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Filogenia e sistemática dos lagartos da família Alopoglosside (Squamata: Gymnophthalmoidea) baseada na análise combinada de sequências de DNA e morfologia

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Dissertação apresentada ao Programa de Pós-Graduação em Zoologia, do convênio da Universidade Federal do Pará e Museu Paraense Emílio Goeldi, como requisito parcial para obtenção do título de Mestre em Zoologia.
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Co-orientador: Prof. Dr. Marcelo José Sturaro

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Dedicado a Natalia Ferro*,*
quem foi a minha companheira nesta
viagem apesar da distância.

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SUMÁRIO

Phylogeny of the microteiid lizards of the family Alopoglossidae (Squamata: Gymnophthalmoidea) based combined analyses of DNA sequences and morphology

ABSTRACT

Alopoglossidae is a family of Neotropical lizards composed of 22 species allocated in two genera (*Alopoglossus* and *Ptychoglossus*). There is a lack of knowledge about the phylogenetic relationships and systematics of this family. Published phylogenies that include alopoglossid species had the objective to generate a hypothesis of the relationships on major groups (i.e., Gymnophthalmoidea), therefore they have very low taxon coverage within the family, and are usually based on limited character sampling. Considering these limitations, this thesis aimed to infer the phylogenetic relationship of Alopoglossidae—including all species in the family—based on combined analyses of DNA sequences and morphological characters. The genes used were the mitochondrial (12S, 16S and ND4), the nuclear (*C-mos*) and a matrix of 143 phenotypic characters from scutelation, tongue morphology, hemipenis morphology, and osteology. The data was analyzed by Maximum Parsimony optimality criteria, performing three alternative weighting schemes under Extended Implied Weighting and an equal weighting search. The generated topologies were compared in a sensitivity analysis. The preferred topology shows the paraphyly of the *Ptychoglossus* genera. *Ptychoglossus vallensis* and *Ptychoglossus billineatus* nearly related to the *Alopoglossus* clade, the Central American species *Ptychoglossus plicatus* and *Ptychoglossus myersi* as the sister clade of *Ptychoglossus* and *Alopoglossus*, and last *Ptychoglossus danieli* and *Ptychoglossus kugleri* were recovered as the sister group of all others alopoglossids. In consequence, was decided that *Ptychoglossus* is a junior synonym of *Alopoglossus*. Also, it is described the more recently discovered *Alopoglossus* species, from the pacific region of Colombia. The paper was already published at South American Journal of Herpetology (IF 0.837, Qualis = B2).

Keywords: Microteiids, systematics, new species, sensitivity analysis

Filogenia dos lagartos microteídeos da família Alopoglosside (Squamata: Gymnophthalmoidea) baseada em uma análise combinada de sequências de DNA e morfologia

RESUMO

Alopoglossidae é uma família de lagartos neotropicais composta por 22 espécies alocadas em dois gêneros (*Alopoglossus* e *Ptychoglossus*). Existe um vácuo no conhecimento sobre as relações filogenéticas e a sistemática desta família. As filogenias publicadas que incluem espécies de alopoglossídeos tiveram o objetivo de gerar uma hipótese das relações em grupos maiores (i. e., Gymnophthalmoidea), por isso têm uma amostragem taxonómica baixa dentro da família e geralmente são baseadas em amostragem limitada de caracteres. Considerando estas limitações, esta tese tem como objetivo inferir a relação filogenética de Alopoglossida—incluindo todas as espécies da família—com uma análise combinada de sequências de DNA e caracteres morfológicos. Os genes utilizados foram mitocondriais (12S, 16S e ND4), o nucleares (*C-mos*) e uma matriz de 143 caracteres fenotípicos da escamação, morfologia da língua, morfologia dos hemipênis e osteologia. Os dados foram analisados seguindo critérios de otimização de Máxima Parcimónia, executando três esquemas de pesagem alternativos Ponderação Implícita Extendida e uma busca com pesos iguais. As topologias geradas foram comparadas em uma análise de sensibilidade. A topologia preferida mostra a parafilia do gênero *Ptychoglossus*. *Ptychoglossus vallensis* e *Ptychoglossus billineatus* estão relacionados com *Alopoglossus*, as espécies centro-americanas *Ptychoglossus plicatus* e *Ptychoglossus myersi* formam o clado irmão de *Ptychoglossus* e *Alopoglossus* e finalmente *Ptychoglossus danieli* e *Ptychoglossus kugleri* foram recuperados como o grupo irmão de todos os outros alopoglossídeos. Em consequência, consideramos que *Ptychoglossus* é um sinônimo de *Alopoglossus*. Além disso, descrevemos uma espécie de *Alopoglossus*, da região do Pacífico da Colômbia. Este artigo foi publicado na revista South American Journal of Herpetology.

