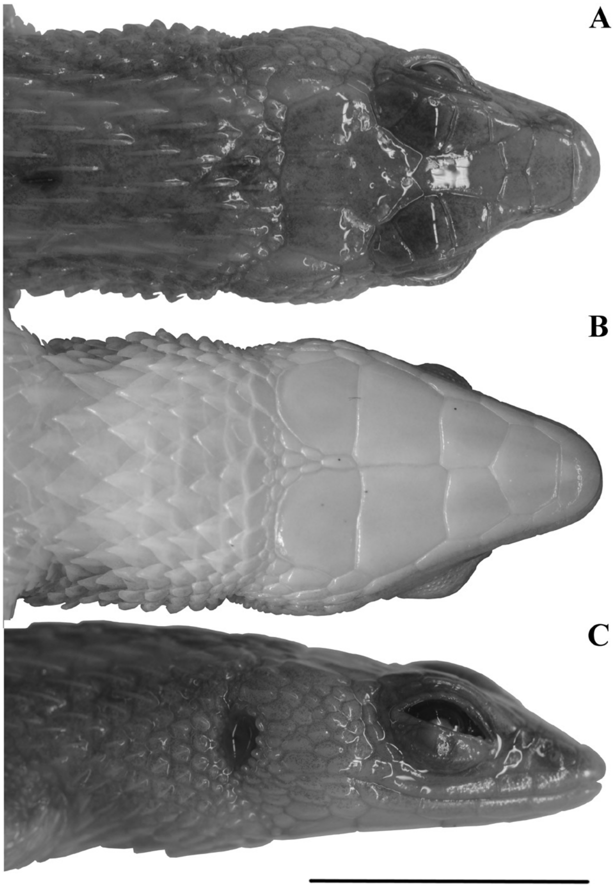

Figure 6. Dorsal (A), ventral (B) and (C) lateral views of the head and neck of the neotype of *Alopoglossus angulatus* (RMNH 15200). Scale bar: 10 mm.

bare skin between conical scales in *A. copii*); it also differs from *A. embera*, *A. festae* and *A. viridiceps* in not having gulars arranged in two longitudinal rows (vs. a double longitudinal row of widened gular scales); from *A. lehmanni* in having dorsal scales rhomboidal, in oblique rows (vs. dorsal scales hexagonal with parallel lateral edges, in transverse rows). *Alopoglossus angulatus* differs from *A. amazonius* and *A. meloi* in having three pairs of chin shields (vs. four pairs) and the third pair of chin shields with rounded posterior margins, in direct contact with gulars or separated from them by a row of small scales (vs. third pair of chin shields irregularly trapezoidal, separated from gulars by large scales). It differs from *A. andeanus* in having scales on the sides of the neck in six to nine transverse rows (vs. 11 or 12) and in lacking a pair of medial enlarged pregular scales. *Alopoglossus angulatus* differs from *Alopoglossus avilapiresae* and *A. carinicaudatus* in having scales on the sides of the neck in six to nine transverse rows (vs. 10–13 in *A. avilapiresae*; 11 or 12 in *A. carinicaudatus*), scales on the medial gular region smooth to feebly keeled (vs. scales on medial gular region strongly keeled, in *A. carinicaudatus*), and the third pair of chin shields with rounded posterior margins [vs. third pair of chin shields irregularly quadrangular (anterior and posterior margins almost parallel) with straight posterior margins, in *A. carinicaudatus*]. *Alopoglossus angulatus* differs from *Alopoglossus collii* in having scales on the gular region subequal in size, with anterior, medial and posterior ones varying from smooth to feebly keeled, phylloid, and anteriormost transverse row with scales varying from similar in size to slightly smaller than those in the proceeding rows (vs. scales on gular region varying in size, with medial and posterior ones smooth, almost rounded, bluntly pointed, larger than lateral ones, and the first three anterior transverse rows with scales smooth, almost rounded, larger than those in the proceeding row, and anteriormost row with the largest scales), lower number of ventral scales (14–18 vs. 18 or 19), and higher total number of femoral pores in males (20–29 vs. 19–22).

Description of neotype

Body cylindrical, snout rounded, neck almost as wide as head and anterior part of body, limbs well developed, broken tail (Fig. 5). Female.

Rostral hexagonal, in broad contact with frontonasal, but also contacting first supralabial and nasal. Viewed dorsally, the rostral is about three times as wide as long. Frontonasal pentagonal, about twice as wide as long (wider posteriorly), anteriorly in contact with rostral, laterally with nasal, and posteriorly with prefrontals. Prefrontals irregularly pentagonal, wider than long, with a long medial suture; laterally in contact with loreal and first supraocular, and touching nasal; posteriorly in contact with frontal. Frontal irregularly hexagonal (almost pentagonal), longer than wide (distinctly wider anteriorly); laterally in contact with first, second and third supraoculars; posteriorly in contact with frontoparietals. Frontoparietals irregularly pentagonal, longer than wide (wider posteriorly), with a long medial suture; laterally in contact with third and fourth supraoculars; posteriorly in contact with interparietal and parietal. Interparietal pentagonal, lateral borders parallel to each other, about twice as long as wide. A pair of irregularly hexagonal parietals, wider than, and as long as, interparietal; laterally in contact with fourth supraocular, first and second supratemporals. The parietal and interparietals form a slightly undulating (almost straight) posterior head margin. Occipitals absent. Four supraoculars; first (anteriormost) smallest, contacting frontal, prefrontal, loreal, first superciliary and second supraocular; second supraocular slightly smaller than third one, wider than long, contacting frontal, first and third supraoculars and first and second superciliaries; third supraocular largest, contacting frontal, frontoparietal, second and fourth supraoculars and second and third superciliaries; fourth supraocular in contact with parietal, frontoparietal, third supraocular, third, fourth and fifth superciliaries and first supratemporal. Five superciliaries, first four elongated, first two longest, fifth irregularly triangular; first (anteriormost) longest, contacting loreal (and frenocular on the left side), first and second supraoculars and second superciliary; second in contact with first and third superciliaries and second and third supraoculars; third in contact with second and fourth superciliaries and third and fourth supraoculars; fourth smallest, contacting third and fifth superciliaries and fourth supraocular; fifth in contact with fourth superciliary, fourth supraocular, first supratemporal and upper postocular. Three suboculars; first longer than tall, contacting frenocular, second and third supralabials and second subocular; second longest, about six times longer than tall and about three times longer than first and third suboculars, contacting first and third suboculars, third, fourth and fifth supralabials; third longer than tall, contacting second subocular, fifth supralabial and the lower postocular. Two postoculars similar in size and shape, continuous with third subocular. Lower eyelid with semitransparent disc of three large palpebrals on the right side, four on the left side. Nasal semidivided, irregularly pentagonal, longer than tall. Nostril in the lower part of nasal, directed lateroposteriorly. Loreal rectangular, contacting nasal, prefrontal, first supraocular, first superciliary and frenocular. Frenocular irregularly pentagonal, contacting loreal, nasal, second supralabial and first subocular. Seven supralabials; third, fourth and fifth under the orbital region; third longest, about three times longer than tall; fifth tallest. Post-supralabial absent. Temporals irregularly polygonal, juxtaposed, keeled. Two large, keeled supratemporal scales bordering the parietal; second largest. Ear opening vertically oval, with anterior margin denticulate. Tympanum recessed into a short auditory meatus. Except for supratemporals and temporals, all dorsal and lateral head scales smooth and juxtaposed. Fourth supraocular, parietals and interparietal with lateral ridges.

Mental trapezoidal, about twice as wide as long, with convex anterior margin. Postmental heptagonal, wider than long. Three pairs of chin shields; first two pairs in broad contact medially and with second, third and fourth infralabials; scales of the third pair separated from each other by six small, granular scales and separated from infralabials by large scales; scale of the third pair on the left side in contact with gulars posteriorly, and scale of the right side separated from gulars by a row of small scales; third pair of chin shields with rounded posterior margins. Five infralabials on the right side, six on the left, all longer than tall; second, third and fourth about twice as long as first; fifth and sixth smallest; suture between third and fourth below centre of eye. Post-infralabials absent. Gular scales smaller, but similar in shape to dorsals, imbricate, phylloid (except that the anteriormost transverse row is almost rounded posteriorly, with scales smaller than, or similar in size to, those posteriad it); scales on anterior, medial and posterior gular regions smooth to feebly keeled; scales on lateral gular region strongly keeled; gular scales in nine transverse rows. Posterior row of gulars (collar) with eight scales, not differentiated from preceding rows. No gular fold. Scales on nape similar to dorsals, except that the anterior ones are shorter. Two transverse rows of granular scales posterior to ear opening. Scales on sides of neck distinctly smaller than dorsals, keeled, imbricate, phylloid; in seven transverse rows on the right side and eight on the left; scales on anterior region shorter than scales on posterior region. A distinctive area with scales much shorter than, but similar in shape to, neck scales surrounds the area of arm insertion.

Dorsal scales rhomboid, strongly keeled and mucronate, imbricate and disposed in oblique rows; 27 scales along a middorsal line from parietals to the level of the hindlimbs. Scales on flanks similar in shape and size to dorsals. Twenty-one scales around midbody. Ventral scales feebly keeled, mucronate and imbricate; posterior margins bluntly pointed; in 18 transverse rows and four longitudinal rows between collar and preanals. Four smooth scales in preanal plate; medial scales larger than lateral ones; preanal plate scales preceded by two large scales. Preanal and femoral pores absent (female).

Dorsal limb scales rhomboid, imbricate, strongly keeled and mucronate; ventral limb scales feebly keeled; ventral aspect of upper arms and posterior aspect of thighs with tuberculate scales. Five clawed digits on each limb. Lamellae under fingers single, transversely enlarged and smooth, 14 under the fourth finger; lamellae under toes divided, 20 or 21 under the fourth toe. Scales on tail keeled, slightly mucronate, imbricate, arranged in transverse rows (not counted; broken tail) and in 12 longitudinal rows; scales in the two paravertebral rows wider than long near the base of the tail and longer than wide in other rows. Keels mostly sharp on tail (feebly keeled and almost rounded on anteriormost ventral rows), forming four dorsal, two lateral (on each side) and four ventral distinct longitudinal ridges.

Measurements of neotype (in millimetres): SVL = 48; AGL = 23.1; HD = 5.4; HW = 7.8; HL = 11.5; NL = 7.3; FL = 13; HLL = 19; ShL = 5.6; TL = 20 (broken).

Coloration in preservative (based on neotype)

Dorsal surface of head, back and tail light brown; head homogeneously light brown; from nape and along middorsum, a rather inconspicuous series of small, dark brown spots; on the posterior dorsal surface of body, between the hindlimbs, the dark spots merge, forming a dark brown medial band; dorsal surface of forelimbs uniformly light brown; dorsal surface of hindlimbs light brown with some small, dark brown spots; dorsal surface of tail with dark brown and cream spots. Lateral aspect of head and neck light brown, becoming gradually cream ventrally; lateral surface of body (flanks) and tail slightly darker than dorsal surface, becoming gradually cream ventrally. A dashed dark brown line extending posteriorly from the nostril, passing above eyes and forelimbs, dorsolaterally on flanks, above hindlimbs and reaching dorsolaterally the tail, bordered dorsolaterally by a light brown stripe from posterior corner of eye to shoulder. An inconspicuous dashed cream line extending from the supralabials under the eye, passing through the lower part of the ear opening and neck, above the forelimbs, ventrolaterally on flanks and reaching the anterior surface of the hindlimbs. Ventral surface of body homogeneously cream; preanal plate and ventral aspect of tail with some small, irregular dark brown spots.

Colouration in life (based on photographs in life)

AAGARDA 6416 (Fig. 7A), adult male: dorsal surface of head and anterior surface of back mahogany, with small, blackish spots; dorsolateral stripe slightly lighter than dorsal surface of head, from posterior corner of eye to anterior part of body; posterior surface of body, dorsal surfaces of limbs and tail bistre; tail with a dorsolateral mahogany stripe anteriorly, becoming gradually bistre with small mahogany spots posteriorly. Lateral surface of head and neck lion; lateral surface of body (flanks) lion with large bistre spots; lateral surfaces of limbs and tail bistre. A continuous bistre line extending from the nostril, above the eyes, ear opening and neck to the shoulders; rather inconspicuous above ear opening. A dashed cream line extending from the supralabials under the eye, passing through the lower part of ear opening and neck, above the forelimbs, ventrolaterally on flanks to the anterior surface of the hindlimbs (rather inconspicuous on head and neck). Iris vividly amber.

Variation

Specimens INPA-H 26241 and MPEG 27543 have five supraoculars. Interparietal, parietals and fourth supraocular are either smooth or with lateral ridges. INPA-H 26240 has four superciliaries on one side and five on the other; MPEG 25441 has six on one side and five on the other. MPEG 26240 has four suboculars on one side and three on the other; MPEG 24911 has four on one side and five on the other. MPEG 19311, MPEG 19376 and MPEG 29602 have one elongated postocular on each side (twice as high); MPEG 15127, MPEG 21453, MPEG 24908–09 and MPEG 2956 have one elongated postocular on one side and two on the other; MPEG 19942, MPEG 25433 and MPEG 28502 have three postocular on one side and two on the other. A single post-supralabial scale is rarely present on specimens. Scales of the third pair of chin shields are in contact medially or separated from each other by one to 13 small, granular scales; they are in direct contact with gulars or separated from them by a row of small, granular scales. Specimen MPEG 22764 has seven transverse rows of gulars. In MPEG 21853, the keels on the ventral scales are stronger than those in other individuals. Scales in the preanal plate vary from smooth to slightly keeled; in MPEG 24908 they are strongly keeled. Preanal and femoral pores are absent in females. In males, the femoral pores are arranged in a continuous, well-separated series on each side; two pores on each side are in the preanal position; each pore is between two scales; total number of pores 20–29. Tables 1 and 2 present a summary of the variation in meristic characters and measurements, respectively.

The pale dorsolateral stripe from the posterior corner of the eye to the shoulders either disappears completely posteriad, or it continues until the base of the tail. Tails are light brown dorsally, with dark brown and cream spots, or have alternate dark brown and cream transverse bands. Flanks are either similar in colour to the back or darker than it; they are usually light brown in females and dark brown with a cream stripe between the limbs in males. Ventral region in females is completely cream or has small, irregular, dark brown spots. In males, the ventral region can be: completely cream; cream with irregular, dark brown spots; cream with the peripheral portion of scales dark brown; or dark brown with the posterior portion of scales cream (except on limbs, preanal plate and tail, which are cream with dark brown spots).

Distribution and habitat

Alopoglossus angulatus is distributed in eastern Amazonia (east of the Negro and Madeira rivers) in Brazil (states of Amapá, Pará and Amazonas), Suriname, Guyana and French Guiana (Supporting Information, Fig. S8). Although in southern Amazonia it occurs east of the Madeira River, westernmost records of *A. angulatus* are restricted to the Tapajós river basin, not reported in the Madeira river basin. *Alopoglossus angulatus* is terrestrial and diurnal,

Figure 7. A, living specimen of *Alopoglossus angulatus*, AAGARDA 6416, from Maísa Farm, Moju (3°14′20″S, 49°20′23″W), State of pará, brazil; photograph by Sarah mângia. B, C, Living specimen of *Alopoglossus amazonius* from Guajará-Mirim (11°24′0.42″S, 64°54′0.02″W), State of rondônia, brazil; photographs by Guarino Colli. D, Living specimen of *Alopoglossus andeanus* from EcoAmazonia, Tambopata province; photoraph by Tiffany Doan. E, F, living specimen of *Alopoglossus avilapiresae* from Chandless State Park, Manuel Urbano (9°56′08″S, 70°09′17.3″W), State of Acre, Brazil; photographs by Marco Antônio de Freitas. G, Living specimen of *A. avilapiresae* from Chico Mendes Extractive Reserve, Brasiléia (10°37′54″S, 69°19′27.9″W), State of Acre, Brazil; Photograph by Marco Antônio de Freitas. H, living specimen of *Alopoglossus collii* from

inhabits primary terra firme and flooded (varzea) forests, and disturbed forest (Martins, 1991; Ribeiro-Júnior *et al.*, 2008). It is most often found in shaded spots among leaf litter near water and, occasionally, on open ground, in water, on logs floating in the water and in plantations (Martins, 1991; Vitt *et al.*, 2008; Ribeiro-Júnior & Amaral, 2017).

ALOPOGLOSSUS AMAZONIUS RUTHVEN, 1924

[FIGS 2–4 (*A. ANGULATUS* 'G. MIRIM'), FIGS 7B, C, 8, 9; TABLES 1 AND 2]

Pantodactylus amazonius Burt & Burt (1931: 358).
Pantodactylus amazonicus Amaral (1937: 1741).
Alopoglossus carinicaudatus Ruibal (1952: 508, part); Peters & Donoso-Barros (1970: 15, part).
Alopoglossus angulatus Ávila-Pires (1995: 307, part); Köhler *et al.* (2012: 176, part).
Holotype: UMMZ 56853, male, Brazil, VILLA MURTINHO, MATTO GROSSO (= VILA MURTINHO, Nova Mamoré municipality, State of RONDÔNIA; 10°23′58.6″S, 65°21′51.8″W), 6 APRIL 1922, JESSE Williamson (Figs 8, 9).

Material examined: Twenty-seven (*N* = 27) referred specimens for morphological analyses and one sample for molecular analyses from Brazil (see Supporting Information; Table S1 and Referred Specimens).

Diagnosis

Alopoglossus amazonius is distinguished from all other species of *Alopoglossus* by the combination of the following characters: (1) scales on sides of neck non-granular, keeled, imbricate (at least medial and posterior ones phylloid), in nine to 13 transverse rows; (2) four pairs of chin shields; (3) third pair of chin shields irregularly trapezoidal, separated from gulars by large scales; (4) absence of a pair of medial enlarged pregular scales; (5) scales on gular region varying in shape and size: lateral ones strongly keeled, pointed, phylloid; anterior and medial ones varying from smooth to feebly keeled, phylloid; posterior ones varying from smooth to feebly keeled, almost rounded posteriorly, larger than lateral, anterior and medial ones; (6) ventral scales mucronate, imbricate, with bluntly pointed posterior margins (almost rounded), varying from smooth to feebly keeled; (7) total number of femoral pores in males 24–28.