Palavras-chave: Microteideos, sistemática, espécie nova, análise de sensibilidade

INTRODUÇÃO GERAL

Alopoglossidae é uma família de lagartos de distribuição Neotropical que foi recentemente reconhecida (Goicoechea *et al.*, 2016). Essa família é composta por dois gêneros: *Alopoglossus* (oito espécies válidas) e *Ptychoglossus* (14 espécies validas)—conjuntamente, os dois gêneros estão distribuídos desde a Costa Rica, ao longo do norte dos Andes e por toda a Amazônia (Harris, 1994; Köhler *et al.*, 2012; Uetz and Hallerman, 2014). Alopoglossidae permanece escassamente conhecida, e a descrição de novas espécies nos últimos anos (Torres-Carvajal and Lobos, 2014; Peloso and Hernandez-Morales, 2017) sugere que a diversidade do grupo pode estar subestimada (Torres-Carvajal and Lobos, 2014). Particularmente, o estudo das relações de parentesco dentro de Alopoglossidae são poucos, e o existentes apresentam uma baixa amostragem de táxons e caracteres.

A família tem sido tradicionalmente reconhecida como uma subfamília dentro de Gymnophthalmidae (Pellegrino *et al.*, 2001; Castoe *et al.*, 2004; Pyron *et al.*, 2013), mas recentemente foi elevada ao nível de família no trabalho de Goicoechea *et al.* (2016)—baseado numa análise filogenética que usou exclusivamente dados de sequencias de DNA. A hipótese mais recente propôs Alopoglossidae como grupo irmão de Teiidae+Gymnophthalmidae, justificando assim o reconhecimento de uma nova família (Alopoglossidae).

Apesar de existir incerteza nas relações de parentescos de Alopoglossidae com Gymnophthalmidae e Teiidae, a monofilia de Alopoglossidae tem sido consistentemente recuperada, tanto com caracteres morfológicos (Presch, 1980) como por dados moleculares (Castoe *et al.*, 2004; Pyron *et al*, 2013). Porém, até agora, não existe uma análise filogenética que inclua a maioria de espécies válidas de alopoglossídeos. Além disso, as análises feitas para Gymnophthalmoidea que incorporam dados morfológicos e moleculares são muito limitadas (Presch, 1980; Hoyos, 1998; Rodrigues *et al.*, 2007, 2009; Peloso *et al.*, 2011).

O estudo mais abrangente sobre a filogenia de Alopoglossidae foi exclusivamente baseado dados moleculares, com um único gene mitocondrial (ND4) e limitado a *Alopoglossus* (Torres-Carvajal and Lobos, 2014). O banco de dados deste trabalho inclui a maioria das espécies válidas de *Alopoglossus*, exceto *Alopoglossus lehmanni* Ayala and Harris 2012 (conhecida só pelo holótipo) e a recentemente descrita *Alopoglossus embera* Peloso and Hernandez-Morales, 2017. Só uma espécie de *Ptychoglossus* fez parte desta análise, usada para enraizar a árvore, assim assumindo a monofilia de *Alopoglossus*. Por outro lado, para *Ptychoglossus*, só *Ptychoglossus brevifrontalis* Boulenger, 1912 foi incluída em alguma análise molecular publicada (Pellegrino *et al.*, 2001; Castoe *et al.*, 2004; Colli *et al.*, 2015; Goicoechea *et al.*, 2016).

Dois estudos filogenéticos geraram hipóteses estritamente baseadas em caracteres morfológicos, os quais incluem alopoglossideos. Presch (1980) analisou quatro espécies de Alopoglossidae e codificou 26 caracteres (24 osteológicos e dois miológicos). Hoyos (1998) realizou uma análise filogenética de algumas espécies colombianas de Gymnothalmidae entre as quais estava *Ptychoglossus stenolepis* (Boulenger, 1908), usando 15 caracteres, sendo nove osteológicos e seis miológicos.

Somente alguns estudos fizeram uma análise combinada de dados morfológicos e genotípicos, os quais incluem duas espécies de alopoglossideos, utilizando no máximo 77 caracteres morfológicos e 2333 pares de base (Rodrigues *et al.*, 2005, 2007, 2009; Peloso *et al.*, 2011). Porém, todos esses estudos tem uma amostragem taxonômica bastante limitada em Alopoglossidae e ajudam pouco na compreensão das relações de parentesco dentro da família, embora suportam consistentemente uma relação de grupos irmãos entre *Ptychoglossus* e *Alopoglossus*.

Como foi exposto acima, as relações filogenéticas das espécies dentro de *Alopoglossus* e *Ptychoglossus* estão escassamente conhecidas. Atualmente não existem estudos que testem as relações de parentesco de *Ptychoglossus* e a filogenia disponível para *Alopoglossus* não inclui todas as espécies válidas. Com o objetivo de testar a monofilia de Alopoglossidae e dos grupos dentro desta família foi realizada uma análise filogenética que inclui todas as espécies válidas de alopoglossideos e uma abrangente amostragem de caracteres composto por evidência genéticas e morfológica.

A incluisão de todas as espécies validas de Alopoglossidae nas análises filogenética apresentou alguns desafios. O mais importante é a impossibilidade de obter uma amostragem de caracteres completos para varias espécies. Três espécies de alopoglossídeos (*A. lehmanni*, *Ptychoglossus erylepis* Harris & Rueda 1985 and *Ptychoglossus grandisquamatus* Rueda 1985) são conhecidas somente por um único espécime, e muitas outras espécies são representadas por poucos espécimes coletados há varias décadas (Harris, 1994; Peloso and Hernandez-Morales, 2017). Isso gera uma importante repercussão na completude do banco de dados. No caso da partição genômica, não foi possível obter amostras de tecido para varias espécies, especialmente para *Ptychoglossus*. A partição de caracteres morfológicos também foi afeitada, pois não foi possível dissecar espécimes de espécies escassamente representadas nas coleções.

Durante a coleta de dados morfológicos foi identificada uma nova espécie de *Alopoglossus* do Chocó da Colômbia. Esta espécie é similar com as outras duas espécies, *Alopoglossus festae* Peracca, 1904 e *Alopoglossus viridiceps* Torres-Carvajal e Lobos, 2014, mas apresenta diferenças evidentes no padrão de coloração e de ornamentação das escamas. Neste trabalho, foi exposto a importância de estudar detalhadamente os espécimes depositados nas coleções biológicas e de fazer novas coletas científicas, já que esta espécie nova de *Alopoglossus* é conhecida de poucos espécimes, que foram mal identificados por décadas. A descrição foi publicada no periódico South American Journal of Herpetology.

REFERÊNCIAS BIBLIOGRÁFICAS

Ayala, S.C., Harris, D.M. 1984. A new microteiid lizard (*Alopoglossus*) from the pacific rainforest Of Colombia. Herpetologica. 40, 154–158.

Boulenger, G.A. 1912. Descriptions of new batrachians from the Andes of South America, preserved in the British Museum. The Annals and Magazine of Natural History. ser. 8, 185–191.

Boulenger, G.A. 1908. Descriptions of new batrachians and reptiles discovered by Mr. M. G. Palmer in south-western Colombia. The Annals and Magazine of Natural History. ser. 8, 515–522.

Castoe, T., Doan, T., Parkinson, C. 2004. Data partitions and complex models in bayesian analysis: the phylogeny of gymnophthalmid lizards. Systematic Biology. 53, 448–469.

Goicoechea, N., Frost, D.R., De la Riva, I., Pellegrino, K.C.M., Sites, J., Rodrigues, M.T., Padial. 2016. Molecular systematics of teioid lizards (Teioidea: Gymnophthalmoidea: Squamata) based on the analysis of 48 loci under tree-alignment and similatity. Cladistics. 32, 1–48.

Harris, D.M. 1994. Review of the teiid lizard genus *Ptychoglossus*. Herpetological Monographs. 8, 226–275.

Harris, D.M., Rueda, J. V. 1985. A new microteiid lizard (Sauria: *Ptychoglossus*) with exceptionally wide scales from southwestern Colombia.. Lozania. Acta Zoologica Colombiana. 48, 1–6.

Hoyos, J.M. 1998. A reapraisal of the phylogeny of lizards of the family Gymnophthalmidae

(Sauria, Scincomorpha). Revista Espeñola de Herpetologia. 12, 27–43.

Köhler, G., Diethert, H.-H., Vesely̋, M. 2012. A contribution to the knowledge of the lizard genus *Alopoglossus* (Squamata: Gymnophthalmidae). Herpetological Monographs. 26, 173–188.