Comparison with other species

Alopoglossus amazonius differs from *A. atriventris*, *A. buckleyi*, *A. copii*, *A. embera*, *A. festae*, *A. lehmanni* and *A. viridiceps* (in parentheses) in having scales on the sides of the neck similar in shape to dorsals, non-granular, keeled, imbricate (granular in *A. atriventris* and *A. buckleyi*; mostly granular in *A. embera*, *A. festae*, *A. lehmanni* and *A. viridiceps*; conical with apparent bare skin between conical scales in *A. copii*); it also differs from *A. embera*, *A. festae* and *A. viridiceps* in not having gulars arranged in two longitudinal rows (vs. a double longitudinal row of widened gular scales); from *A. lehmanni* in having dorsal scales rhomboidal, in oblique rows (vs. dorsal scales hexagonal with parallel lateral edges, in transverse rows). *Alopoglossus amazonius* differs from *A. angulatus*, *A. andeanus*, *A. avilapiresae*, *A. carinicaudatus* and *A. collii* in having four pairs of chin shields (vs. three pairs), and third pair of chin shields irregularly trapezoidal, separated from gulars by large scales [vs. third pair of chin shields with rounded posterior margins, in direct contact with gulars or separated from them by a row of small scales in *A. angulatus*, *A. andeanus*, *A. avilapiresae* and *A. collii*; third pair of chin shields irregularly quadrangular (anterior and posterior margins almost parallel) with straight posterior margins, separated from gulars by a row of small scales, in *A. carinicaudatus*]. *Alopoglossus amazonius* differs from *A. meloi* in having scales on sides of neck in nine to 13 transverse rows (vs. six to eight) and a higher total number of femoral pores in males (24–28 vs. 20–23).

Redescription of holotype

Body cylindrical, snout rounded, neck almost as wide as head and anterior part of body, limbs well developed, broken tail (Fig. 8). Male.

Rostral hexagonal, in broad contact with frontonasal, but also contacting first supralabial and nasal. Viewed dorsally, the rostral is about three times as wide as long. Frontonasal pentagonal, about twice as wide as long (wider posteriorly), anteriorly in contact with rostral, laterally with nasal and posteriorly with prefrontals. Prefrontals irregularly triangular,

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Pimenta Bueno (11°51′45.22″S, 60°56′17.99″W), State of Rondônia, Brazil; photograph by Guarino Colli. I, J, living specimen of *Alopoglossus carinicaudatus* from Parque Nacional Yasuní, Estación Científica Yasuní Pontificia Universidad Católica del Ecuador sendero Ceiba (0°40′32.74″S, 76°23′45.81″W), Department of Orellana, Ecuador; photographs available at: https://bioweb.bio/faunaweb/reptiliaweb/QCAZ/Especimen/24703. *Photographs of specimens of *A. amazonius*, *A. andeanus* and *A. collii* were not used to describe coloration in life because they were old scanned photographic slides (not at sactisfatory resolution).

Table 1. Summary of the variation in meristic characters among species of the *Alopoglossus angulatus* species complex

	A. angulatus (*N* = 201)	*A. amazonius* (*N* = 28)	*A. andeanus* (*N* = 6)	*A. avilapiresae* (*N* = 64)	*A. carinicaudatus* (*N* = 7)	*A. collii* (*N* = 9)
Dorsals	22–29 (26 ± 1.8)	25–31 (27.8 ± 1.5)	27–30 (28.7 ± 1)	23–30 (27.7 ± 1.7)	22–27 (25.3 ± 1.8)	26–29 (27.2 ± 1.3)
Ventrals	14–18 (16.3 ± 1)	16–19 (17 ± 0.8)	15–20 (16.8 ± 1.8)	14–18 (16.3 ± 0.9)	15–17 (15.6 ± 0.8)	18–19 (18.3 ± 0.5)
Midbody	18–22 (20.1 ± 0.7)	19–22 (20.7 ± 1.1)	19–20 (19.7 ± 0.5)	19–22 (20.6 ± 0.8)	15–21 (18.4 ± 2.5)	19–21 (20.2 ± 0.8)
Supraoculars	4–5 (4 ± 0.2)	4	4	4	4	4
Superciliaries	4–5 (5 ± 0.1)	5–6 (5.1 ± 0.3)	5	4–5 (5 ± 0.2)	5	5
Suboculars	3–4 (3 ± 0.1)	3	3–4 (3.2 ± 0.4)	2–3 (3 ± 0.2)	2–4 (3 ± 0.6)	3
Postoculars	1–2 (1.9 ± 0.3)	1–3 (2.3 ± 0.7)	2–3 (2.7 ± 0.5)	2–3 (2.3 ± 0.5)	2–3 (2.4 ± 0.5)	1–3 (2 ± 0.7)
Palpebrals	2–5 (3.6 ± 0.6)	3–5 (3.8 ± 0.9)	4–6 (4.7 ± 0.8)	4–7 (4.5 ± 0.7)	4–5 (4.4 ± 0.5)	3–6 (4.2 ± 0.8)
Supralabials	7	7	7	7–8 (7.1 ± 0.3)	7	7
Infralabials	6	6	6	6–7 (6 ± 0.2)	6	6
Scales on sides of neck	6–9 (8.4 ± 0.6)	9–13 (11.8 ± 0.7)	11–12 (11.3 ± 0.5)	10–13 (11.4 ± 0.8)	11–12 (11.4 ± 0.5)	8–9 (8.2 ± 0.4)
Pairs of chin shields	3	4	3	3	3	3
Pair of medial enlarged pregulars	0	0	1	0	0	0–1*
Scales between third pair of chin shields	1–13 (5.3 ± 1.9)	1–4 (2.2 ± 0.8)	4–8 (5.8 ± 1.5)	1–7 (4.2 ± 1.9)	4–9 (5.9 ± 2)	1–6 (2.8 ± 2)
Scales between fourth pair of chin shields	–	0–5 (2.4 ± 1.6)	3–7 between pregular scales (4.7 ± 1.5)	–	–	0–2* between pregular scales
Gulars	7–10 (8.6 ± 0.7)	7–10 (8.7 ± 0.8)	7–9 (8.2 ± 0.8)	7–10 (8.6 ± 0.8)	7–10 (8.1 ± 1.1)	9–10 (9.3 ± 0.5)
Lamellae under fourth finger	11–16 (13.9 ± 1.3)	13–16 (14.8 ± 1)	13–17 (14.8 ± 1.8)	12–18 (14.3 ± 1.3)	12–16 (14.6 ± 1.6)	12–14 (13.1 ± 0.8)
Lamellae under fourth toe	14–23 (19.2 ± 1.6)	17–23 (20.7 ± 1.5)	17–21 (19.7 ± 1.8)	17–23 (19.9 ± 1.6)	20–23 (21.9± 1.1)	18–23 (20.8 ± 1.5)
Femoral pores in males	20–29 (24.2 ± 1.7)	24–28 (25.5 ± 1.9)	24–28 (25.7 ± 2.1)	23–29 (25.7 ± 1.7)	22–26 (24.6 ± 1.7)	19–22 (21.2 ± 0.7)

Counts are presented as minimum–maximum (mean ± SD); *N* = total number of specimens studied. Counts for scales around the tail, number of loreal and frenocular scales presented similar values among specimens and species (*N* = 12; *N* = 1; *N* = 1; respectively).
*Only one individual with a pair of medial enlarged pregular scales.

Table 2. Summary of the variation in measurements among species of the *Alopoglossus angulatus* species complex

	A. angulatus (*N* = 82)	*A. amazonius* (*N* = 12)	*A. andeanus* (*N* = 3)	*A. avilapiresae* (*N* = 26)	*A. carinicaudatus* (*N* = 7)	*A. collii* (*N* = 5)
Snout–vent length	37.6–60.5 (49.3 ± 5.1)	34.6–62 (51.2 ± 9.1)	40.3–58 (46.6 ± 9.9)	36.1–58.7 (50 ± 7)	33.5–58.9 (47.7 ± 8.3)	40–52.5 (48.7 ± 5)
Axilla–groin length	15.2–28.8 (22.1 ± 3.2)	16.6–30.7 (25.2 ± 5.2)	18.3–29 (22.7 ± 5.6)	14.7–30.4 (23.3 ± 4.3)	15.2–30.1 (23.1 ± 4.7)	19.2–24.9 (22.3 ± 2.4)
Head depth	4.5–7.8 (5.9 ± 0.8)	4.1–7.5 (6 ± 1.1)	5.4–7.7 (6.2 ± 1.3)	4.4–7.1 (6 ± 0.7)	4.8–6.5 (5.5 ± 0.6)	4.9–7.5 (6.3 ± 1.1)
Head width	5.7–9.9 (7.5 ± 0.9)	5.2–9.8 (8.2 ± 1.6)	6.4–10.5 (7.9 ± 2.3)	5.8–9.4 (7.7 ± 0.9)	5.9–8.7 (7.7 ± 1.1)	7.6–9.4 (8.4 ± 0.7)
Head length	9.1–13.1 (10.9 ± 0.9)	7.7–13.5 (10.9 ± 1.6)	9.1–13.8 (11 ± 2.5)	8.5–13.3 (11 ± 1.3)	8.1–12.1 (10.4 ± 1.4)	8.4–11.5 (9.6 ± 1.3)
Neck length	4.9–9.8 (7.3 ± 0.9)	5.1–9.6 (7.5 ± 1.6)	5.6–9 (7.4 ± 1.7)	5.4–9.8 (7.5 ± 1)	5.9–9.3 (7.4 ± 1.2)	5–9 (7.7 ± 1.6)
Forelimb length	8.4–16.3 (13.1 ± 1.6)	8.8–17 (13.9 ± 2.6)	8.8–16.5 (11.7 ± 4.2)	6.7–18.8 (11.9 ± 2.7)	6.4–17.3 (13.3 ± 4.3)	12.3–15.9 (14.4 ± 1.5)
Hindlimb length	14.3–27.2 (21.5 ± 2.4)	15.4–27 (22.8 ± 4.1)	12.7–29.5 (18.6 ± 9.4)	11.2–25.5 (18.6 ± 4.8)	10.1–28.7 (21.5 ± 7.2)	18.5–23 (20.3 ± 1.9)
Shank length	4.5–10.1 (7.6 ± 0.9)	5.2–7.8 (6.5 ± 0.8)	6.2–6.8 (6.5 ± 0.3)	5.4–8.7 (7.2 ± 1)	4.9–8.4 (6.7 ± 1.1)	5.4–6.3 (6 ± 0.4)
Tail length	58–106.9 (81.9 ± 9.6; *N* = 52)	57.3–82.3 (76.9 ± 16.6; *N* = 8)	–	50.3–97 (78.2 ± 15.2; *N* = 16)	54.9–76.5 (65.7 ± 15.3; *N* = 2)	74.2–99.8 (87 ± 11.5; *N* = 5)

Measurements are presented as minimum–maximum (mean ± SD); *N* = total number of specimens measured. Only intact and non-regenerated tails were considered (in *A. andeanus*, all specimens had a broken tail). Measurements in millimetres.

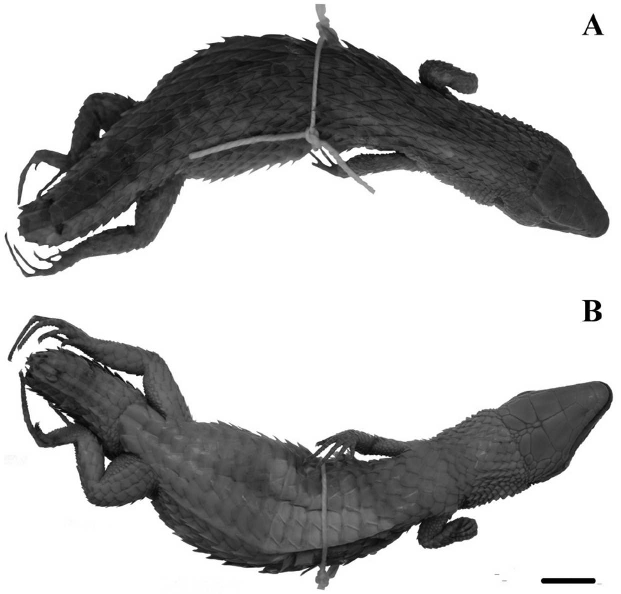

Figure 8. Dorsal (A) and ventral (B) views of the holotype of *Alopoglossus amazonius* (UMMZ 56853). Scale bar: 10 mm.

wider than long, only touching each other medially (not forming a medial suture); laterally in contact with loreal and first supraocular, and touching nasal; posteriorly in contact with frontal. Frontal irregularly hexagonal, longer than wide (distinctly wider anteriorly); laterally in contact with first and second supraoculars (touching third supraocular on the right side); posteriorly in contact with frontoparietals. Frontoparietals irregularly pentagonal, longer than wide (wider posteriorly), with a long medial suture; laterally in contact with third and fourth supraoculars; posteriorly in contact with interparietal and parietal. Interparietal pentagonal, lateral borders parallel to each other, about one and a half times as long as wide. A pair of irregularly hexagonal parietals, as long as, and wider anteriorly than, interparietal; laterally in contact with fourth supraocular, first and second supratemporals. The parietal and interparietals form a slightly undulating (almost straight) posterior head margin. Occipitals absent. Four supraoculars; first (anteriormost) smallest, contacting frontal, prefrontal, loreal, first superciliary and second supraocular; second supraocular largest, wider than long, contacting frontal, first and third supraoculars and first and second superciliaries; third supraocular slightly smaller than second one, contacting frontoparietal, second and fourth supraoculars and second and third superciliaries (touching frontal on the right side of head); fourth supraocular in contact with parietal, frontoparietal, third supraocular, third, fourth and fifth superciliaries and first supratemporal. Five

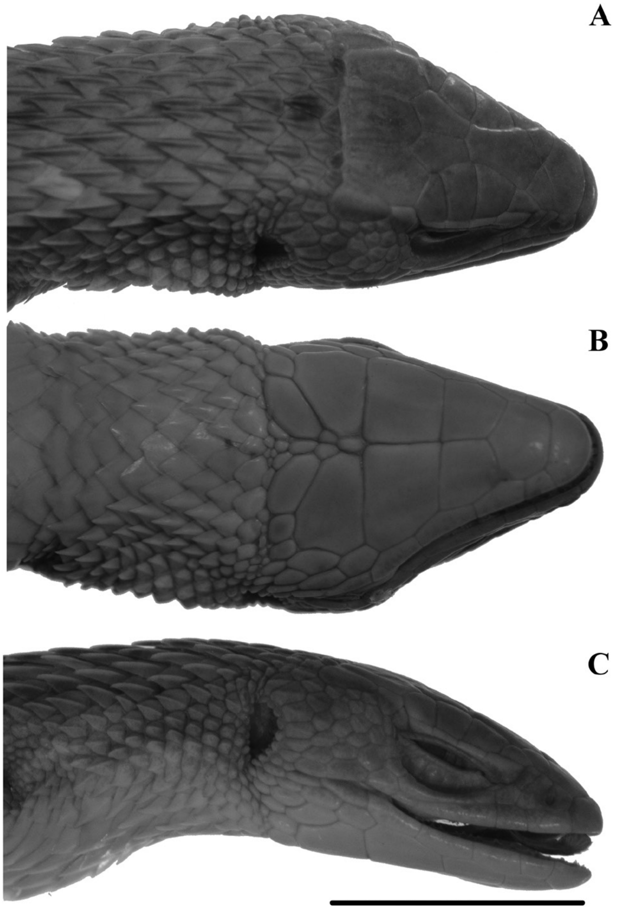

Figure 9. Dorsal (A), ventral (B) and lateral (C) views of the head and neck of the holotype of *Alopoglossus amazonius* (UMMZ 56853). Scale bar: 10 mm.

superciliaries, first four elongated, fifth irregularly triangular; first (anteriormost) longest (about three times as long as tall), contacting loreal, frenocular, first and second supraoculars and second superciliary; second in contact with first and third superciliaries and second and third supraoculars; third in contact with second and fourth superciliaries and third and fourth supraoculars; fourth in contact with third and fifth superciliaries and fourth supraocular; fifth in contact with fourth superciliary, fourth supraocular, first supratemporal and upper postocular. Three suboculars; first longer than tall, contacting frenocular, third supralabial (touching second supralabial) and second subocular; second as long as, but shorter than, first, contacting first and third suboculars and third supralabial; third longest, about three times longer than first and second suboculars, contacting second subocular, third, fourth and fifth supralabials and the lower postocular. One small preocular between first superciliary, loreal and frenocular. Three postoculars continuous with third subocular; the lower ones wider than the upper one. Lower eyelid with semitransparent disc of three large palpebrals. Nasal semidivided, irregularly pentagonal, longer than tall. Nostril in the lower part of nasal, directed posterodorsally. Loreal rectangular, contacting nasal, prefrontal, first supraocular, first superciliary and frenocular. Frenocular irregularly pentagonal, contacting loreal, nasal, second supralabial and first subocular. Seven supralabials, third, fourth and fifth under the orbital region; second, fifth and sixth tallest; third longest, about three times longer than tall. Post-supralabial absent. Temporals irregularly polygonal, juxtaposed, keeled. Two large, keeled, supratemporal scales bordering the parietal; second largest. Ear opening vertically oval, with anterior margin denticulate. Tympanum recessed into a short auditory meatus. Except for supratemporals and temporals, all dorsal and lateral head scales smooth and juxtaposed. Parietals and interparietal with lateral ridges.

Mental trapezoidal, about twice as wide as long, with convex anterior margin. Postmental heptagonal, wider than long. Four pairs of chin shields; first two pairs in broad contact medially and with second, third and fourth infralabials; scales of the third pair irregularly trapezoidal (octagonal), separated from each other by three small, granular scales, from infralabials by large scales, from gulars by the fourth pair of chin shields and two large scales on each side; scales of the fourth pair separated from each other by four small, granular scales and partly separated from gulars by some small scales. Six infralabials, all longer than tall; first and sixth smallest; second, third, fourth and fifth about twice as long as first; suture between third and fourth below centre of eye. Post-infralabials absent. Gular scales smaller than dorsals, pointed, imbricate, differentiated in size toward collar; scales on anterior, medial and lateral gular regions, varying from smooth to feebly keeled, phylloid; anteriormost transverse row and scales on posterior gular region wider than scales on anterior, medial and lateral gular regions, smooth to feebly keeled, almost rounded; gular scales in nine transverse rows. Posterior row of gulars (collar) with nine smooth scales, larger than preceding rows. No gular fold. Scales on nape similar to dorsals, except that the anterior ones are shorter. One transverse row of granular scales posterior to ear opening. Scales on sides of neck distinctly smaller than dorsals, keeled, imbricate, phylloid; in 11 transverse rows; scales on anterior region shorter than scales on posterior region. A distinctive area with scales much shorter than, but similar in shape to, neck scales surrounds the area of arm insertion.