Pellegrino, K.C.M., Rodrigues, M.T., Tonenaga-Yassuda, Y., Jr, J.W.S. 2001. A molecular perspective on the evolution of microteiid lizards (Squamata, Gymnophthalmidae), and a new classification for the family. Biological Journal of the Linnean Society. 74, 315–338.

Peloso, P.L. V, Hernandez-Morales, C. 2017. Description of a new species of *Alopoglossus* Boulenger , 1885 from western Colombia (Gymnophthalmoidea). South American Journal of Herpetology. 12, 89–98.

Peracca, M.G. 1904. Rettili ed amfibii. Bollettino dei Musei di Zoologia ed Anatomia comparata della R. Universita´ di Torino 19:1–41.

Presch, W. 1980. Evolutionary history of the south american microteiid lizards (Teiidae: Gymnophthalmidae). Copeia. 1980, 36–56.

Pyron, R.A., Burbrink, F.T., Wiens, J.J. 2013. A phylogeny and revised classification of Squamata, including 4161 species of lizards and snakes. BMC evolutionary biology. 13, 1–53.

Rodrigues, M.T., Cassimiro, J., Pavan, D. 2009. A new genus of microteiid lizard from the Caparaó mountains, southeastern Brazil, with a discussion of relationships among Gymnophthalminae (Squamata). American Museum Novitates. 1–28.

Rodrigues, M.T., Freire, E.M.X., Pellegrino, K.C.M., Sites Jr., J.W. 2005. Phylogenetic relationships of a new genus and species of microteiid lizard from the Atlantic forest of north-eastern Brazil (Squamata, Gymnophthalmidae). Zoological Journal of the Linnean Society. 144, 543–557. doi:10.1111/j.1096-3642.2005.00177.x

Rodrigues, M.T., Machado, K.C., Dixo, M., Verdade, V.K., Sites, J.W. 2007. A new genus of microteiid lizard from the Atlantic Forests of state of Bahia, Brazil, with a new generic name for *Colobosaura mentalis*, and a discussion of relationships among the Heterodactylini (Squamata, Gymnophthalmidae). American Museum Novitates. 1–27.

Rueda, J.V. 1985. Acerca de las especies colombianas del genero *Ptychoglossus* (Sauria: Gymnophthalmidae) con la descripción de una nueva especie. Lozania. 51, 1–12.

Torres-Carvajal, O., Lobos, S.E. 2014. A new species of *Alopoglossus* lizard (Squamata, Gymnophthalmidae) from the tropical andes, with a molecular phylogeny of the genus.

ZooKeys. 120, 105–120. doi:10.3897/zookeys.410.7401

Uetz, P., Hallerman, J. 2014. The reptile database. Disponível em: http:// www.reptile-database.org/. Acessado em Setembro de 2017.

Capítulo 1

Filogenia dos lagartos da família Alopoglossidae (Squamata: Gymnophthalmoidea) baseada na combinação de dados moleculares e morfológicos

O capítulo I desta dissertação foi elaborado e formatado conforme as normas da publicação científica *Cladistics (Qualis A2)*, as quais se encontram em anexo (Anexo I)

A species-level total evidence phylogeny of the microteiid lizard family Alopoglossidae (Squamata: Gymnophthalmoidea)

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Running title: Phylogeny of Alopoglossidae

Abstract

Alopoglossidae is a family of Neotropical lizards composed of 22 species allocated in two genera (*Alopoglossus* and *Ptychoglossus*). There is a lack of knowledge about the phylogenetic relationships and systematics of this family. Published phylogenies that include alopoglossid species have very low taxon coverage within the family, and are usually based on limited character sampling. Considering these limitations, we inferred the phylogenetic relationship of Alopoglossidae—including all species in the family—based on the combined analyses of DNA sequences and morphological characters. We used four loci (the mitochondrial *12S*, *16S* and *ND4*; the nuclear *C-mos*) and a matrix of 143 phenotypic characters from scutelation, tongue morphology, hemipenis morphology, and osteology. The dataset was analyzed with Maximum Parsimony, with four alternative weighting schemes: three under Extended Implied Weighting, and one with equal weighting—topologies were compared in a sensitivity analysis framework. Our analyses strongly support the paraphyly of *Ptychoglossus*, with *Alopoglossus* nested within it. We provide an updated classification for the subfamily, where *Ptychoglossus* Boulenger, 1890 is considered a junior synonym of *Alopoglossus* Boulenger, 1885.