Dorsal scales rhomboid, strongly keeled and mucronate, imbricate and disposed in oblique rows; 29 scales along a middorsal line from parietals to the level of hindlimbs. Scales on flanks similar in shape and size to dorsals. Twenty-one scales around midbody. Ventral scales smooth anteriorly, feebly keeled posteriorly, mucronate and imbricate; posterior margins bluntly pointed; in 17 transverse rows and four longitudinal rows between collar and preanals. Six feebly keeled scales in preanal plate; posterior scales slightly larger than anterior and lateral ones; anterior scales longer than preceding ventral scales. Preanal and femoral pores absent (female).

Dorsal limb scales rhomboid, imbricate, strongly keeled, and mucronate; ventral limb scales feebly keeled; ventral aspect of upper arms and posterior aspect of thighs with tuberculate scales. Five clawed digits on each limb. Lamellae under fingers single, transversely enlarged and smooth, with 14 under the fourth finger; lamellae under toes divided, with 23 under the fourth toe. Scales on tail keeled, slightly mucronate, imbricate, arranged in transverse rows (not counted; broken tail) and in 12 longitudinal rows; scales in the two paravertebral rows wider than long near the base of the tail, and longer than wide in other rows. Keels mostly sharp on tail (feebly keeled and almost rounded on anteriormost ventral rows), forming four dorsal, two lateral (on each side) and four ventral distinct longitudinal ridges.

Measurements of holotype (in millimetres): SVL = 49; AGL = 24.5; HD = 6; HW = 9.5; HL = 13.5; NL = 8; FL = 15; HLL = 27; ShL = 6.1; TL = 17 (broken).

Coloration in preservative (based on holotype)

Dorsal surface of head, back and tail light brown; head homogeneously light brown; from nape and along middorsum, a rather inconspicuous series of small, dark brown spots; on the posterior dorsal surface of body, between the hindlimbs and the base of tail, the dark spots merge to form a dark brown medial band; dorsal surface of forelimbs uniformly light brown; dorsal surface of hindlimbs light brown with some small dark brown spots. Lateral aspect of head and neck light brown, becoming gradually cream ventrally; lateral surface of body (flanks) and tail homogeneous light brown (slightly darker than dorsal), becoming gradually cream ventrally. A continuous dark brown line extending posteriorly from the nostril, passing above the eyes and forelimbs, dorsolaterally on flanks, above hindlimbs, and reaching dorsolaterally the tail, bordered dorsolaterally by a cream stripe from posterior corner of eye to base of tail; narrower from the nostril to the anterior portion of the neck, and wider from the posterior portion of the neck to the shoulders. A dashed light cream line extending posteriorly from the supralabials under the eye, passing through the lower part of the ear opening and neck, above the forelimbs, ventrolaterally on flanks, and reaching the anterior surface of hindlimbs; rather inconspicuous between the limbs. Ventral surface of body cream, with some small, irregular light cream spots on the gular region.

Variation

Interparietal and parietals are either smooth or with lateral ridges. Specimen MPEG 31439 has six superciliaries. A single post-supralabial scale is rarely present on specimens. Scales of the third pair of chin shields are in contact medially or separated from each other by one to four small, granular scales. Scales of the fourth pair of chin shields are in broad contact medially or separated from each other by one to five small, granular scales; they are in direct contact with gulars or separated from them by a row of small scales. Medial gular scales vary from similar in shape to dorsals (strongly keeled) to similar in shape to ventrals (feebly keeled to smooth). Ventral scales vary from smooth to feebly keeled. Scales in preanal plate vary from smooth to slightly keeled. Preanal and femoral pores are absent in females. In males, the femoral pores are arranged in a continuous, well-separated series on each side; two pores on each side are in the preanal position; each pore is between two scales; total number of pores 24–28. Tables 1 and 2 present a summary of the variation in meristic characters and measurements, respectively.

The pale dorsolateral stripe from the posterior corner of the eye to the shoulders either disappears completely posteriad or it becomes rather inconspicuous until the base of the tail. Tails are from light brown to dark brown dorsally, with dark brown and cream spots; they are bordered dorsolaterally by a light brown stripe or by irregular cream spots. In females, flanks are homogeneous light brown (slightly darker than dorsal) or with some dark brown spots; in males, they are light brown (slightly darker than dorsal) with some dark brown spots or completely dark brown. Ventral region in females is completely cream or with some small, irregular dark brown spots; in males, it is from completely cream to dark brown with cream spots (when body is dark brown, under the tail and limbs are cream with dark brown spots).

Distribution and habitat

Alopoglossus amazonius is distributed in southwestern Amazonia (upper Madeira river basin, south of the Amazon River), in Brazil (State of Rondônia) (Supporting Information, Fig. S9). The revision of the Bolivian specimens of the *A. angulatus* species complex (see Langstroth, 2005) may reveal the presence of *A. amazonius* also in that country, owing to its presence in Brazil near the frontier with Bolivia (see Supporting Information, Fig. S9). The information available about the habitat of *A. amazonius* is poor and consists mainly of museum data. The specimens were encountered in leaf litter, in terra firme forest, and in patches of forest in savannas, during the day.

More than 39 000 fires have ignited in the Brazilian Amazonia from January to August 2019 (Andrade, 2019), most of them in the state of Rondônia. In Bolivia, about one million hectares of forest burned only during August 2019. *Alopoglossus amazonius*, here revalidated, occurs in a restricted area in Rondônia, Brazil, along the border with Bolivia, and studies on how the fires have affected its populations are imperative.

ALOPOGLOSSUS ANDEANUS RUIBAL, 1952

[FIGS 4 (*A. ANGULATUS* 'WESTERNMOST'), 7D, 10, 11; TABLES 1 AND 2]

Alopoglossus angulatus Köhler *et al.* (2012: 174, 176, their fig. 2); Ribeiro-Júnior (2018: 32, part).

Holotype: *MCZ 45590*, male, Peru, LA PAMPA, DEPARTMENT OF PUNO (13°39′S, 69°36′W), AT AN ELEVATION OF 760 M A.S.L., 23 JANUARY 1940, G. P. Gardner (Figs 10, 11).

Material examined: Five referred specimens for morphological analyses from Peru (see Supporting Information; Appendix S2).

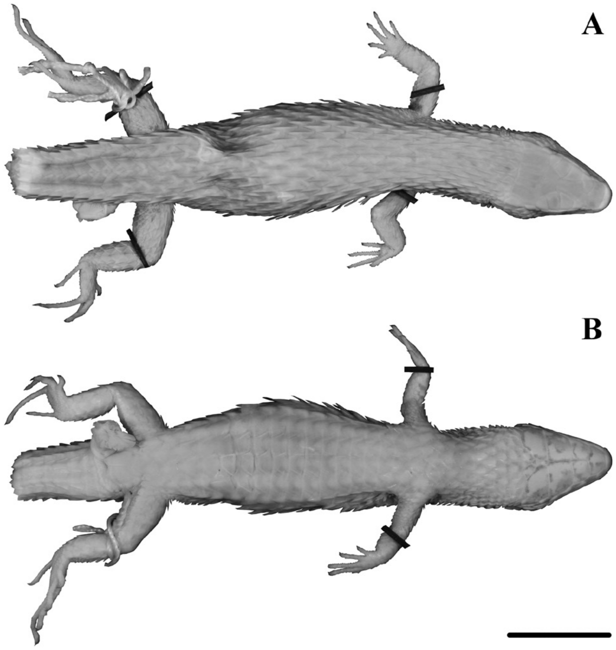

Figure 10. Dorsal (A) and ventral (B) views of the holotype of *Alopoglossus andeanus* (MCZ 45590). Scale bar: 10 mm.

Diagnosis

Alopoglossus andeanus is distinguished from all other species of *Alopoglossus* by the combination of the following characters: (1) scales on the sides of the neck non-granular, keeled, imbricate (at least medial and posterior ones phylloid), in 11 or 12 transverse rows; (2) three pairs of chin shields; (3) third pair of chin shields with rounded posterior margins, in direct contact with gulars; (4) presence of a pair of medial enlarged pregular scales; (5) scales on gular region varying in shape and size: lateral ones strongly keeled, pointed, phylloid; anterior, medial and posterior ones varying from smooth to feebly keeled, bluntly pointed; medial and posterior ones larger than anterior and lateral ones; (6) ventral scales smooth, mucronate, imbricate, with bluntly pointed posterior margins; (7) total number of femoral pores in males 24–28.

Comparison with other species

Alopoglossus andeanus differs from *A. atriventris*, *A. buckleyi*, *A. copii*, *A. embera*, *A. festae*, *A. lehmanni*

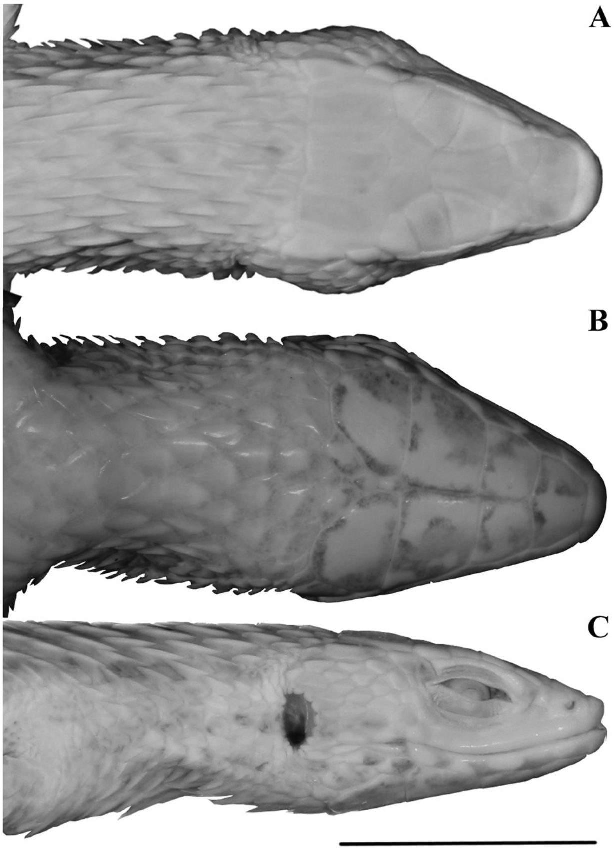

Figure 11. Dorsal (A), ventral (B) and lateral (C) views of the head and neck of the holotype of *Alopoglossus andeanus* (MCZ 45590). Scale bar: 10 mm.

and *A. viridiceps* (in parentheses) in having scales on the sides of the neck similar in shape to dorsals, non-granular, keeled, imbricate (granular in *A. atriventris* and *A. buckleyi*; mostly granular in *A. embera*, *A. festae*, *A. lehmanni* and *A. viridiceps*; conical with apparent bare skin between conical scales in *A. copii*); it also differs from *A. embera*, *A. festae* and *A. viridiceps* in not having gulars arranged in two longitudinal rows (vs. a double longitudinal row of widened gular scales); from *A. lehmanni* in having dorsal scales rhomboidal, in oblique rows (vs. dorsal scales hexagonal with parallel lateral edges, in transverse rows). *Alopoglossus andeanus* differs from *A. angulatus*, *A. amazonius*, *A. avilapiresae*, *A. carinicaudatus* and *A. meloi* in having a pair of medial enlarged pregular scales (vs. absent). It also differs from *A. angulatus* in having scales on sides of neck in 11 or 12 transverse rows (vs. six to nine), and scales on medial and posterior gular regions larger than anterior and lateral ones (vs. scales on medial and posterior gular regions subequal in size to anterior and lateral ones); from *A. carinicaudatus* in having the third pair of chin shields in direct contact with gulars (vs. third pair of chin shields separated from gulars by a row of small, granular scales), anterior ventral scales smooth (vs. anterior ventral scales strongly keeled), and scales on medial gular region larger than scales on lateral gular region, varying from smooth to feebly keeled, bluntly pointed (vs. scales on medial gular region subequal in size to scales on lateral gular region, strongly keeled, pointed). *Alopoglossus andeanus* also differs from *A. amazonius* and *A. meloi* in having three pairs of chin shields (vs. four pairs), and third pair of chin shields with rounded posterior margins, in direct contact with gulars (vs. third pair of chin shields irregularly trapezoidal, separated from gulars by large scales). It differs from *A. collii* in having scales on the sides of the neck in 11 or 12 transverse rows (vs. eight or nine) and the total number of femoral pores 24–28 in males (vs. 19–22).

Redescription of the holotype

Body cylindrical, snout rounded, neck almost as wide as head and anterior part of body, limbs well developed, broken tail (Fig. 10). Male.

Rostral hexagonal, in broad contact with frontonasal, but also contacting first supralabial and nasal. Viewed dorsally, the rostral is about three times as wide as long. Frontonasal pentagonal, about twice as wide as long (wider posteriorly), anteriorly in contact with rostral, laterally with nasal and loreal, and posteriorly with prefrontals. Prefrontals irregularly trapezoidal, wider than long, with a relatively long medial suture; laterally in contact with loreal and first supraocular; posteriorly in contact with frontal. Frontal irregularly hexagonal, longer than wide (distinctly wider anteriorly); laterally in contact with first, second and third supraoculars; posteriorly in contact with frontoparietals. Frontoparietals irregularly pentagonal, longer than wide (wider posteriorly), with a long medial suture; laterally in contact with third and fourth supraoculars; posteriorly in contact with interparietal and parietal. Interparietal pentagonal, lateral borders parallel to each other, about one and a half times as long as wide. A pair of irregularly hexagonal parietals, as long as, and wider anteriorly than, interparietal; laterally in contact with fourth supraocular, first and second supratemporals. The parietal and interparietals form a slightly undulating (almost straight) posterior head margin. Occipitals absent. Four supraoculars; first (anteriormost) smallest, contacting frontal, prefrontal, loreal, first superciliary and second supraocular; second supraocular largest, wider than long, contacting frontal, first and third supraoculars and first and second superciliaries; third supraocular slightly smaller than second, contacting frontal, frontoparietal, second and fourth supraoculars and second and third superciliaries; fourth supraocular in contact with parietal, frontoparietal, third supraocular, third, fourth and fifth superciliaries and first supratemporal. Five superciliaries; first four elongated, fifth irregularly triangular; first longest (about two times as long as tall), contacting loreal, first and second supraoculars and second superciliary; second in contact with first and third superciliaries and second and third supraoculars; third in contact with second and fourth superciliaries and third and fourth supraoculars; fourth in contact with third and fifth superciliaries and fourth supraocular; fifth in contact with fourth superciliary, fourth supraocular, first supratemporal, and touching upper postocular. Four suboculars; first three elongated, fourth tallest; first in contact with frenocular, second and third supralabials and second subocular; second longest, about two times longer than the others, contacting first and third suboculars and third and fourth supralabials; third in contact with second and fourth suboculars, third, fourth and fifth supralabials; fourth in contact with third subocular, fifth supralabial and the lower postocular. One rectangular preocular between first superciliary, loreal, frenocular and first subocular. Two postoculars continuous with fourth subocular; lower one larger than upper one. A series of small, granular scales preceding postoculars. Lower eyelid with semitransparent disc of three large palpebrals. Nasal semidivided, irregularly pentagonal, longer than tall. Nostril in the lower part of nasal, directed posterodorsally. Loreal rectangular, contacting prefrontal, frontonasal, nasal, frenocular, first supraocular and first superciliary. Frenocular irregularly pentagonal, contacting loreal, nasal, second supralabial and first subocular. Seven supralabials;

third, fourth and fifth under the orbital region; first, second and fifth tallest; third longest, about three times as long as tall; fourth smallest. One post-supralabial on right side; absent on the other. Temporals irregularly polygonal, juxtaposed, keeled. Two large, keeled, supratemporal scales bordering the parietal; second largest. Ear opening vertically oval, with anterior margin denticulate. Tympanum recessed into a short auditory meatus. Except for supratemporals and temporals, all dorsal and lateral head scales smooth and juxtaposed. Frontal, frontoparietals, parietals and interparietal with lateral ridges.

Mental trapezoidal, about twice as wide as long, with convex anterior margin. Postmental heptagonal, wider than long. Three pairs of chin shields; first two pairs in broad contact medially and with second, third and fourth infralabials; scales of the third pair irregularly trapezoidal (hexagonal), separated from each other by two small, granular scales and separated from infralabials by large scales; third pair of chin shields with rounded posterior margins, in direct contact with gulars. Presence of a pair of medial enlarged pregular scales between the scales of the third pair of chin shields, separated from each other by one small, granular scale, in direct contact with gulars. Six infralabials, all longer than tall (about two times as long as tall); third infralabial below centre of eye; sixth smallest. Post-infralabials absent. Gular scales smaller than dorsal scales, imbricate, differentiated in size towards collar; scales on lateral gular region smaller, but similar in shape to dorsals, strongly keeled, pointed, phylloid; scales on anterior, medial and posterior gular regions varying from smooth to feebly keeled, bluntly pointed, phylloid (except for the anteriormost row almost rounded posteriorly, smooth); scales on medial and posterior gular regions larger than those on anterior and lateral gular regions; gular scales in eight transverse rows. Posterior row of gulars (collar) with six smooth scales, larger than preceding rows. No gular fold. Scales on nape similar to dorsals, except the anterior ones are shorter. One transverse row of granular scales posterior to ear opening. Scales on sides of neck distinctly smaller than dorsals, keeled, imbricate, phylloid; in 11 or 12 transverse rows; scales on anterior region shorter than scales on posterior region. A distinctive area with scales much shorter than, but similar in shape to, neck scales surrounds the area of arm insertion.

Dorsal scales rhomboid, strongly keeled and mucronate, imbricate and disposed in oblique rows; 28 scales along a middorsal line from parietals to the level of hindlimbs. Scales on flanks similar in shape and size to dorsals. Twenty scales around midbody. Ventral scales smooth, imbricate, bluntly pointed, with rounded posterior margins; in 17 transverse rows and four longitudinal rows between collar and preanals. Six pointed, smooth scales in preanal plate; posterior scales larger than anterior and lateral ones; anterior scales longer than preceding ventral scales. A continuous, well-separated series of femoral pores on each side; each pore between two scales; two pores on each side in preanal position; total number of pores 24, with 12 on each side.

Dorsal limb scales rhomboid, imbricate, strongly keeled and mucronate; ventral limb scales varying from feebly keeled to smooth; ventral aspect of upper arms and posterior aspect of thighs with tuberculate scales. Five clawed digits on each limb. Lamellae under fingers single, transversely enlarged and smooth, 15 or 16 under the fourth finger; lamellae under toes divided, 21–23 under the fourth toe. Scales on tail keeled, slightly mucronate, imbricate, arranged in transverse (not counted; broken tail) and in 12 longitudinal rows; scales in the two paravertebral rows wider than long near the base of the tail, and longer than wide in other rows. Keels mostly sharp on tail (feebly keeled and almost rounded on anteriormost ventral rows), forming four dorsal, two lateral (on each side) and four ventral distinct longitudinal ridges.