Introduction

Alopoglossidae, as currently defined, is composed by two genera: *Alopoglossus* Boulenger, 1885 (eight valid nominal species) and *Ptychoglossus* Boulenger, 1890 (14 valid nominal species). These lizards are distributed from Costa Rica, through northern South America, both east and west of the Andes, and across Amazonia (Harris 1994; Köhler *et al*. 2012; Uetz & Hallerman 2014). This family was, for a long time, recognized as a sub-family of a more inclusive Gymnophthalmidae (Pellegrino *et al.*, 2001; Castoe *et al.*, 2004; Pyron *et al.*, 2013), but was recently separated from the latter and elevated to full family status by Goicoechea *et al.* (2016)—based on the results of phylogenetic analyses of DNA sequence data. Goicoechea *et al.* (2016) performed several analyses on their dataset, but based their taxonomic decision on a preferred phylogenetic hypothesis—i.e., derived from a parsimony analysis and the direct optimization (*sensu* Wheeler, 1996) of sequence characters. Based on that hypothesis, Alopoglossidae was recovered as the sister clade of Teiidae + Gymnophthalmidae, thus justifying its recognition as a separate family. Whether the intimate evolutionary relationships of Alopoglossidae lies with Gymnophthalmidae or Teiidae is still somewhat undefined, but the monophyly of Alopoglossidae has been consistently supported by both morphological (Presch, 1980) and molecular data (Castoe *et al.*, 2004; Pyron *et al*, 2013). Nevertheless, to date, there are no published phylogenetic analyses that include the majority of the valid species of Alopoglossidae, whereas phylogenetic analyses of Gymnophthalmoidea that incorporate both phenotypic and genomic data simultaneously are very limited.

The most comprehensive study on alopoglossid phylogeny was an exclusively molecular-based study which relied on a single mitochondrial gene (ND4)—the study was, however limited to *Alopoglossus* (Torres-Carvajal and Lobos, 2014). Their dataset included most recognized species of *Alopoglossus* (except *Alopoglossus lehmanni* Ayala & Harris 2012, known only from the holotype, and the recently named *Alopoglossus embera* Peloso and Hernandez-Morales, 2017). A single species of *Ptychoglossus* was included, to root the tree, therefore assuming the monophyly of *Alopoglossus*. On the other hand, for *Ptychoglossus*, only *Ptychoglossus brevifrontalis* Boulenger 1912 was ever used in any published genomic analyses (Pellegrino *et al.*, 2001; Castoe *et al.*, 2004; Colli *et al.*, 2015; Goicoechea *et al.*, 2016).

Two phylogenetic studies based strictly on morphological characters included alopoglossid species. Presch (1980) included four alopoglossid species and coded 26 characters

(24 osteological and two myological). Hoyos (1998) performed a phylogenetic analysis of some Colombian Gymnophthalmid species among which was included *Ptychoglossus stenolepis* (Boulenger, 1908) using 15 characters, nine osteological and six myological. A few additional studies combined morphological and genotypic data and which included at least two alopoglossids—using up to 77 morphological characters and 2333 base pairs of molecular data (Rodrigues *et al.*, 2005, 2007, 2009; Peloso *et al.*, 2011). All of these studies, however, included very limited taxonomic sampling of alopoglossids and help little in understanding the relationships within these taxa—although they overwhelmingly support the sister taxon relationship between the two genera.

As exposed above the phylogenetic relationships of species within both *Alopoglossus* and *Ptychoglossus* are considerably poorly understood. There are no available studies specifically designed to test the phylogenetic relationships of *Ptychoglossus* and the phylogeny available for *Alopoglossus* does not include all of the valid species. With the aim of testing both the monophyly of Alopoglossidae and of the groups within this family, we carried out a phylogenetic study including all recognized alopoglossid species and a comprehensive character sampling composed by genomic and phenomic evidences. With the phylogeny in hand, we are able to describe the morphological synapomorphies that support the different clades within the Alopoglossidae tree.

Material and methods

Our objective to include all known Alopoglossidae taxa in the phylogeny was met with significant challenges. Most importantly, the impossibility to obtain a complete character sampling for several ingroup taxa. Three alopoglossid species (*A. lehmanni*, *Ptychoglossus erylepis* Harris and Rueda 1985 and *Ptychoglossus grandisquamatus* Rueda 1985) are known from single specimens, and many other species are represented only by a handful of collection specimens, collected decades ago (Harris, 1994; Peloso and Hernandez-Morales, 2017). This had significant repercussions on the completeness of the data set. For the genomic partition, we were unable to obtain tissue samples for several species, especially within *Ptychoglossus*. The anatomical character partitions were also affected, as several internal morphology characters could not be sampled due to our inability to dissect or scan specimens of species scantly represented in collections. Nonetheless, we were able to obtain a species-level phylogeny for the group.