Measurements of holotype (in millimetres): SVL = 58; AGL = 29; HD = 7.7; HW = 10.5; HL = 13.8; NL = 9; FL = 16.5; HLL = 29.5; ShL = 6.5; TL = 15 (broken).

Coloration in preservative (based on holotype)

Dorsal surface of head, back and tail light brown; head homogeneously light brown; from nape along the middorsum to the shoulders, a rather inconspicuous series of small, cream and dark brown spots; on the posterior dorsal surface of body, between the hindlimbs and the base of tail, the dark spots merge to form a dark brown medial band; dorsal surface of forelimbs uniformly light brown; dorsal surface of hindlimbs light brown, with some small, dark brown spots; dorsal surface of tail, with a cream dorsolateral stripe. Lateral aspect of head and neck light brown with some irregular cream and dark brown spots; lateral surface of body (flanks) dark brown with some small cream spots anteriorly, becoming gradually light brown posteriorly and cream ventrally; lateral surface of tail slightly darker than dorsal surface with some dark brown spots. A continuous dark brown line extending posteriorly from the nostril, above the eyes to the shoulders; narrower from the nostril to the anterior portion of the neck, and wider from the posterior portion of the neck to the shoulders; bordered dorsolaterally by a light brown stripe. A dashed cream stripe extending from the supralabials under the eye, passing through the lower part of the ear opening and neck, above the forelimbs, ventrolaterally on the flanks, and reaching the anterior surface of hindlimbs;

rather inconspicuous between the limbs. Ventral surface of body cream, with some small, irregular dark brown spots on the head, and with some cream spots on gulars.

Variation

There is little variation among the examined specimens. Except for the holotype, all other specimens have three suboculars (holotype has four). Frontal and frontoparietals are either smooth or with lateral ridges. Scales on medial gular region vary from smooth to feebly keeled. Preanal and femoral pores are absent in females; males have 24–28 total number of pores. Tables 1 and 2 present a summary of the variation in meristic characters and measurements, respectively.

The pale dorsolateral stripe, from the posterior corner of eye to the shoulders, either disappears completely posteriad or it continues until the base of the tail. The middorsal series of small cream and dark brown spots, from nape to at least the shoulders, either disappears completely posteriad or it continues until the tail. Tails are bordered dorsolaterally by a light brown stripe or by irregular cream spots. Sides of neck are light brown in females and light to dark brown in males. Flanks are light brown (slightly darker than dorsal) with some dark brown spots in females and from light to dark brown with some cream spots or homogeneously dark brown in males. Ventral region in females is cream with some small, irregular dark brown spots. In males, the ventral region can be dark brown with cream spots on chin shields and gulars, or cream with dark brown spots on body, preanal plate and tail.

Remarks

A pair of medial enlarged pregular scales is present in all specimens of *A. andeanus* and not found on all examined specimens of *A. angulatus* species complex, except on CHUNB 18040 (*A. collii*) from the state of Rondônia, Brazil. However, specimens of *A. andeanus* have 11 or 12 transverse rows of scales on the sides of the neck and 24–28 total number of pores in males, and the specimen CHUNB 18040 has eight transverse rows of scales on the sides of the neck and 22 total number of pores. Both species, *A. andeanus* and *A. collii*, have restricted distributions, and they are poorly represented in collections. Up to this study, we consider the presence of a pair of enlarged pregular scales on one specimen of *A. collii* as an anoumalous condition of the scales between the third pair of chin shields, in contrast to *A. andeanus*, in which the presence of the pair of enlarged pregular scales was considered as one of the diagnostic characters. Increasing the sample size of both species in the future will help us to understand the relevance and importance of this diagnostic character in *A. andeanus*.

Distribution and habitat

Alopoglossus andeanus is distributed in southwesternmost Amazonia (on Madre de Dios upper river basin), in Peru (Madre de Dios and Puno departments) (Supporting Information, Fig. S10). The revision of the Bolivian specimens of *A. angulatus* species complex (cited as *A. carinicaudatus* and *A. angulatus* by Langstroth, 2005; see also Cortez-Fernandez, 2005) from Madre de Dios river basin may reveal the presence of *A. andeanus* also in that country, owing to its presence in Peru near the frontier with Bolivia (see Supporting Information, Fig. S10). The information available about the habitat of *A. andeanus* consists solely of museum data. The specimens were collected in montane Amazonian forest, during the day, at elevations between 250 and 760 m a.s.l.

***ALOPOGLOSSUS AVILAPIRESAE* SP. NOV.**

[FIGS 2–4 (*A. ANGULATUS* 'WEST'), FIGS 7E–G, 12, 13; TABLES 1 AND 2]

LSID: *urn:lsid:zoobank.org:act:0C29C5C2-168E-490F-A9C1-5C44AC6A0553*

Alopoglossus angulatus Ribeiro-Júnior (2018: 32, part).

Holotype: INPA-H 9515, male, BRAZIL, STATE OF AMAZONAS, Maraã municipality, Amanã, Baré (2°28′54.95″S, 64°42′36.98″W), 5 February 2001,

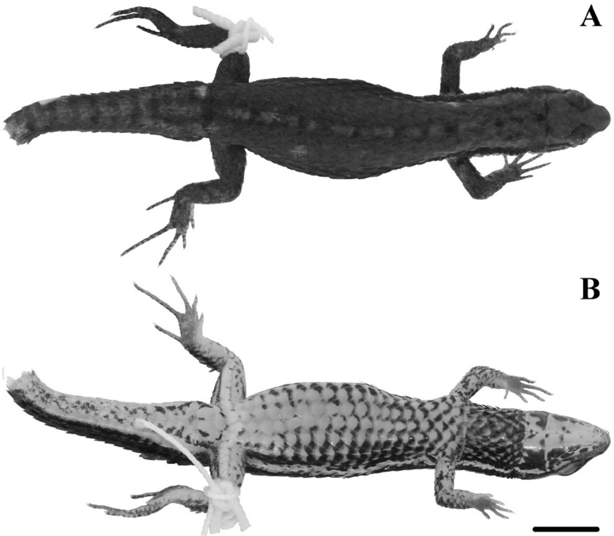

Figure 12. Dorsal (A) and ventral (B) views of the holotype of *Alopoglossus avilapiresae* (INPA-H 9515). Scale bar: 10 mm.

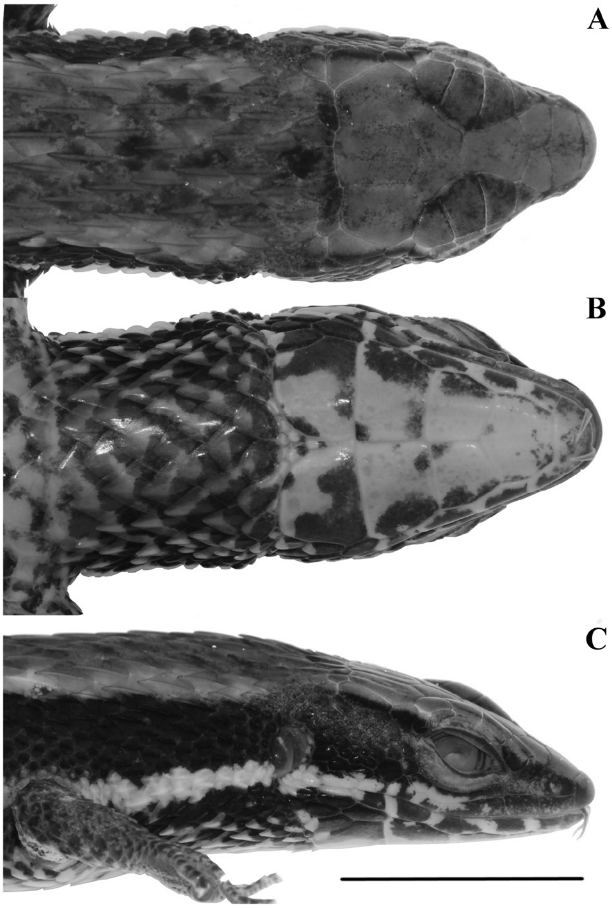

Figure 13. Dorsal (A), ventral (B) and lateral (C) views of the head and neck of the holotype of *Alopoglossus avilapiresae* (INPA-H 9515). Scale bar: 10 mm.

Ana Cristina de Oliveira Cordeiro Duarte, field number RCV 01-322 (Figs 12, 13).

Paratypes: BRAZIL: State of Amazonas: INPA-H 9514, Amanã, Baré (2°28′54.9″S, 64°42′37″W), 30 January 2001, Duarte, field number RCV 01-274; INPA-H 9394, Amanã, Boa Esperança (2°29′17.6″S, 64°45′12.9″W), 1 February 2001, Duarte, field number RCV 01-292; INPA-H 9382, Amanã, Boa Vista (2°20′32.7″S, 64°51′33.8″W), 12 January 2001, Duarte, field number RCV 01-74; INPA-H 11112, 11119, two females, Maraã, Mamirauá Sustainable Development Reserve, Paraná Trail (2°21′42.68″S, 65°15′35.45″W), 9 September 2003 and 6 September 2006, Bernhard.

Material examined: Fifty-eight (N = 58) referred specimens for morphological analyses from Brazil, Colombia and Peru and one sample for molecular analyses from Peru (see Supporting Information; Appendix S2, Table S1).

Etymology

The specific epithet is a noun in the genitive case honoring Teresa Cristina Sauer de Ávila-Pires, in recognition of her valuable contribution to the knowledge of the Amazonian lizards. The first author of this study (M.A.R.-J.) expresses his great appreciation to T. Ávila-Pires for her valuable and constructive contribution to his personal and professional development.

Diagnosis

Alopoglossus avilapiresae is distinguished from all other species of *Alopoglossus* by the combination of the following characters: (1) scales on the sides of the neck non-granular, keeled, imbricate (at least medial and posterior ones phylloid), in ten to 13 transverse rows; (2) three pairs of chin shields; (3) third pair of chin shields with rounded posterior margins, in direct contact with gulars or separated from them by a row of small scales; (4) absence of a pair of medial enlarged pregular scales; (5) scales on gular region subequal in size, but varying in shape: lateral ones strongly keeled, pointed, phylloid; anterior, medial and posterior ones feebly keeled, bluntly pointed; anteriormost transverse row with scales smooth, almost rounded posteriorly, and varying from similar in size to slightly smaller than those in the proceeding rows; (6) ventral scales mucronate, imbricate, with bluntly pointed posterior margins (almost rounded), varying from smooth to feebly keeled; (7) total number of femoral pores in males 23–29.

Comparison with other species

Alopoglossus avilapiresae differs from *A. atriventris*, *A. buckleyi*, *A. copii*, *A. embera*, *A. festae*, *A. lehmanni* and *A. viridiceps* (in parentheses) in having scales on the sides of the neck similar in shape to dorsals, non-granular, keeled, imbricate (granular in *A. atriventris* and *A. buckleyi*; mostly granular in *A. embera*, *A. festae*, *A. lehmanni* and *A. viridiceps*; conical with apparent bare skin between conical scales in *A. copii*); it also differs from *A. embera*, *A. festae* and *A. viridiceps* in not having gulars arranged in two longitudinal rows (vs. a double longitudinal row of widened gular scales); from *A. lehmanni* in having dorsal scales rhomboidal, in oblique rows (vs. dorsal scales hexagonal with parallel lateral edges, in transverse rows). *Alopoglossus avilapiresae* differs from *A. amazonicus* and *A. meloi* in having three pairs of chin shields (vs. four pairs), and the third pair of chin shields rounded medially and posteriorly, contacting gulars or separated from them by a row of small scales (vs. third pair of chin shields irregularly trapezoidal, separated from gulars by large scales). It differs from *A. angulatus* in having scales on sides of neck in ten to

13 transverse rows (vs. six to nine); from *A. andeanus* in lacking a pair of medial enlarged pregular scales; from *A. carinicaudatus* in having the third pair of chin shields rounded medially and posteriorly, contacting gulars or separated by a row of small scales [vs. third pair of chin shields irregularly quadrangular (anterior and posterior margins almost parallel) with straight posterior margins, separated from gulars by a row of small, granular scales in *A. carinicaudatus*], scales on medial gular region feebly keeled (vs. scales on medial gular region strongly keeled), and scales on anterior ventral region varying from smooth to feebly keeled (vs. scales on anterior ventral region strongly keeled). *Alopoglossus avilapiresae* differs from *A. collii* in having scales on sides of neck in ten to 13 transverse rows (vs. eight or nine) and total number of femoral pores 23–29 in males (vs. 19–22).

Description of holotype

Body cylindrical, snout rounded, neck almost as wide as head and anterior part of body, limbs well developed, broken tail (Fig. 12). Male.

Rostral hexagonal, in broad contact with frontonasal, but also contacting first supralabial and nasal. Viewed dorsally, the rostral is about three times as wide as long. Frontonasal pentagonal, about twice as wide as long (wider posteriorly), anteriorly in contact with rostral, laterally with nasal, and posteriorly with prefrontals. Prefrontals irregularly trapezoidal, wider than long, with a long medial suture; laterally in contact with loreal and first supraocular, and touching nasal; posteriorly in contact with frontal. Frontal irregularly heptagonal, longer than wide (distinctly wider anteriorly); laterally in contact with first, second and third supraoculars; posteriorly in contact with frontoparietals. Frontoparietals irregularly pentagonal, longer than wide (wider posteriorly), with a long medial suture; laterally in contact with third and fourth supraoculars; posteriorly in contact with interparietal and parietal. Interparietal pentagonal, lateral borders parallel to each other, about one and a half times as long as wide. A pair of irregularly hexagonal parietals, as long as, and wider anteriorly than, interparietal; laterally in contact with fourth supraocular, first and second supratemporals. The parietal and interparietals form a slightly undulating (almost straight) posterior head margin. Occipitals absent. Four supraoculars; first (anteriormost) smallest, contacting frontal, prefrontal, loreal, first superciliary and second supraocular; second supraocular smaller than third, wider than long, contacting frontal, first and third supraoculars and first and second superciliaries; third supraocular largest, contacting frontal, frontoparietal, second and fourth supraoculars and second and third superciliaries; fourth supraocular in contact with parietal, frontoparietal, third supraocular, third, fourth and fifth superciliaries and first supratemporal. Five superciliaries; first four elongated; first tallest, second, third and fourth about half the height of the first; fifth irregularly rounded; first (anteriormost) in contact with loreal, first and second supraoculars and second superciliary; second in contact with first and third superciliaries and second and third supraoculars; third in contact with second and fourth superciliaries and third and fourth supraoculars; fourth in contact with third and fifth superciliaries and fourth supraocular; fifth in contact with fourth superciliary, fourth supraocular and first supratemporal. Three suboculars; first longer than tall, contacting frenocular, second and third supralabials and second subocular; second longest, about three times longer than first and third suboculars, contacting first and third suboculars and third and fourth supralabials; third as long as, but taller than, first, contacting second subocular, fourth and fifth supralabials and the lower postocular. One small preocular between first superciliary, frenocular and first subocular. Two postoculars continuous with third subocular; lower one about two times wider than upper one. Lower eyelid with semitransparent disc of four large palpebrals on one side and five on the other. Nasal semidivided, irregularly pentagonal, longer than tall, contacting rostral, frontonasal, prefrontal, loreal, frenocular and first and second supralabials. Nostril in the lower part of nasal, directed posterolaterally. Loreal rectangular, contacting nasal, prefrontal, first supraocular, first superciliary and frenocular. Frenocular irregularly pentagonal, contacting loreal, nasal, second supralabial and first subocular. Seven supralabials; third, fourth and fifth under the orbital region; second and fifth tallest; third longest, about three times longer than tall; fourth and sixth smallest. Post-supralabial absent. Temporals irregularly polygonal, juxtaposed, feebly keeled. Two large, smooth, supratemporal scales bordering the parietal; second largest. Ear opening vertically oval, with anterior margin denticulate. Tympanum recessed into a short auditory meatus. Except for some temporals, all dorsal and lateral head scales smooth and juxtaposed. Parietals and interparietal with low lateral ridges.

Mental trapezoidal, about twice as wide as long, with convex anterior margin. Postmental heptagonal, wider than long. Three pairs of chin shields; first two pairs in broad contact medially and with second, third and fourth infralabials; scales of the third pair of chin shields in contact with each other anteriorly, separated from each other by three small, granular scales posteriorly, and separated from infralabials by large scales; third pair rounded medially and posteriorly, in direct contact with gulars on the left side and partly separated from them by small scales on the right. Six infralabials, all longer than tall; first, fourth and fifth about two times as long as tall; second and third longest (about three times as long as tall); sixth smallest; suture between third and fourth below centre of eye. Post-infralabials absent. Gular scales smaller but similar in shape to dorsals, imbricate, phylloid, differentiated in size towards collar (except that the anteriormost transverse row is almost rounded posteriorly, smooth, with scales slightly smaller, or similar in size to, posteriad it); scales on lateral gular region strongly keeled, pointed, phylloid; scales on anterior, medial and posterior gular regions varying from smooth to feebly pointed, imbricate, wider than scales on lateral gular region; gular scales in eight transverse rows. Posterior row of gulars (collar) with seven smooth scales, larger than preceding rows. No gular fold. Scales on nape similar to dorsals, except that the anterior ones are shorter, almost rounded, feebly keeled. One transverse row of granular scales posterior to ear opening. Scales on sides of neck distinctly smaller than dorsals, keeled, imbricate, phylloid; in ten transverse rows; scales on anterior region shorter than scales on posterior region. A distinctive area with scales much shorter than, but similar in shape to, neck scales surrounds the area of arm insertion.

Dorsal scales rhomboid, strongly keeled and mucronate, imbricate and disposed in oblique rows; 28 scales along a middorsal line from parietals to the level of hindlimbs. Scales on flanks similar in shape and size to dorsals. Twenty-one scales around midbody. Ventral scales mucronate and imbricate; scales on anterior and along the midventral portion smooth, bluntly pointed; lateral ones feebly keeled, pointed; in 17 transverse rows and four longitudinal rows between collar and preanals. Seven smooth scales in preanal plate (three anteriors; two laterals; two posteriors); posterior scales larger than anterior and lateral ones; lateroanterior scales shorter than lateral ones; medioanterior larger than preceding ventral scales. A continuous, well-separated series of femoral pores on each side; each pore between two scales; two pores on each side in preanal position; total number of pores 25, 12 on one side and 13 on the other.

Dorsal limb scales rhomboid, imbricate, strongly keeled, and mucronate; ventral limb scales feebly keeled; ventral aspect of upper arms and posterior aspect of thighs with tuberculate scales. Five clawed digits on each limb. Lamellae under fingers single, transversely enlarged and smooth, with 16 under the fourth finger; lamellae under toes divided, with 22 or 23 under the fourth toe. Scales on tail keeled, slightly mucronate, imbricate, arranged in transverse rows (not counted; broken tail) and in 12 longitudinal rows; scales in the two paravertebral rows wider than long near the base of the tail, and longer than wide in other rows. Keels mostly sharp on tail (feebly keeled and almost rounded on anteriormost ventral rows), forming four dorsal, two lateral (on each side) and four ventral distinct longitudinal ridges.

Measurements of holotype (in millimetres): SVL = 53.4; AGL = 25.2; HD = 6.9; HW = 8.4; HL = 10.9; NL = 7.6; FL = 15.5; HLL = 22.9; ShL = 6.3; TL = 22.3 (broken).

Coloration in preservative (based on holotype)

Dorsal surface of head, back and tail light brown; head with some small, irregular dark brown spots, most evident bordering supraocular region; a cream dorsolateral stripe extending posteriorly from the posterior corner of the eye to the shoulders; from nape, along the middorsum to base of tail, a rather inconspicuous series of alternated small, dark brown and cream spots; on the posterior dorsal surface of body, between the hindlimbs and the base of tail, the dark spots merge to form a dark brown medial band; dorsal surface of forelimbs and hindlimbs light brown with some small dark brown spots; dorsal surface of tail with alternating dark brown and cream bands. Lateral aspect of head light brown with small, irregular dark brown spots; lateral aspect of neck dark brown; lateral surface of body (flanks) and tail dark brown, becoming cream ventrally. A dashed dark brown line extending from the nostril to the posterior portion of the head. A continuous cream stripe extending posteriorly from the supralabials under the eye, passing through the lower part of the ear opening and neck, above the forelimbs, ventrolaterally on flanks, and reaching the anterior surface of the hindlimbs (bordered on flanks by a dashed dark brown line). Ventral surface of head, body, limbs and tail cream with some small irregular dark brown spots; gular region dark brown with small irregular cream spots.

Coloration in life (based on photographs in life)

Specimen from the Chandless State Park, Manuel Urbano, State of Acre, adult male (Figs 7E, F): dorsal surface of head and anterior surface of body buff, becoming gradually dark brown towards posterior surface of body; dorsal surface of forelimbs amber; dorsal surface of hindlimbs and tail dark brown; dorsal surfaces of head, body, hindlimbs and tail with amber, buff and black spots. Lateral surface of head, neck and flanks black with amber and buff spots, with white spots ventrally. A continuous white stripe extending posteriorly from the supralabials under the eye, passing through the lower part of the ear opening and neck, above the forelimbs, ventrolaterally on flanks, and reaching the anterior surface of the hindlimbs. Ventral surface of head and gular region black with white and cream spots; ventral surface of body with scales black anteriorly and cream posteriorly; ventral surface of forelimbs grey with black spots; ventral surface of hindlimbs and tail cream with black spots.

Specimen from the Chico Mendes Extractive Reserve, Brasiléia, State of Acre, adult male (Fig. 7G): dorsal surface of head bright amber; anterior surface of body dull amber, becoming gradually dark brown towards posterior surface of body; dorsal surfaces of head and body with blackish spots; on the posterior dorsal surface of body, between the hindlimbs and the base of the tail, the blackish spots merge to form a large, blackish medial band; dorsal surface of forelimbs and hindlimbs dark brown; hindlimbs with some irregular small, black and buff spots; dorsal surface of tail dull dark brown. A continuous dark brown line extending from the nostril to the shoulders. Lateral surface of head bright amber, becoming gradually blackish posteriorly; lateral surface of neck and flanks black with amber and buff spots, with white spots ventrally; lateral surfaces of limbs and tail dark brown with buff and black spots. A buff dorsolateral stripe extending from the posterior corner of the eye to the anterior part of the tail; posteriad, it becomes gradually dark brown with small buff spots. A continuous stripe extending posteriorly from the supralabials under the eye, passing through the lower part of the ear opening and neck, above the forelimbs, ventrolaterally on the flanks, and reaching the anterior surface of the hindlimbs; white from under the eye to the lower part of the ear opening, and cream from the neck to the anterior surface of the hindlimbs. Iris vividly orange.

Variation

Specimen INPA-H 11112 has eight supralabials on one side and seven on the other. Interparietal and parietals are either smooth or with low lateral ridges. MPEG 20671 has the scales of the third pair of chin shields in broad contact medially; other specimens have scales of the third pair separated from each other by one to eight small, granular scales. Scales of the third pair of chin shields are in direct contact with gulars or separated from them by a row of small scales. Medial gular scales vary from smooth to feebly keeled. Ventral scales vary from smooth to feebly keeled. Scales in preanal plate vary from smooth to slightly keeled. Preanal and femoral pores are absent in females; males have 23–29 total number of pores. Tables 1 and 2 present a summary of the variation in meristic characters and measurements, respectively.

The pale dorsolateral stripe extending from the posterior corner of the eye to the shoulders either disappears completely posteriad or it continues until the base of the tail. The dashed dark brown line extending from the nostril to the posterior portion of the head either disappears completely posteriad or it continues, passing through above the forelimbs, dorsolaterally on the flanks, above the hindlimbs, and reaching the tail dorsolaterally; when it continues along lateral surface of body, it is narrower from the nostril to the anterior portion of the neck, and wider from the posterior portion of the neck to the shoulders (rather inconspicuous on flanks); it is rather inconspicuous on females between the nostril and posterior border of the head. The cream line extending from the supralabials under the eye to the anterior surface of the hindlimbs is rather inconspicuous on flanks in females. The rather inconspicuous middorsal series of alternated dark brown and cream spots can begin on the nape or shoulders. Dorsal surface of tail can be: homogeneous light brown; light brown with dark brown and cream spots; light brown with alternating dark brown and cream bands; dorsolaterally, tail has a light brown stripe or irregular cream spots. Lateral surfaces of neck are light brown (slightly darker than dorsal) in females and light or dark brown in males. Flanks are homogeneous light brown (slightly darker than dorsal) or with some dark brown spots in females; dark brown in males. Ventral surface of body is homogeneously cream or it has some small, irregular dark brown spots in females; it is homogeneously cream or dark brown with blackish and/or cream spots in males (when the ventral surface is dark brown, under the tail and limbs are cream).

Distribution and habitat

Alopoglossus avilapiresae is distributed in western Amazonia (west of the Negro and Madeira rivers, on both sides of the Amazon River), in Colombia (Department of Amazonas), Peru (Departments of Cusco, Huánuco, Junín, Loreto, Madre de Dios, Puno and San Martín) and Brazil (States of Amazonas and Acre) (Supporting Information, Fig. S11). The information available about the habitat of *A. avilapiresae* is poor and consists solely of museum data. The specimens were encountered in the leaf litter in montane, terra firme and flooded (varzea) forests, during the day.

ALOPOGLOSSUS CARINICAUDATUS (COPE, 1876)

[FIGS 2–4 (*A. ANGULATUS* 'ECUADOR'), 7I, J, 14, 15; TABLES 1 AND 2]

Lepidosoma carinicaudatum Cope (1876: 160).
Leposoma carinicaudatum O'Shaughnessy (1881: 233).
Alopoglossus carinicaudatus Boulenger (1885: 384); Ruthven (1924: 3); Ruibal (1952: 508, part).
Pantodactylus carinicaudatus Burt & Burt (1931: 358).

Alopoglossus angulatus Köhler *et al.* (2012: 176, part); Ribeiro-Júnior (2018: 32, part).
Holotype: ANSP 11371, male, Marañon, Orton Expedition. Type locality restricted by Ruibal (1952) to Valley of the Marañon River, Peru, but here corrected and restricted to Santa Rosa de Otas, Department of Napo, Ecuador (upper Napo River; 0°58′41.2″S, 77°27′4.4″W; see comments in Remarks below) (Figs 14, 15).

Material examined: Six referred specimens for morphological analyses from Ecuador and Peru and 17 samples for molecular analyses from Ecuador (see Supporting Information; Appendix S2, Table S1).

Diagnosis

Alopoglossus carinicaudatus is distinguished from all other species of *Alopoglossus* by the combination of the following characters: (1) scales on the sides of the neck non-granular, keeled, imbricate (at least medial and posterior ones phylloid), in 11 or 12 transverse rows; (2) three pairs of chin shields; (3) third pair of chin shields irregularly quadrangular (anterior and posterior margins almost parallel), with straight posterior margins, separated from gulars by a row of small scales; (4) absence of a pair of medial enlarged pregular scales; (5) scales on gular region subequal in shape and size: lateral, anterior, medial and posterior ones strongly keeled, pointed, phylloid; anteriormost transverse row feebly keeled; (6) ventral scales mucronate, imbricate, with bluntly pointed posterior margins, varying from strongly keeled on anterior and lateral surfaces to feebly keeled on medial and posterior surfaces; and (7) total number of femoral pores in males 22–26.

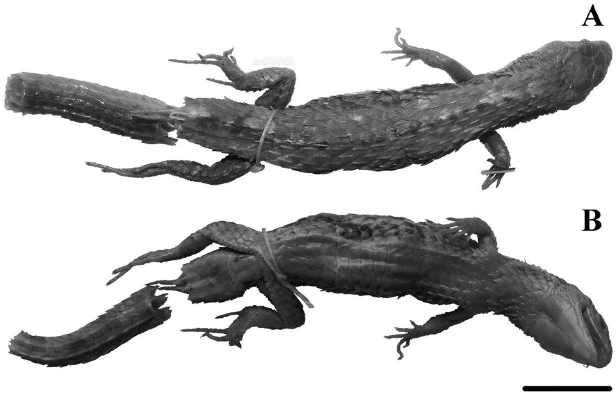

Figure 14. Dorsal (A) and ventral (B) views of the holotype of *Alopoglossus carinicaudatus* (ANSP 11371). Scale bar: 10 mm.

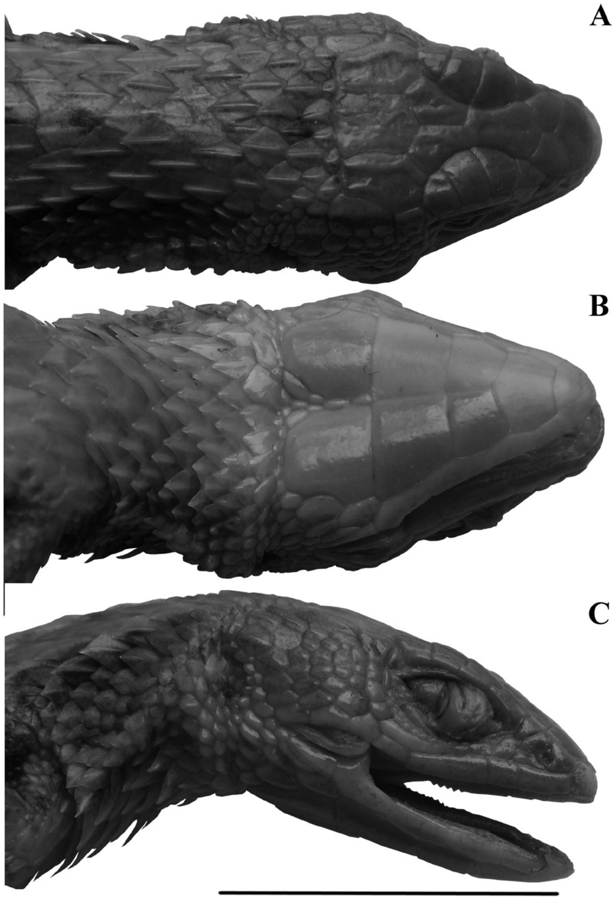

Figure 15. Dorsal (A), ventral (B) and lateral (C) views of the head and neck of the holotype of *Alopoglossus carinicaudatus* (ANSP 11371). Scale bar: 10 mm.

Comparison with other species

Alopoglossus carinicaudatus differs from *A. atriventris*, *A. buckleyi*, *A. copii*, *A. embera*, *A. festae*, *A. lehmanni* and *A. viridiceps* (in parentheses) in having scales on the sides of the neck similar in shape to dorsals, non-granular, keeled, imbricate (granular in *A. atriventris* and *A. buckleyi*; mostly granular in *A. embera*, *A. festae*, *A. lehmanni* and *A. viridiceps*; conical with apparent bare skin between conical scales in *A. copii*); it also differs from *A. embera*, *A. festae* and *A. viridiceps* in not having gulars arranged in two longitudinal rows (vs. a double longitudinal row of widened gular scales); from *A. lehmanni* in having dorsal scales rhomboidal, in oblique rows (vs. dorsal scales hexagonal with parallel lateral edges, in transverse rows). *Alopoglossus carinicaudatus* differs from *A. angulatus*, *A. amazonius*, *A. andeanus*, *A. avilapiresae*, *A. collii* and *A. meloi* in having the third pair of chin shields irregularly quadrangular (anterior and posterior margins almost parallel), with straight posterior margins, separated from gulars by a row of small scales (vs. third pair of chin shields with rounded posterior margins, in direct contact with gulars or separated from them by a row of small scales in *A. angulatus*, *A. andeanus*, *A. avilapiresae* and *A. collii*; third pair of chin shields irregularly trapezoidal, separated from gulars by large scales in *A. amazonius* and *A. meloi*), scales on gular region subequal in shape and size, with lateral, anterior, medial and posterior ones strongly keeled, pointed, phylloid (vs. scales on gular region subequal in size but varying in shape, with anterior, medial and posterior ones varying from smooth to feebly keeled, phylloid in *A. angulatus* and *A. meloi*; scales on gular region varying in shape and size, with posterior ones varying from smooth to feebly keeled, almost rounded, larger than lateral, anterior and medial ones in *A. amazonius*; scales on gular region varying in shape and size, with anterior, medial and posterior ones varying from smooth to feebly keeled, bluntly pointed, and medial and posterior ones larger than anterior and lateral ones in *A. andeanus*; scales on gular region subequal in size but varying in anterior shape, with medial and posterior ones feebly keeled, bluntly pointed in *A. avilapiresae*; scales on gular region varying in shape and size, with medial and posterior ones smooth, almost rounded, bluntly pointed, larger than lateral ones in *A. collii*) and in having ventral scales strongly keeled on anterior region (vs. anterior ventral scales varying from feebly keeled to smooth on all other species). It also differs from *A. angulatus* in having scales on the sides of the neck in 11 or 12 transverse rows (vs. six to nine); from *A. amazonicus* and *A. meloi* in having three pairs of chin shields (vs. four pairs); from *A. andeanus* by lacking a pair of medial enlarged pregular scales; and from *A. collii* in having scales on the sides of the neck in 11or 12 transverse rows (vs. eight or nine).

Redescription of holotype

Body cylindrical, snout rounded, neck almost as wide as head and anterior part of body, limbs well developed, broken tail (Fig. 14). Male.

Rostral hexagonal, in broad contact with frontonasal, but also contacting first supralabial and nasal. Viewed dorsally, the rostral is about three times as wide as long. Frontonasal pentagonal, twice as wide as long (wider posteriorly), anteriorly in contact with rostral, laterally with nasal, and posteriorly with prefrontals. Prefrontals irregularly pentagonal, wider than long, with a short medial suture; laterally in contact with loreal and first supraocular, and touching nasal; posteriorly in contact with frontal. Frontal hexagonal, longer than wide (distinctly wider anteriorly); laterally in contact with first and second supraoculars; posteriorly in contact with frontoparietals. Frontoparietals irregularly pentagonal, longer than wide (wider posteriorly), with a long medial suture; laterally in contact with third and fourth supraoculars, and touching second supraocular on the right side; posteriorly in contact with interparietal and parietal. Interparietal pentagonal, lateral borders parallel to each other, about as long as wide. A pair of irregularly hexagonal parietals (distinctly wider anteriorly), slightly longer than interparietal; laterally in contact with fourth supraocular, first and second supratemporals. The parietals and interparietal form a slightly undulating (almost straight) posterior head margin. Occipitals absent. Four supraoculars; first (anteriormost) smallest, contacting frontal, prefrontal, loreal, first superciliary and second supraocular; second supraocular largest, wider than long, contacting frontal, first and third supraoculars, first and second superciliaries, and touching frontoparietal on the right side; third supraocular slightly smaller than second, contacting frontoparietal, second and fourth supraoculars and second and third superciliaries; fourth supraocular in contact with parietal, frontoparietal, third supraocular, third, fourth and fifth superciliaries and first supratemporal. Five superciliaries; first four elongated, fifth triangular; first (anteriormost) longest, contacting loreal, first and second supraoculars and second superciliary; second in contact with first and third superciliaries and second and third supraoculars; third in contact with second and fourth superciliaries and third and fourth supraoculars; fourth in contact with third and fifth superciliaries and fourth supraocular; fifth in contact with fourth superciliary, fourth supraocular and first supratemporal. Two suboculars on the right side; first smallest, wider than long, contacting frenocular, second supralabial and second subocular; second longest, about five times longer than tall, contacting third, fourth and fifth supralabials and the lower postocular. Three suboculars on the left side; first about two times longer than tall, contacting frenocular, second and third supralabials and second subocular; second smallest, about two times longer than tall, contacting first and third subocular and third supralabial; third longest, about five times longer than tall, contacting second subocular, third, fourth and fifth supralabials and the lower postocular. Three postoculars; upper one smallest; medial one slight larger than lower one. Lower eyelid with semitransparent disc of five large palpebrals. Nasal semidivided, irregularly pentagonal, longer than tall. Nostril in the lower part of nasal, directed lateroposteriorly. Loreal trapezoidal, contacting nasal, prefrontal, first supraocular, first superciliary and frenocular. Frenocular irregularly pentagonal, contacting loreal, nasal, second supralabial and first subocular. Seven supralabials; third and fourth under the orbital region; first, fourth, sixth and seventh about two times longer than tall; second quadrangular; third longest, about three times longer than tall; fifth tallest. Post-supralabial absent. Temporals irregularly polygonal, juxtaposed, keeled. Two large, keeled, supratemporal scales bordering the parietal; second largest. Ear opening vertically oval, with anterior margin denticulate. Tympanum recessed into a short auditory meatus. Except for supratemporals and temporals, all dorsal and lateral head scales smooth and juxtaposed. Frontoparietals, fourth supraoculars, interparietal and parietals with lateral ridges.