Taxon sampling

All currently valid species of Alopoglossidae were included in this study, except the recently described *Alopoglossus meloi* Ribeiro, 2018. The outgroup was selected following three requirements. First, the availability of sequences of the target genes in GenBank (Benson *et al.*, 2013). Secondly, the easy access to specimens that allowed for a complete sampling for the phenotypic characters. Lastly, we choose species of the outgroup aiming a diverse representation of families closely related to Alopoglossidae (i.e., Gymnophthalmidae and Teiidae). For gymnophthalmids, the following subfamilies were represented in our dataset: Cercosaurinae (*Arthrosaura kockii*, *Bachia flavecens, Cercosaura ocellata*, *Loxopholis guianensis* and *Potamites ecpleopus*); Gymnophthalminae (*Colobosaura modesta*, *Iphisa elegans* and *Tretioscincus agilis*). For Teiidae, to two of the three subfamilies were represented: Teiinae (*Ameiva ameiva*, *Cnemidophorus lemiscatus* and *Kentropyx calcarata*); Tupinambinae (*Tupinambis teguixin* and *Salvator merianae*). The tree was rooted with *Lacerta viridis* (Laurenti, 1768), based on the fact that Lacertidae is consistently recovered as the sister taxon of Gymnophthalmoidea (Conrad, 2008; Gauthier *et al.*, 2012; Pyron *et al.*, 2013; Reeder *et al.*, 2015).

For various practical reasons, not all the species have a complete sampling for all sources of evidence, but there is considerable overlap of characters among all species—especially external morphology. The complete list of taxa and the sources of character included for each of them are in Appendix 3. Detailed descriptions of sources of evidence are given below.

Genotypic evidence

Laboratory protocols. Genomic DNA was extracted and isolated from frozen and ethanol-preserved tissues (usually liver or muscle) using the Qiagen DNeasy kit, following the manufacturer's guidelines. Fragments targeted for PCR amplification and sequencing were the nuclear DNA (nDNA) *Oocyte Maturation Factor Gene* (*c-mos*), and the mitochondrial DNA (mtDNA) loci *NADH Dehydrogenase Subunit IV* (ND4), and mitochondrial *rRNA subunits 12S* (12S) and *16S* (16S). The primers used for PCR amplification and sequencing have been largely used in lizard phylogenetic studies, including Alopoglossidae (Kocher *et al.*, 1989; Arevalo *et al.*, 1994; Saint *et al.*, 1998; Pellegrino *et al.*, 2001)—PCR primers and conditions are listed in the Table 1. The PCR products were sequencing in both directions using an ABI automated sequencer at Museu Paraense Emílio Goeldi. The sequences were checked and edited in Geneious, version 9 (Kearse *et al.*, 2012).

Genotypic sampling. We had access to tissue samples from four *Alopoglossus* and seven *Ptychoglossus* species, i.e., 50% of the diversity within Alopoglossidae. Our data was complemented with sequences of 16S and ND4 of *Alopoglossus buckleyi* (O'Shaughnessy, 1881), *Alopoglossus copii* Boulenger (1885), *Alopoglossus festae* Peracca, 1904 and *Alopoglossus viridiceps* Torres-Carvajal and Lobos, 2014 deposited by Torres-Carvajal and Lobos (2014) and Arteaga *et al.* (2016) in GenBank (Benson *et al.*, 2013). Therefore 14 of 22 ingroup species have genotypic evidence available.

Morphological evidence

The morphological dataset aimed to accommodate the variation within Alopoglossidae, but also accounted for variation within the whole Gymnophthalmoidea. We used the program Mesquite, version 3.4 (Maddison and Maddison, 2010) to construct the morphological character sets. We coded a total of 143 morphological characters, which can be grouped into seven different character sets, depending on the sources of information, as follows: five characters from tongue morphology, 68 from scutellation, 10 from hemipenis, 39 from cranium, five from mandible, eight of post-cranium and eight from the hyoid apparatus. The complete list of characters, including a brief description and delimitation of putatively homologous character states are listed in Appendix 1.

Tongue characters were largely coded based on the morphological studies of Boulenger (1885) and Harris (1985), whereas they were scored on specimens preserved with the mouth opened—in rare cases, when permitted, the tongue was extracted and analyzed separately. For *Alopoglossus viridiceps*, *Ptychoglossus kugleri*, *Ptychoglossus romalaeos* we did not have access to tongue morphology. The scutellation was coded following the nomenclature proposed by Harris (1994) and was scored for all the alopoglossid taxa.