Mental trapezoidal, about twice as wide as long, with convex anterior margin. Postmental heptagonal, as wide as long. Three pairs of chin shields, first two pairs in broad contact medially and with second, third and fourth infralabials; scales of the third pair separated from each other by nine small, granular scales and separated from infralabials by larger scales; third pair of chin shields irregularly quadrangular (anterior and posterior margins almost parallel), with straight posterior margins, separated from gulars by a row of small scales. Six infralabials, all longer than tall; second and third about twice as long as first; fourth about three times as long as first; fifth slightly longer than first; sixth smallest; suture between third and fourth below centre of eye. One small post-infralabial. Gular scales smaller but similar in shape to dorsals, strongly keeled, pointed, imbricate, phylloid (except the anteriormost transverse row is feebly keeled); gular scales in ten transverse rows, not differentiated in size or shape towards collar. Posterior row of gular scales (collar) with eight scales, not differentiated from preceding rows. No gular fold. Scales on nape similar to dorsals, except that the anterior ones are shorter. Two transverse rows of granular scales posteriorly to ear opening. Scales on sides of neck distinctly smaller than dorsals, keeled, imbricate, phylloid; in 11 transverse rows; scales on anterior region similar in size to scales on posterior region. A distinctive area with scales much shorter than, but similar in shape to, neck scales, surrounds the area of arm insertion.

Dorsal scales rhomboid, strongly keeled and mucronate, imbricate and disposed in oblique rows; 26 scales along a middorsal line from parietals to the level of the hindlimbs. Scales on flanks similar to dorsals. Twenty-one scales around midbody. Ventral scales keeled, mucronate and imbricate; posterior margin bluntly pointed; scales along midventral and posterior regions feebly keeled; scales on anterior and lateral regions strongly keeled; in 15 transverse rows and four longitudinal rows between collar and preanals. Nine feebly keeled, bluntly pointed scales in preanal plate, five on anterior region and four on posterior region; posteromedial scales much larger than posterolateral ones; anteromedial scale larger than anterolateral ones, but similar in size to preceding ventral scales. A continuous, well-separated series of femoral pores on each side; each pore between two scales; two pores on each side in preanal position; total number of pores 22, 11 on each side.

Dorsal limb scales rhomboid, imbricate, strongly keeled and mucronate; ventral limb scales feebly keeled; ventral aspect of upper arms and posterior aspect of thighs with tuberculate scales. Five clawed digits on each limb. Lamellae under fingers single, transversely enlarged, and smooth, with 12 under the fourth finger; lamellae under toes divided, with 22 under the fourth toe. Scales on tail keeled, slightly mucronate, imbricate, arranged in transverse rows (not counted; broken tail) and in 12 longitudinal rows; scales in the two paravertebral rows wider than long near the base of the tail, and longer than wide in other rows. Keels mostly sharp on tail (feebly keeled and almost rounded on anteriormost ventral rows), forming four dorsal, two lateral (on each side) and four ventral distinct longitudinal ridges.

Measurements of holotype (in millimetres): SVL = 53.5; AGL = 26; HD = 6.5; HW = 8.5; HL = 11; NL = 6.8; FL = 14.5; HLL = 23.5; ShL = 6.2; TL = 9 + 23 (broken, in two parts).

Coloration in preservative (based on neotype)

Dorsal surface of head, back and tail brown; head homogeneously brown; from nape and along middorsum, a continuous series of small, dark brown spots; on the posterior dorsal surface of body, between the hindlimbs, the dark brown spots merge to form a dark brown medial band; dorsal surface of forelimbs uniformly brown; dorsal surface of hindlimbs mottled brown and dark brown; tail with dark brown spots dorsally. Lateral aspect of head, neck and tail brown, becoming gradually light brown and cream ventrally; a cream ventrolateral line on neck; lateral surface of body (flanks) completely covered by a wide, dark brown band, bordered ventrally by an indistinct cream line. A dashed dark brown line extending from the nostril to the dorsolateral region of the neck. Ventral surface of body homogeneously cream; preanal plate and tail with some small, irregular dark brown spots.

Coloration in life (based on photographs in life)

QCAZR6263 (Fig. 7H, I), adult male: dorsal surface of head bright mahogany; anterior surface of body dull mahogany, becoming gradually bistre towards posterior surface of body and tail; dorsolateral amber stripe from the posterior corner of the eye to the anterior part of the body; posterior surface of body, dorsal surfaces of limbs and tail bistre (forelimbs slightly lighter than hindlimbs); from above the hindlimbs to the tail, a rather inconspicuous dorsolateral amber stripe. Lateral surface of head bright lion and lateral surface of neck dull lion, becoming gradually cream ventrally; lateral surface of body (flanks) bistre, with a continuous white, wide band from fore- to hindlimbs, bordered dorsally and ventrally by a blackish band (continuous dorsally, inconspicuous ventrally); lateral surfaces of limbs and tail bistre, with some amber dots. A continuous bistre line extending from the nostril, above the eyes, ear opening and neck to the shoulders; bordering ventrally the dorsolateral amber stripe. Ventral surface of head, gular region and ventral surface of forelimbs homogeneous white; ventral surface of body white, with some blackish spots on lateral region; ventral surface of hindlimbs, tail and preanal plate white with some blackish spots. Iris vividly amber.

Variation

There is little variation among the examined specimens. Except for the holotype, all other specimens have a lower number of scales between the third pair of chin shields (nine vs. three to seven) and gular scales (ten vs. seven to nine); the holotype has two and three suboculars, whereas all others have three. Preanal and femoral pores are absent in females; males have 22–26 total number of pores. Tables 1 and 2 present a summary of the variation in meristic characters and measurements, respectively. Females have a similar coloration pattern to males, but they are generally lighter.

Remarks

The species was described based on only one specimen collected during Prof. Orton Expedition in Andean region and western Amazonia, in Ecuador, Peru and Brazil. The type locality was presented by Cope (1876: 161) as 'from the Marañon' and later modified to 'Upper Amazons' by Boulenger (1885: 385). Burt & Burt (1931: 358) cited 'Valley of the Marañon River' as the type locality. Ruibal (1952: 508) included 'Peru' in Burt and Burt's designation without any reason for the restriction. Subsequent studies followed Ruibal (1952), citing the type locality of *A. carinicaudatus* as Valley of the Marañon River, Peru. However, according to Cope (1868: 96; published 8 years before the description of *A. carinicaudatus*) the Prof. Orton Expedition collected reptiles chiefly in seven localities: three in the Andean region (Guayaquil, Ambato and Antisana, in Ecuador) and four in the Amazonian region ('Archiaona' and Santa Rosa in Ecuador; Pebas in Peru; and Tabatinga in Brazil); snakes were mainly collected in Brazil and Peru, and lizards in Ecuador. After revising great series of *Alopoglossus* previously identified as *A. angulatus* from Peru, we disagree with Ruibal in suggesting that *A. carinicaudatus* was collected in the valley of the Marañon River in Peru during the Prof. Orton Expedition in that country (in Pebas); in addition, we rule out the possibility of it being collected in the upper Marañon River (whence only *A. avilapiresae* is known), in the Andean region in Ecuador (*A. angulatus* species complex does not occur in that region) or in Tabatinga, Brazil (whence only *A. avilapiresae* is known). Therefore, based on the combination of the lines of evidence, and owing to the proximity of Santa Rosa to the nearest known record of *A. carinicaudatus* (see Species distribution below) and its location on Napo river basin (river used by the Prof. Orton Expedition to access the Amazon River from the Andean region), here we restrict the type locality of *A. carinicaudatus* to Santa Rosa de Otas, upper Napo River, Ecuador, from which the specimens probably came. The new restriction of the type locality presented here, which means a modification from Peru to Ecuador, also represents a tentative correction of the distribution of *A. carinicaudatus*.

Distribution and habitat

Alopoglossus carinicaudatus is distributed in the westernmost Amazonia, in the upper Napo river basin, occurring in northeastern Ecuador (Department of Napo, Pastaza, Orellana and Sucumbíos) and northernmost Peru (Department of Loreto) (Supporting Information, Fig. S12). The information available about the habitat of *A. carinicaudatus* is poor. P.V. found CORDIBI 0297 in a lowland forest and CORDIBI 12663 in an upland forest.

***ALOPOGLOSSUS COLLII* SP. NOV.**

[FIGS 2–4 (*A. ANGULATUS* 'SOUTH'), 7H, 16, 17; TABLES 1 AND 2]

LSID: *urn:lsid:zoobank.org:act:F30F039E-935C-4D6D-BDFD-FCDF5E160BD2*

Holotype: *CHUNB 18038*, female, Brazil, State of Rondônia, Pimenta Bueno (11°51′45.2″S, 60°56′18 ″W), between 1 July and 24 August 2000, Guarino Colli, field number GRCOLLI 5572 (Figs 16, 17).

Paratypes: Brazil: State of Mato Grosso: UFMT 4105, PCH Ombreiras Margem direita do Rio Jauru (15°19′2.3″S, 58°51′42.8″W); State of Rondônia: CHUNB 18037, CHUNB 18039–18040 and CHUNB 18599, males, Pimenta Bueno (11°51′45.2″S, 60°56′18 ″W), between 1 July and 24 August 2000, Colli, field numbers GRCOLLI 5816, 5757, 5681 and 5684, respectively; CHUNB 11472, male, Vilhena

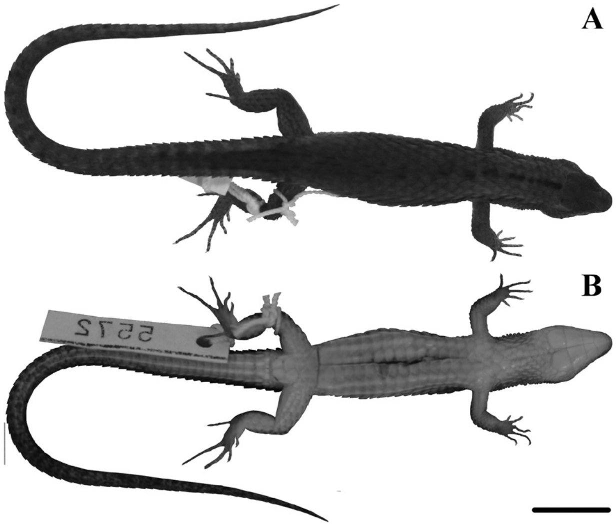

Figure 16. Dorsal (A) and ventral (B) views of the holotype of *Alopoglossus collii* (CHUNB 18038). Scale bar: 10 mm.

(12°07′19.1″S, 60°16′39.1″W), between 20 August and 22 September 1999, Mesquita, field number GRCOLLI 4041.

Material examined: Three referred specimens for morphological analyses and five samples for molecular analyses from Brazil (see Supporting Information; Appendix S2, Table S1).

Etymology

The specific epithet is a noun in the genitive case honouring herpetologist Guarino Rinaldi Colli in recognition of his valuable contribution to the knowledge on the lizards of the Cerrado, especially in the State of Rondônia, Brazil.

Diagnosis

Alopoglossus collii is distinguished from all other species of *Alopoglossus* by the combination of the following characters: (1) scales on the sides of the neck non-granular, keeled, imbricate (at least medial and posterior ones phylloid), in eight or nine transverse rows; (2) three pairs of chin shields; (3) third pair of chin shields with rounded posterior margins, in direct contact with gulars or separated from them by small scales; (4) absence of a pair of medial enlarged pregular scales (see Remarks below); (5) scales on gular region varying in shape and size: lateral ones strongly keeled, pointed, phylloid (except the anterior ones); the first three anterior transverse rows with scales smooth, almost rounded, larger than those in the proceeding row (anteriormost row with the largest scales); medial and posterior ones smooth, almost rounded, bluntly pointed, larger than lateral ones; (6) ventral scales mucronate, imbricate, with bluntly pointed posterior margins, varying from smooth to feebly keeled; (7) total number of femoral pores in males 19–22.

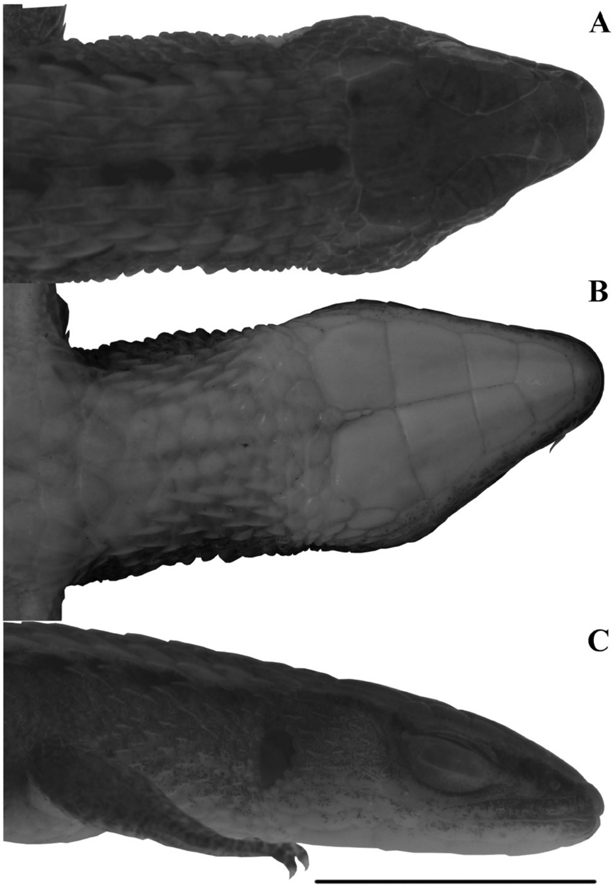

Figure 17. Dorsal (A), ventral (B) and lateral (C) views of the head and neck of the holotype of *Alopoglossus collii* (CHUNB 18038). Scale bar: 10 mm.

Comparison with other species

Alopoglossus collii differs from *A. atriventris*, *A. buckleyi*, *A. copii*, *A. embera*, *A. festae*, *A. lehmanni* and *A. viridiceps* (in parentheses) in having scales on the sides of the neck similar in shape to dorsals, non-granular, keeled, imbricate (granular in *A. atriventris* and *A. buckleyi*; mostly granular in *A. embera*, *A. festae*, *A. lehmanni* and *A. viridiceps*; conical with apparent bare skin between conical scales in *A. copii*); it also differs from *A. embera*, *A. festae* and *A. viridiceps* in not having gulars arranged in two longitudinal rows (vs. a double longitudinal row of widened gular scales); from *A. lehmanni* in having dorsal scales rhomboidal, in oblique rows (vs. dorsal scales hexagonal with parallel lateral edges, in transverse rows). *Alopoglossus collii* differs from *A. angulatus* in having scales on medial and posterior gular regions bluntly pointed, almost rounded, larger than scales on lateral gular region (vs. scales on medial and posterior gular regions phylloid, subequal in size to lateral ones), scales in the first transverse row (anteriormost) of the gular region larger than those in proceeding rows on the anterior region [vs. scales in the first transverse row (anteriormost) of gular scales similar in size to, or slightly smaller than, those in proceeding rows], higher number of ventral scales (18 or 19 vs. 14–18) and a lower total number of femoral pores in males (19–22 vs. 20–29). *Alopoglossus collii* differs from *A. amazonicus* and *A. meloi* in having three pairs of chin shields (vs. four pairs), and the third pair of chin shields in direct contact with gulars or separated from them by a row of small scales (vs. third pair of chin shields separated from gulars by large scales). *Alopoglossus collii* differs from *A. andeanus* and *A. avilapiresae* in having scales on the sides of the neck in eight or nine transverse rows (vs. 11 or 12 in *A. andeanus*; 10–13 in *A. avilapiresae*), 19–22 total number of femoral pores in males (vs. 24–28 in *A. andeanus*; 23–29 in *A. avilapiresae*). *Alopoglossus collii* differs from *A. carinicaudatus* in having scales on the sides of the neck in eight or nine transverse rows (vs. 11 or 12), third pair of chin shields with rounded posterior margins, in direct contact with gulars or separated from them by small scales [vs. third pair of chin shields irregularly quadrangular (anterior and posterior margins almost parallel), with straight posterior margins, separated from gulars by a row of small scales], and scales on the medial gular region bluntly pointed, almost rounded (vs. scales on medial gular region strongly keeled, phylloid).

Description of holotype

Body cylindrical, snout rounded, neck almost as wide as head and anterior part of body, limbs well developed, tail longer than body (Fig. 16). Female.

Rostral hexagonal, in broad contact with frontonasal, but also contacting first supralabial and nasal. Viewed dorsally, the rostral is about three times as wide as tall. Frontonasal pentagonal, about twice as wide as long (wider posteriorly), anteriorly in contact with rostral, laterally with nasal, and posteriorly with prefrontals. Prefrontals irregularly triangular, wider than long, with a relatively short medial suture; laterally in contact with loreal and first supraocular, and touching nasal on the right side; posteriorly in contact with frontal. Frontal irregularly hexagonal, longer than wide (wider and almost rounded anteriorly); laterally in contact with second and third supraoculars; posteriorly in contact with frontoparietals. Frontoparietals irregularly pentagonal, longer than wide (wider posteriorly), with a long medial suture; laterally in contact with third and fourth supraoculars; posteriorly in contact with interparietal and parietal. Interparietal pentagonal, lateral borders parallel to each other, about one and a half times as long as wide (wider posteriorly). A pair of irregularly heptagonal parietals, wider anteriorly than, and slightly longer than, interparietal; laterally in contact with fourth supraocular, first and second supratemporals. The parietals and interparietal form a slightly undulating (almost straight) posterior head margin. Occipitals absent. Four supraoculars; first (anteriormost) smallest, contacting prefrontal, loreal, first superciliary and second supraocular; second supraocular largest, wider than long, contacting frontal, first and third supraoculars and first and second superciliaries; third supraocular slightly smaller than second, contacting frontal, frontoparietal, second and fourth supraoculars and second and third superciliaries; fourth supraocular in contact with parietal, frontoparietal, third supraocular, third, fourth and fifth superciliaries and first supratemporal. Five superciliaries, first tallest; first four elongated; second, third, and fourth about half the tall of first; fifth irregularly triangular; first in contact with loreal, frenocular, first and second supraoculars and second superciliary; second in contact with first and third superciliaries and second and third supraoculars; third in contact with second and fourth superciliaries and third and fourth supraoculars; fourth in contact with third and fifth superciliaries and fourth supraocular; fifth in contact with fourth superciliary, fourth supraocular and first supratemporal. Three suboculars; first longer than tall, contacting frenocular, third supralabial and second subocular; second longest, about three times longer than first and third suboculars, contacting first and third suboculars and third and fourth supralabials; third as long as, but taller than, first, contacting second subocular, fourth and fifth supralabials and the lower postocular. Two postoculars continuous with third subocular; lower one about two times taller than upper one. Lower eyelid with semitransparent disc of four large palpebrals on one side and five on the other. Nasal semidivided, irregularly pentagonal, longer than tall. Nostril in the median part of nasal, directed posterolaterally. Loreal rectangular, contacting nasal, prefrontal, first supraocular, first superciliary and frenocular. Frenocular irregularly pentagonal, contacting loreal, nasal, second supralabial, first subocular, and touching third supralabial. Seven supralabials, third, fourth and fifth under the orbital region; third longest, about three times as long as tall; fifth tallest; seventh shortest. Post-supralabial absent. Temporals irregularly polygonal, juxtaposed, strongly keeled. Two large, keeled, supratemporal scales bordering the parietal; second largest. Ear opening vertically oval, with anterior margin denticulate. Tympanum recessed into a short auditory meatus. Except for supratemporals and temporals, all dorsal and lateral head scales smooth and juxtaposed. Frontoparietals, parietals and interparietal with low lateral ridges.

Mental trapezoidal, about twice as wide as long, with convex anterior margin. Postmental pentagonal, wider than long. Three pairs of chin shields; first two pairs in broad contact medially and with second, third and fourth infralabials; scales of the third pair in contact anteriorly, separated from each other by two small, granular scales and one large scale posteriorly, and from infralabials by large scales; third pair with irregular rounded posterior margins, in direct contact with gulars. Six infralabials, all longer than tall; first, second and fifth about two times as long as tall; third and fourth longest, about three times as long as tall; sixth smallest; suture between third and fourth below centre of eye. Post-infralabials absent. Gular scales smaller than dorsals, imbricate, differentiated in size and shape towards collar; scales in the first three transverse rows of gulars smooth, almost rounded, wider than those in proceeding rows (the first transverse row; anteriormost with the largest scales on the anterior gular region); scales on lateral gular region smaller than, but similar in shape to dorsals, strongly keeled, pointed, imbricate, phylloid (except for the anterior ones smooth, almost rounded); scales on medial gular region larger than scales on lateral gular region, smooth, imbricate, bluntly pointed, almost rounded; scales on posterior gular region larger than scales on lateral, anterior and medial gular regions, smooth, almost rounded; gular scales in nine transverse rows. Posterior row of gular scales (collar) with eight smooth scales, not differentiated from preceding rows. No gular fold. Scales on nape similar to dorsals, except that the anterior ones are shorter, almost rounded. One transverse row of granular scales posterior to ear opening. Scales on sides of neck distinctly smaller than dorsals, keeled, imbricate, phylloid; in eight transverse rows; scales on anterior region shorter than scales on posterior region. A distinctive area with scales much shorter than, but similar in shape to, neck scales surrounds the area of arm insertion.

Dorsal scales rhomboid, strongly keeled and mucronate, imbricate and disposed in oblique rows; 26 scales along a middorsal line from parietals to the level of the hindlimbs. Scales on flanks similar in shape and size to dorsals. Twenty scales around midbody. Ventral scales mucronate and imbricate; scales on anterior and along the midventral region smooth, bluntly pointed; scales on lateral region feebly keeled, pointed; in 18 transverse rows and four longitudinal rows between collar and preanals. Six feebly keeled scales in preanal plate; four antero- and posteromedial scales much larger than lateral ones, slightly larger than preceding ventral scales. Preanal and femoral pores absent (female).

Dorsal limb scales rhomboid, imbricate, strongly keeled and mucronate; ventral limb scales feebly keeled; ventral aspect of upper arms and posterior aspect of thighs with tuberculate scales. Five clawed digits on each limb. Lamellae under fingers single, transversely enlarged and smooth, with 13 or 14 under the fourth finger; lamellae under toes divided, with 20–23 under the fourth toe. Scales on tail keeled, slightly mucronate, imbricate, arranged in transverse rows (not counted) and in 12 longitudinal rows; scales in the two paravertebral rows wider than long near the base of the tail, and longer than wide in other rows. Keels mostly sharp on tail (feebly keeled, almost rounded on anteriormost ventral rows), forming four dorsal, two lateral (on each side) and four ventral distinct longitudinal ridges.

Measurements of holotype (in millimetres): SVL = 51.8; AGL = 24.6; HD = 7.5; HW = 9.4; HL = 10; NL = 8.8; FL = 15.9; HLL = 21.4; ShL = 6.3; TL = 98.5 (1.9 times SVL).

Coloration in preservative (based on holotype)

Dorsal surface of head, back and tail light brown; head with some small, irregular dark brown spots, most evident on supraocular region and frontoparietals; from nape and along the middorsum, a rather inconspicuous series of dark brown spots; on the posterior dorsal surface of body, between the hindlimbs and the base of tail, the dark spots merge to form a dark brown medial band; dorsal surface of forelimbs and hindlimbs light brown with some small dark brown spots; dorsal surface of tail with alternating dark brown and cream spots. Lateral aspect of head and neck light brown, becoming gradually cream ventrally; lateral surface of body (flanks) and tail light brown, becoming gradually cream ventrally. A dashed dark brown line extending posteriorly from the nostril, passing above eyes and forelimbs, dorsolaterally on flanks, above hindlimbs and reaching the tail dorsolaterally; rather inconspicuous on flanks; bordered dorsolaterally by a stripe slightly lighter than dorsal surface from the posterior corner of the eye to the base of the tail, more evident on shoulders and above hindlimbs. A rather inconspicuous cream stripe extending from the supralabials under the eye, passing through the lower part of the ear opening and neck, above the forelimbs, ventrolaterally on flanks, and reaching the anterior surface of the hindlimbs. Ventral surface of head, body, limbs and anterior portion of tail cream; posterior portion of tail cream with small, irregular dark brown spots.

Variation

There is little variation among the type series. Specimen CHUNB 18039 has nine transverse rows of scales on the sides of the neck. CHUNB 18039–18040 have three postoculars on one side and two on the other. CHUNB 11472 and 18599 have only one small scale between the third pair of chin shields posteriorly. CHUNB 18039 has one enlarged pregular scale, and CHUNB 18040 has a pair of medial enlarged pregular scales (see Remarks below). Frontoparietals are either smooth or with low lateral ridges. Third pair of chin shields is in direct contact with gulars or separated from them by small scales. Ventral scales vary from smooth to feebly keeled. Scales in preanal plate vary from smooth to feebly keeled. Preanal and femoral pores are absent in females. In males, the femoral pores are arranged in a continuous, well-separated series on each side; two pores on each side are in the preanal position; each pore is between two scales; total number of pores 19–22. Tables 1 and 2 present a summary of the variation in meristic characters and measurements, respectively. The preanal plate and ventral region of the base of the tail are homogeneously cream or with some small, irregular dark brown spots.

Remarks

Except for all specimens of *A. andeanus*, enlarged pregular scales between the third pair of chin shield scales are also present in CHUNB 18040 (a pair of medial enlarged pregular scales) and CHUNB 18039 (one enlarged pregular scale). However, CHUNB 18039 and CHUNB 18040, both males, have eight or nine transverse rows of scales on the sides of the neck and 22 total number of pores, whereas *A. andeanus* has 11 or 12 transverse rows of scales on the sides of the neck and 24–28 total number of pores in males. We consider the presence of enlarged pregular scales on specimens of *A. collii* as an anoumalous condition of the scales between the third pair of chin shields, in contrast to *A. andeanus*, in which the presence of the pair of enlarged pregular scales was considered as one of the diagnostic characters. As mentioned above (see Remarks for *A. andeanus*), increasing the sample size of *A. andeanus* and *A. collii* in the future will help us to elucidade the condition of pregular scales as an informative character.

Distribution and habitat

Alopoglossus collii is distributed in southern Amazonia, in a region at the transition with the Cerrado, occurring only in Brazil (States of Mato Grosso and Rondônia) (Supporting Information, Fig. S13). Detailed information about the region can be found in the papers by Gainsbury & Colli (2003), Colli *et al.* (2003) and Freitas *et al.* (2011). The information available about the habitat of *A. collii* is poor; Macedo *et al.* (2008) found one specimen in the leaf litter in a dry open forest in the State of Rondônia. The area of occurrence of the new species *A. collii* was directly affected by fires in August and September 2019, and as for *A. amazonius*, studies on how the fires have affected *A. collii* populations are imperative.

DISCUSSION

Given that Amazonia is a megadiverse domain, the species richness in the region remains superficially known and poorly understood (Nunes *et al.*, 2012; Ribeiro-Júnior & Amaral, 2016b), with many small terrestrial vertebrates having surprisingly widespread distributions (Ribeiro-Júnior, 2015a, b; Ribeiro-Júnior & Amaral, 2016a, b, 2017). Some recent studies using morphological or molecular datasets have revealed widespread species as a complex of closely related species (Geurgas & Rodrigues, 2010; Nunes *et al.*, 2012; Oliveira *et al.*, 2016; Ribeiro-Júnior & Amaral, 2016a, 2017; Ribeiro-Júnior, 2018; Silva *et al.*, 2018), but the adoption of integrative taxonomy, combining both approaches, could greatly improve the reliability and efficiency of species delineation (Bergmann & Russel, 2007; Murphy *et al.*, 2016).

Our study combines evidence from morphological and molecular datasets and indicates the presence of a species complex in *A. angulatus*, contrasting with Ávila-Pires (1995) and Köhler *et al.* (2012) (the most recent and detailed studies with *A. angulatus*). The original and ambiguous diagnosis, the absence of standardization of the nomenclatural characters in *Alopoglossus* (see Ribeiro-Júnior, 2018: 34–35) and replication of the characters collected (Köhler *et al.*, 2012 examined the same characters as Ávila-Pires, 1995) are, possibly, the main reasons why previous studies underestimated the real diversity in *A. angulatus*. The overall congruence between two independent lines of evidence (external morphology and mitochondrial/nuclear data) in our study provides strong support for the existence

Illustrated key to the species of the genus *Alopoglossus* and map of distribution of species previously recognized as *A. angulatus*

The key is adapted from Köhler *et al.* (2012), Torres-Carvajal & Lobos (2014) and Ribeiro-Júnior (2018) and does not reflect the phylogenetic relationships of the species. We present in Figure 18 differences between scales on theside of, and along, the neck in *A. angulatus* and *A. atriventris*, commonly misindetified in collections; and in Figure 19 qualitative differences of the gular scales between species of the *A. angulatus* species group, in addition to the presence/absence of the fourth pair of chin shields and the enlarged pair of pregular scales. Figure 20 presents distributional records of species that have scales on the side of, and along, the neck non-granular, keeled and imbricate; all of them were previously recognized as *A. angulatus*.

1. A double longitudinal row of widened gular scales; dorsal scales lanceolate in transverse rows only 2

– No double longitudinal row of widened gular scales; dorsal scales hexagonal in transverse rows only or rhomboidal in oblique and transverse rows 4

2. Presence of distinct light stripe from mouth commissure to shoulder .... *A. viridiceps* (west of Andes in ....Ecuador)

– No distinct light stripe from mouth commissure to shoulder 3

3. Ventral scales keeled, pointed .... *A. embera* (west of Andes in Colombia)

– Ventral scales smooth, rounded .... *A. festae* (west of Andes in Peru, Ecuador and Colombia)

4. Dorsal scales hexagonal with parallel lateral edges, in transverse rows only; transverse ventral count ten .... *A. lehmanni* (west of Andes in Colombia)

– Dorsal scales rhomboidal or lanceolate, in oblique and transverse rows; transverse ventral count four to eight .. 5

5. Keels on posterior part of dorsum form longitudinal ridges; scales on side of neck large and conical with apparent bare skin between conical scales .... *A. copii* (western Amazonia in Ecuador and Peru)

– Keels on posterior part of dorsum do not form longitudinal ridges; scales on side of neck small and granular or keeled and somewhat imbricate without apparent bare skin between scales 6

6. Scales on side of, and along, the neck small and granular (Fig. 18A) 7

– Scales on side of, and along, the neck non-granular, keeled, imbricate (at least medial and posterior ones phylloid) (Fig. 18B) 8

7. Ventral scales distinctly keeled .... *A. atriventris* (western Amazonia in Brazil, Colombia, Peru and Ecuador)

– Ventral scales smooth.................................... *A. buckleyi* (western Amazonia in Brazil, Peru and Ecuador)

8. Four pairs of chin shields; third pair of chin shields separated from gulars by large scales (Fig. 19B, G) 9

– Three pairs of chin shields; third pair of chin shields in direct contact with gulars or separated from them by small or granular scales (Fig. 19A, C–F) 10

9. Scales on sides of neck in nine to 13 transverse rows; total number of femoral pores in males 24–28 ....A. amazonius (south-western Amazonia in Brazil; Fig. 20)

– Scales on sides of neck in six to eight transverse rows; total number of femoral pores in males 20–23 ....*A. meloi* [north-eastern Amazonia (southern Guiana Shield) in Brazil; Fig. 20]

10. Scales on sides of neck in six to nine transverse rows 11

– Scales on sides of neck in ten to 13 transverse rows 12

11. Scales on medial and posterior gular regions phylloid, subequal in size to lateral ones (Fig. 19A); number of ventral scales 14–18; number of femoral pores in males 20–29 ....*A. angulatus* (eastern Amazonia in Brazil, French Guiana, Suriname and Guyana; Fig. 20)

– Scales on medial and posterior gular regions bluntly pointed, almost rounded, larger than scales on lateral gular region (Fig. 19F); number of ventral scales 18 or 19; number of femoral pores in males 19–22 ....*A. collii* (south-western Amazonia in Brazil; Fig. 20)

12. Third pair of chin shields irregularly quadrangular (anterior and posterior margins almost parallel), with an almost straight posterior margin; scales on medial gular region strongly keeled, phylloid and similar to those on lateral gular region (Fig. 19E) ....*A. carinicaudatus* (north-western Amazonia in Peru and Ecuador; Fig. 20)

– Third pair of chin shields with rounded posterior margins; scales on medial gular region varying from smooth to feebly keeled, bluntly pointed (Fig. 19C, D) 13

13. Presence of a distinct pair of enlarged medial pregular scales between the third pair of chin shields (Fig. 19C) .... *A. andeanus* (south-western Amazonia in Peru; Fig. 20)

– Absence of a pair of enlarged medial pregular scales between the third pair of chin shields (Fig. 19D) ....*A. avilapiresae* (western Amazonia in Brazil and Peru; Fig. 20)

of eight distinct evolutionary units (de Queiroz, 2007): *Alopoglossus angulatus s.s.*, *A. amazonius*, *A. andeanus*, *A. avilapiresae*, *A. carinicaudatus*, *A. collii* and two distinct lineages (one from French Guiana and one from Southwest Amazonia). Six distinct lineages with high genetic differentiation measured by genetic distances were recognized by DNA analyses and six morphological units by morphology (quantitative analyses and qualitative examination). Two independent lineages (one in French Guiana and one in southwest Amazonia) were signalized as two new putative species (not described here, but under morphological revision), and one species (*A. andeanus*) was recognized and resurrected based only on morphological evidence. Five species (*A. angulatus*, *A. amazonius*, *A. avilapiresae*, *A. carinicaudatus* and *A. collii*) had representatives in both analyses, with samples examined for morphology and sequencing data.

The descriptions and redescriptions presented here, along with the most recent contribution to the genus (Ribeiro-Júnior, 2018), represent a solution for the complex taxonomic history and nomenclatural problem that recognized several species as *A. angulatus* (see Ruibal, 1952; Hoogmoed, 1973; Ávila-Pires, 1995; Köhler *et al.*, 2012). Until now, the diagnosis of *A. angulatus* has been ambiguous (see Ribeiro-Júnior, 2018: 34), allowing *A. carinicaudatus*, *A. amazonius* and *A. andeanus* to be considered as synonyms of *A. angulatus* (see Köhler *et al.*, 2012). Furthermore, a new species described recently (*A. meloi*) and the two new species described here (i.e. *A. avilapiresae* and *A. collii*) would also have been identified as *A. angulatus*. We show that the remarkable genetic differentiation and variability in the number of transverse rows of neck scales, number of pairs of chin shields, number of preanal pores and shape and size of gular scales between species are useful diagnostic characters to distinguish among species previously nested within *A. angulatus*. The descriptions and redescriptions presented in the present paper represent a major advance in the knowledge of *Alopoglossus* taxonomy and systematics, increasing the total number of known species of *Alopoglossus* from nine to 14.

The phylogenetic tree of *Alopoglossus* presented by Torres-Carvajal & Lobos (2014) recovered *A. angulatus* and *A. copii* as sister species, within a cis-Andean clade also containing *A. atriventris* and *A. buckleyi*. Recently, Goicoechea *et al.* (2016) recovered a similar topology for the Alopoglossidae phylogenetic tree. Both studies support a clade composed by species that have scales on the sides of the neck that are similar in shape to dorsals, non-granular, keeled and imbricate (*A. angulatus* species complex). Owing to a more thorough sampling used within the *A. angulatus* species complex, we were able to detect six distinct evolutionary units encompassed within the complex. The uncertain relationship between *A. angulatus* and *A. atriventris* + *A. copii* in the concatenated and mtDNA inferences is probably caused by the reduced sampling of *A. copii* (i.e. only one sample). Despite the partial recovery of mitochondrial lineages by the nuclear markers, there are also incongruences, such as paraphyly for *A. angulatus* in *SNCAIP* and for *A. atriventris* and *A. carinicaudatus* in *PRLR*. These

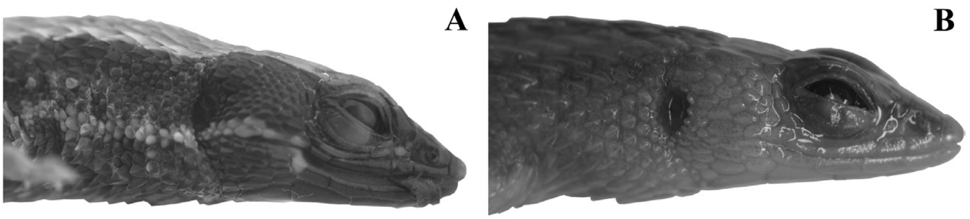

Figure 18. Lateral view of the head and neck of the holotype of *Alopoglossus atriventris* (KU 126783; A) and *Alopoglossus angulatus* (RMNH 15200; B), showing differences between scales on the side of and along the neck.