Hemipenial characters were coded from the direct observation of the organ. We used some of the hemipenial characters and terminology defined by Nunes (2011: Unpublished PhD

Thesis). For some species where material was not immediately available, we prepared hemipenes following the protocols of Pesantes (1994) and Zaher & Prudente (2003).

Two techniques were used to investigate and code characters related to the osteological partition. For some specimens, we used high-resolution computed tomography scan (CT scans) whereas for others we used clear and double staining technique. We obtained CT scans of *A. angulatus*, *A. buckleyi*, *A. embera*, *A. festae*, *P. danieli*, *P. plicatus* and *P. vallensis* in GE Pheonix Vtome Xs Micro Computed Tomography machines. Most were done at the Microscopy and Image Facility (MIF) at the American Museum of Natural History, whereas the scan of *A. lehmanni* was performed at the Nanoscale Research Facility at the University of Florida. Compilation of the individual x-rays, and image 3D visualizations were done in VGStudio MAX version 2.2 (Volume Graphics, Heidelberg, Germany). TIFF images from 3D rendering were used herein for descriptions and comparisons. Osteology of six taxa (*A. angulatus*, *A. atriventris*, *P. bicolor*, *P. brevifrontalis*, *P. vallensis* and *P. stenolepis*) was analysed from cleared and double stained specimens. For newly prepared specimens, we followed the protocol in Maisano (2008).

Table 1. List of primers and summary of PCR conditions used in this study.

				PCR conditions			
Gene	Primer	Primer sequence (5'–3)	Reference	denaturation	annealing	extension	cycles
12S	12Sa	CTG GGA TTA GAT ACC CCA CTA	modified from Kocher *et al.* (1989)	94°C(1:00)	52°C(1:00)	72°C(1:00)	40
	12Sb	TGA GGA GGG TGA CGG GCG GT	modified from Kocher *et al.* (1989)				
16S	16SF	CTG TTT ACC AAA AAC ATM RCC TYT AGC	Pellegrino *et al* (2001)	94°C(1:00)	53°C(1:00)	72°C(1:00)	40
	16SR	TAG ATA GAA ACC GAC CTG GAT T	Pellegrino *et al* (2001)				
ND4	ND4F	CAC CTA TGA CTA CCA AAA GCT CAT GTA GAA GC	Arévalo *et al.*(1994)	94°C(1:00)	53°C(1:00)	72°C(1:00)	40
	ND4R	CAT TAC TTT TAC TTG GAT TTG CAC CA	Arévalo *et al* (1994)				
c-mos	G73	GCG GTA AAG CAG GTG AAG AAA	Saint *et al.* (1998)	94°C(1:00)	53°C(1:00)	72°C(1:00)	40
	G74	TGA GCA TCC AAA GTC TCC AAT C	Saint *et al.* (1998)				

Phylogenetic analysis

Sequence homology was established automatically for each targeted gene using multiple sequence alignment (MSA) in MAFFT (Katoh *et al.*, 2005). We performed analyses under the parsimony (PAR) optimality criteria, using extended implied weighting (EIW; Goloboff, 1993, 2014) and the more widely used equally weighted parsimony—all analyses performed in TNT (Goloboff *et al.*, 2008). Tree searches were performed with ten replicates, with a minimum of ten hits under the *xmult* command, which implements a variety of tree search algorithms—Random Addition Sequences (RAS), Tree Bisection and Reconnection branch swapping (TBR), Parsimony Ratchet (Nixon, 1999), Tree Fusing (Goloboff, 1999), Sectorial Searches (Goloboff, 1999), and Tree Drifting (Goloboff, 1999).

EIW analyses weights characters, during tree search, according to their homoplasy, assigning greater weights to the hierarchic characters and down-weighting homoplastic characters. Given that different sources of characters can have different levels of homoplasy, the data set was divided in four partitions to better accommodate such variation—dataset was split into a morphological set, an rRNA set, where the 12S and 16S markers were concatenated in SequenceMatrix (Vaidaya *et al.*, 2011), and two for the protein coding sets, ND4 and *C-mos* respectively. To access the effect of the weighting scheme on the topologies, we tested four alternative approaches: (i) weighting each single character separately (SEP); (ii) in the morphological partition each character weighted independently, each ribosomal marker and the 1st, 2nd and 3rd positions for protein coding genes weighted collectively (WC); (iii) same partition scheme as ii but without extrapolating the average homoplasy to the missing entries (NEM); and (iv) equal weighted (EQ).