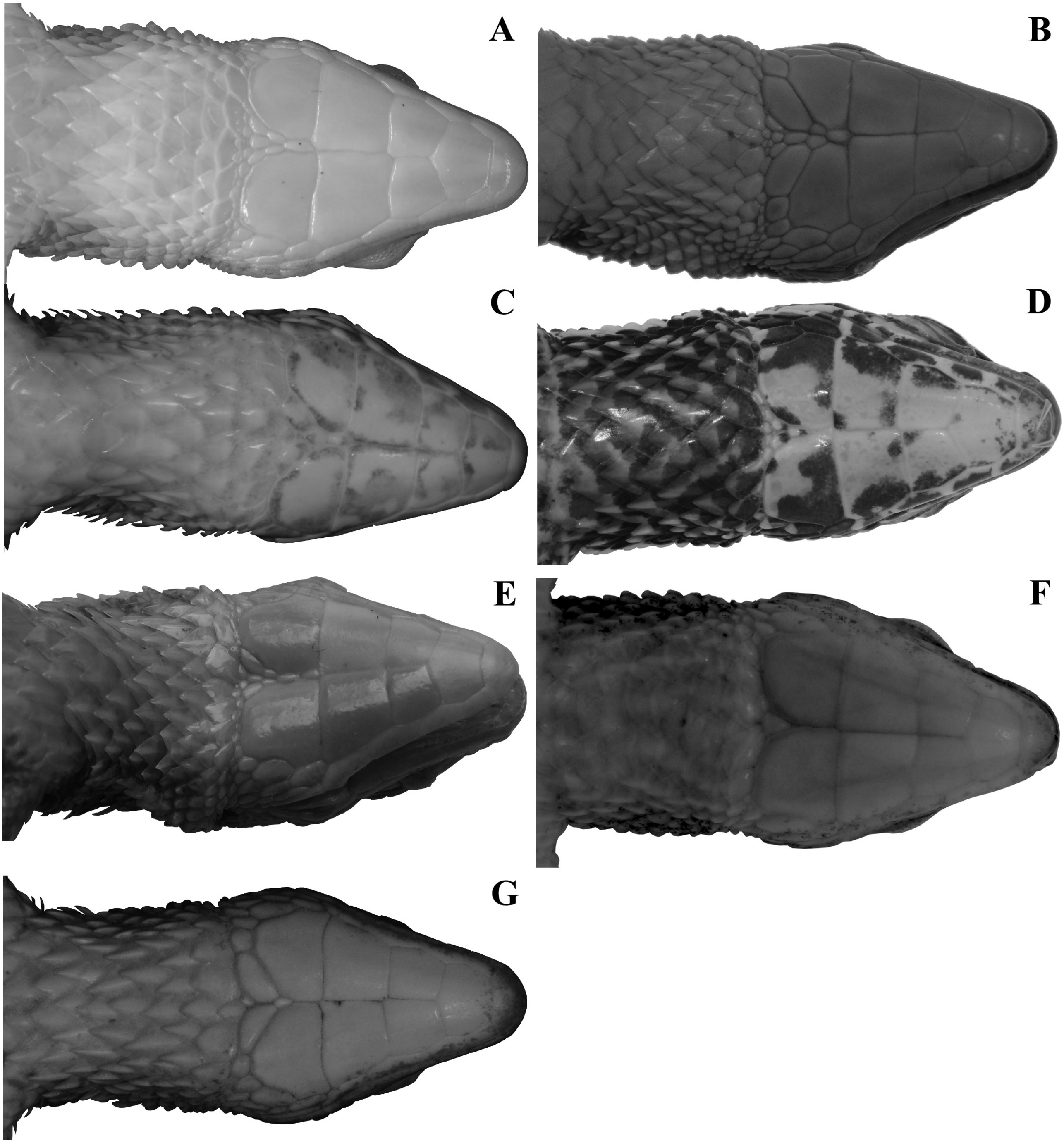

Figure 19. Ventral view of the head of the holotype of *Alopoglossus angulatus* (*RMNH 15200*; A), *Alopoglossus amazonius* (*UMMZ 56853*; B), *Alopoglossus andeanus* (MCZ 45590; C), *Alopoglossus avilapiresae* (INPA-H 9515; D), *Alopoglossus carinicaudatus* (ANSP 11371; E), *Alopoglossus collii* (CHUNB 18038; F) and *Alopoglossus meloi* (MPEG 24372; G) showing differences of the gular scales, presence/absence of the fourth pair of chin shields and presence/absence of enlarged pregular scales in species of the *A. angulatus* species group.

incongruences were probably caused by incomplete lineage sorting of nuclear markers and were reflected in a sister relationship between *A. atriventris* and *A. angulatus s.s.* recovered on the species tree, albeit with low nodal support. Furthermore, population structure analyses indicated that despite the

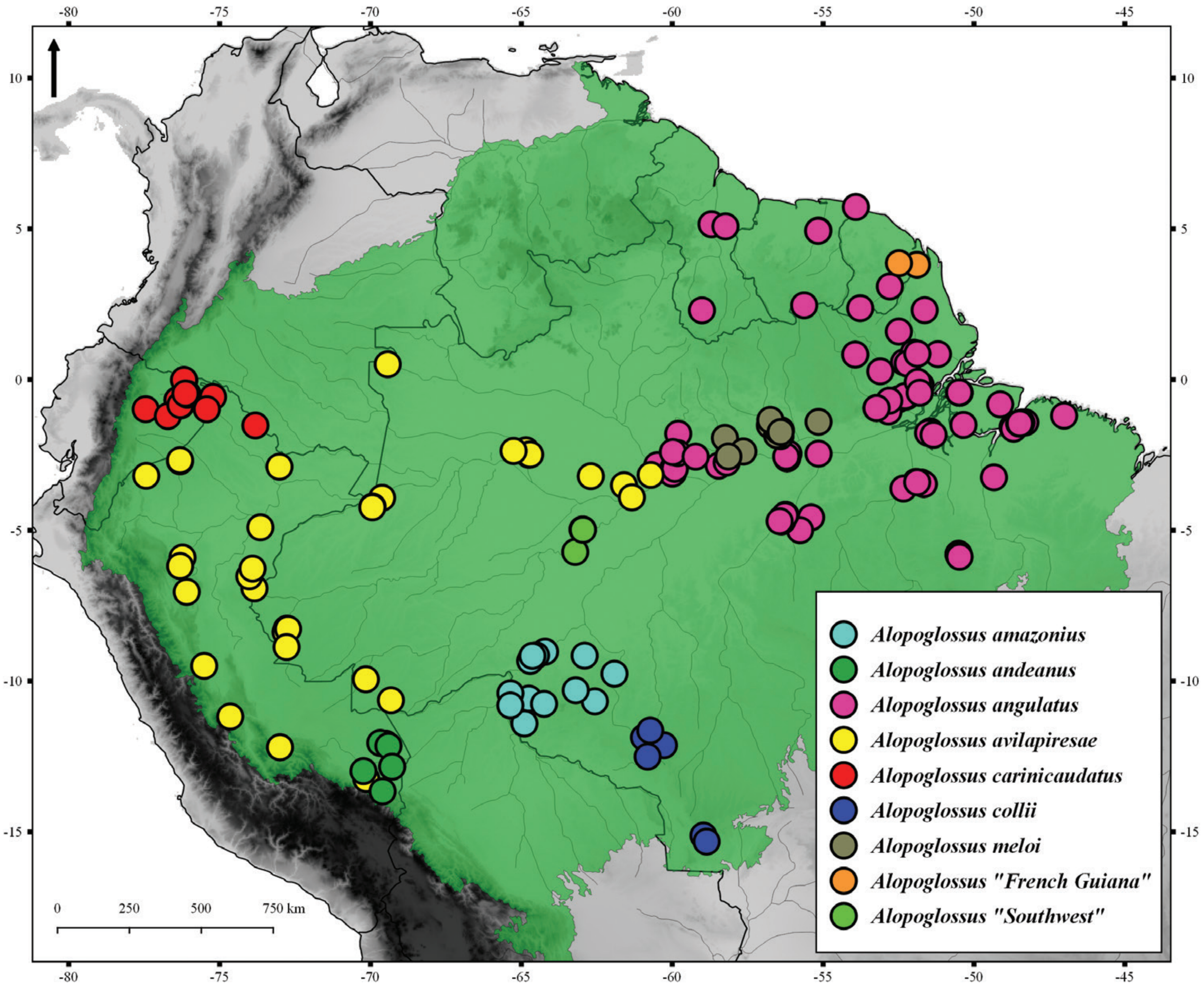

Figure 20. Distributional records of species previously recognized under *Alopoglossus angulatus*, including *Alopoglossus meloi*.

distinction between populations, certain samples still show signals of genetic mixture.

Results from species delimitation analyses overall are congruent with the pattern of spatial structure and organization obtained by morphological data. Despite this, some phylogenetic relationships were not fully resolved by the species tree. The positioning of *A. amazonius* and the candidate species of Southwestern Amazonia was uncertain owing to low support, also observed for the divergence of *A. carinicaudatus* and for the ancestral node between the clades (*A. amazonius* + Southwest lineage) + *A. collii* and *A. avilapiresae* + French Guiana lineage. The relatively low support of the species tree and disagreements between mtDNA and nuDNA gene trees might be a consequence of incomplete lineage sorting or horizontal transfer of genes between different species. Mitochondrial genes are usually more likely to fix differentiations thanks to their uniparental origin, lower effective population sizes and faster coalescent times, which avoid recombination and result in the most effective lineage sorting. Nuclear DNA, in turn, allows recombination owing to its biparental origin, which makes it harder to distinguish between lineages and enables gene transfer between organisms that are in the process of differentiation. Moreover, it also presents efficient strategies for correction of replication errors, reducing the probability of mutations and, consequently, differentiation times (Toews & Brelsford, 2012).

Speciation mechanisms typically involve the continuous accumulation of differentiations between populations initially isolated by ecological processes or by the influence of abiotic factors on the connectivity and distribution of organisms (de Queiroz, 2007).

Biological aspects intrinsic to organisms, such as generation times, dispersal potential and ecological plasticity, also interfere directly in the rates of speciation. Thus, disagreements between distinct characters can be expected during the continuous process of divergence and speciation (de Queiroz, 2007; Wang, *et al.*, 2013); likewise, lower support values on the species tree are expected (McCormack *et al.*, 2011; Werneck *et al.*, 2012). Denser taxonomic, geographical and molecular sampling is needed to clarify the phylogenetic relationships between the *A. angulatus* species complex and other *Alopoglossus* species.

Most of the divergence events within the *A. angulatus* species complex took place during the late Miocene and Miocene–Pliocene transition, which agrees with interpecific-level speciation times of other deeply divergent Amazonian lizards (Gamble *et al.*, 2008; Geurgas *et al.*, 2008; Werneck *et al.*, 2009; Miralles & Carranza, 2010). Further sampling and biogeographical analyses will help us understand the historical and/or ecological mechanisms involved in the evolutionary history of the species complex.

Here, we have provided the most comprehensive assessment to date on the molecular and morphological differentiation of the *A. angulatus* species complex. We showed that the current diversity within the genus *Alopoglossus* was underestimated in several orders, increasing the total species diversity of the genus to 14 species. We also recognized at least two differentiated lineages as putative species (under the species descriptions) and that *A. carinicaudatus* was substructured into three supported subclades, indicating that the perceived diversity of the species complex (and genus) should increase even more in the near future. Some questions regarding the evolution of *Alopoglossus* are still open, such as the phylogenetic relationships between species of the *A. angulatus* complex and other species within the genus, and the ecological and historical determinants of the Alopoglossidae biogeography.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Appendix S1. Data Availability.
Appendix S2. Referred Specimens.
Table S1. Tissue samples.
Table S2. Primers and polymerase chain reaction conditions.
Table S3. Estimates of evolutionary divergence over sequence pairs between groups. Uncorrected p-distance values are shown in the upper diagonal. Corrected distances are shown in the lower diagonal. Values in square brackets are the standard deviations.
Table S4. Results of species delimitation analyses. Species codes are as follows: Aatri, *Alopoglossus atriventris*; aE, '*A. angulatus* East'; aEc, '*A. angulatus* Ecuador'; aFG, '*A. angulatus* F. Guiana'; aGM, '*A. angulatus* Guajará Mirim'; aS, '*A. angulatus* South'; aSW, '*A. angulatus* Southwest'; aW, '*A. angulatus* West'.
Table S5. Mann–Whitney pairwise comparisons of measurements between pairs of groups. Significance (*P*-value; asterisk/bold marking) was assessed with Bonferroni correction. Measurement codes: AGL, axilla–groin length; FL, forelimb length; HD, head depth; HL, head length; HLL, hindlimb length; HW, head width; NL, neck length; ShL, shank length; SVL, snout–vent length. Group codes: E, East; Ec, Ecuador; GM, G. Mirim; S, South; W, West; Wm, Westernmost.
Table S6. Mann–Whitney pairwise comparisons of scalation characters between pairs of groups. Significance (*P*-value; asterisk/bold marking) was assessed with Bonferroni correction (except pores). Scalation codes: BtwP, granular scales between the pairs of chin shields; D, dorsals; F, lamellae under fourth finger; G, gulars; Mb, midbody; Neck, scales in transverse rows on sides of neck; Pal, palpebrals; Po, postoculars; Pores, femoral pores in males; T, lamellae under fourth toe; V, ventrals. Group codes: E, East; Ec, Ecuador; GM, G. Mirim; S, South; W, West; Wm, Westernmost.
Table S7. Summarized loadings for the first three factors in the linear discriminant analysis using measurements and only adults (SVL ≥ 40 mm). Measurement codes: AGL, axilla–groin length; FL, forelimb length; HD, head depth; HL, head length; HLL, hindlimb length; HW, head width; NL, neck length; ShL, shank length; SVL, snout–vent length.
Table S8. Summarized loadings for the first three factors in the linear discriminant analysis using scalation characters and all individuals. Scalation codes: BtwP, granular scales between the pairs of chin shields; D, dorsals; F, lamellae under fourth finger; G, gulars; Il, infralabials; Mb, midbody; Neck, scales in transverse rows on sides of neck; Pairs, pairs of chin shields; Pal, palpebrals; Po, postoculars; Sbo, suboculars; Sc, superciliaries; Sl, supralabials; So, supraoculars; T, lamellae under fourth toe; V, ventrals.

Table S9. Summarized loadings for the first three factors in the linear discriminant analysis using scalation characters and only males. Scalation codes: BtwP, granular scales between the pairs of chin shields; D, dorsals; F, lamellae under fourth finger; G, gulars; Il, infralabials; Mb, midbody; Neck, scales in transverse rows on sides of neck; Pairs, pairs of chin shields; Pal, palpebrals; Po, postoculars; Sbo, suboculars; Sc, superciliaries; Sl, supralabials; So, supraoculars; T, lamellae under fourth toe; V, ventrals.

Table S10. Summarized loadings for the first three factors in the linear discriminant analysis using scalation characters and only females. Scalation codes: BtwP, granular scales between the pairs of chin shields; D, dorsals; F, lamellae under fourth finger; G, gulars; Il, infralabials; Mb, midbody; Neck, scales in transverse rows on sides of neck; Pairs, pairs of chin shields; Pal, palpebrals; Po, postoculars; Sbo, suboculars; Sc, superciliaries; Sl, supralabials; So, supraoculars; T, lamellae under fourth toe; V, ventrals.

Figure S1. *SNCAIP* gene tree. Branch colours represent the different delimited lineages. Values close to nodes correspond to the phylogenetic support (bootstrap/posterior probability).

Figure S2. *PRLR* gene tree. Branch colours represent the different delimited lineages. Values close to nodes correspond to the phylogenetic support (bootstrap/posterior probability).

Figure S3. Population structure results of mitochondrial DNA and nuclear markers *PRLR* and *SNCAIP*. Letters below the bars represent lineages delimited of *Alopoglossus angulatus* species complex, being: A, '*A. angulatus* Ecuador'; B, '*A. angulatus* Southwest'; C, '*A. angulatus* Guajará Mirim'; D, '*A. angulatus* South'; E, '*A. angulatus* French Guiana'; F, '*A. angulatus* West'; G, '*A. angulatus* East'; H, *Alopoglossus atriventis*.

Figure S4. Comparisons of measurement data between groups of *Alopoglossus angulatus*: A, axilla–groin length (AGL); B, head depth (HD); C, head width (HW); D, head length (HL); E, neck length (NL); F, forelimb length (FL); G, hindlimb length (HLL); H, shank length (ShL); I, snout–vent length (SVL). Group codes: E, '*A. angulatus* East'; EC, '*A. angulatus* Ecuador'; GM, '*A. angulatus* G. Mirim'; S, '*A. angulatus* South'; W, '*A. angulatus* West'; WM, '*A. angulatus* Westernmost'. Significant differences between pairwise comparisons are presented by group codes below or above data.

Figure S5. Comparisons of scalation characters between groups of *Alopoglossus angulatus*: A, dorsals (D); B, ventrals (V); C, midbody (Mb); D, postoculars (Po); E, palpebrals (Pal); F, scales in transverse rows on sides of neck (Neck); G, granular scales between the pairs of chin shields (BtwP); H, gulars (G). Group codes: E, '*A. angulatus* East'; EC, '*A. angulatus* Ecuador'; GM, '*A. angulatus* G. Mirim'; S, '*A. angulatus* South'; W, '*A. angulatus* West'; WM, '*A. angulatus* Westernmost'. Significant differences between pairwise comparisons are presented by group codes below or above data.

Figure S6. Comparisons of scalation characters between groups of *Alopoglossus angulatus*: A, femoral pores in males (Pores); B, lamellae under fourth finger (F); C, lamellae under fourth toe (T). Group codes: E, '*A. angulatus* East'; EC, '*A. angulatus* Ecuador'; GM, '*A. angulatus* G. Mirim'; S, '*A. angulatus* south'; W, '*A. angulatus* West'; WM, '*A. angulatus* Westernmost'. Significant differences between pairwise comparisons are presented by group codes below or above data.

Figure S7. Discriminant analysis of scalation characters between female (A–C) and male (D–F) specimens of the *Alopoglossus angulatus* groups recognized by molecular analyses. Colours used in linear discriminant analyses are the same as those used in molecular trees: pink, '*A. angulatus* East'; light blue, '*A. angulatus* G. Mirim'; dark blue, '*A. angulatus* South'; yellow, '*A. angulatus* West'; red, '*A. angulatus* Ecuador'; green, '*A. angulatus* Westernmost' (here included, but not represented in the molecular analyses).

Figure S8. Distributional records of *Alopoglossus angulatus*. Star, neotype; black dots, specimens (morphological analyses); pink dots, tissue samples (molecular analyses).

Figure S9. Distributional records of *Alopoglossus amazonius*. Star, holotype; black dots, specimens (morphological analyses); blue dot, tissue sample (molecular analyses).

Figure S10. Distributional records of *Alopoglossus andeanus*. Star, holotype; black dots, specimens (morphological analyses).

Figure S11. Distributional records of ***Alopoglossus avilapiresae*** Star, holotype; black dots, specimens (morphological analyses); yellow dot, tissue sample (molecular analyses).

Figure S12. Distributional records of *Alopoglossus carinicaudatus*. Star, holotype; black dots, specimens (morphological analyses); red dots, tissue samples (molecular analyses).

Figure S13. Distributional records of ***Alopoglossus collii*** Star, holotype; black dots, specimens (morphological analyses); blue dots, tissue samples (molecular analyses).