The EIW needs a reference constant value (*k*), whereas the lowest the *k*, the stronger the down-weighting on the homoplastic characters will be. Choosing the optimal *k* value remains as one the most critical steps in EIW, due to different *k* values can generating different topologies. We follow the Mirande's (2009) strategy, where *k* values implemented are those that have an average character fit of 50, 54, 58, 62, 66, 70, 74, 78, 82, 86 and 90% of the fit of a perfectly hierarchic one (see also Reemer & Ståhls, 2013). With this we can avoid the artificially biased impression of stability generated towards higher values when regular distributed *k* values are used. This also permits to avoid the overweighting because the stronger *k* value implemented is that in which the “average” character have 50% of the weight of a perfectly hierarchical one. In the case that more than a tree was found for a *k* value, a strict consensus was calculated.

The choosing criterion to select among generated trees was stability and support. For to measure the stability was calculated using the SPR distance (Goloboff, 2008), considering as the most stable trees those that have the lowest average differences in relation with the remains trees. Nodal support was measured with bootstrapping, with 1000 replicates for each *k* value, with the best-supported tree being that with the greater average bootstrap support. Once the optimal tree was selected for each scheme, the same procedure based on stability and support was implemented for to choose among the these and an equal weighted tree.

All these trees were compared with the MPS’s tree using the software YBYRÁ (Machado, 2015), which allows for a visual congruence analysis (through Navajo Rug plots) among all trees generated for the study.

Results

Phylogenetic analyses

For the EIW analysis, we obtained that in the SEP scheme the interval of the most stable trees was 58–78% of average character fit, with an average SPR distance of 0.95758 and the optimal *k* value among this interval was 3.72, due to the greater average nodal support (56.3). In the case of the WC scheme, the interval was 74–82% that had tha same averange SPR distance of SEP scheme and the optimal *k* value was 5.96 that generated a tree with 53 of average nodal support. Last, in the NEM scheme the optimal *k* value was 4.64 (52.4 of average nodal support) that belong to the 70–78% interval of average character fit. See Table 2 for a resume of these parameters.

When the stability of the selected weighted and the unweighted trees was explored, we found that the more stable tree was the one generated by the WC weighted scheme that has an average SPR distance of 0.9495 in relation to the other two weighted trees and the unweighted one. Although SEP scheme tree has the greater average nodal support (Table 2), its average SPR distance is the lowest (0.8788). We gave larger importance to stability, hence, the WC tree was preferred.

Table 2. Resume of the parameters used for to choose among the different *k* values in the phylogenetic analyzes of Alopoglossidae, based on molecular and morphological data.

Scheme	**Interval of the more stable trees**	**Average SPR distance**	**Optimal *k* value**	**Fit**	**Average nodal support**	**Total steps**
SEP	58–78%	0.95758	3.72	376.24065	56.3	5458
WC	74–82%	0.95758	5.96	382.51760	53.0	5454
NEM	70–78%	0.96061	4.64	471.36637	52.4	5454
EQ	Not applicable	Not applicable	Not applicable	Not applicable	51.1	5464

A visual congruence analysis of the topologies by means Navajo Rug plots, using as a reference the WC tree, is presented in the Figure 1, whereas each single tree is shown separately in Figure 2. The congruence analysis shows that the WC and the NEM schemes generated the same topology, but incongruences appear when these are compared with SEP and EQ schemes. In the case of EQ, its topology is very similar to the preferred scheme. Within the in-group the two incongruent nodes of the EQ scheme are not because the members of that node change, but due to that nodes are collapsed (Fig. 2D). In the out-group, EQ and WC have incongruences within Gymnophthalmidae. For EQ, Gymnophthalminae (*Colobosaura modesta*, *Iphisa elegans* and *Tretioscincus agilis*) is sister group of *Bachia flavescens*, *Cercosaura ocellata* and *Potamites ecpleopus*. For WC, it is sister group of *Arthrosaura kockii* and *Loxopholis guianense*. In both cases Gymnophthalmidae is maintained monophyletic, but both are incongruent with the recently accepted relationship of Gymnopthalmidae (Goicoechea *et al.*, 2016). We realized that our out-group sampling is not enough for to decide some update on wide accepted inner relationship of Gymnophthalmidae, our comments on this topic are only to show the topological variants among the different implemented schemes.

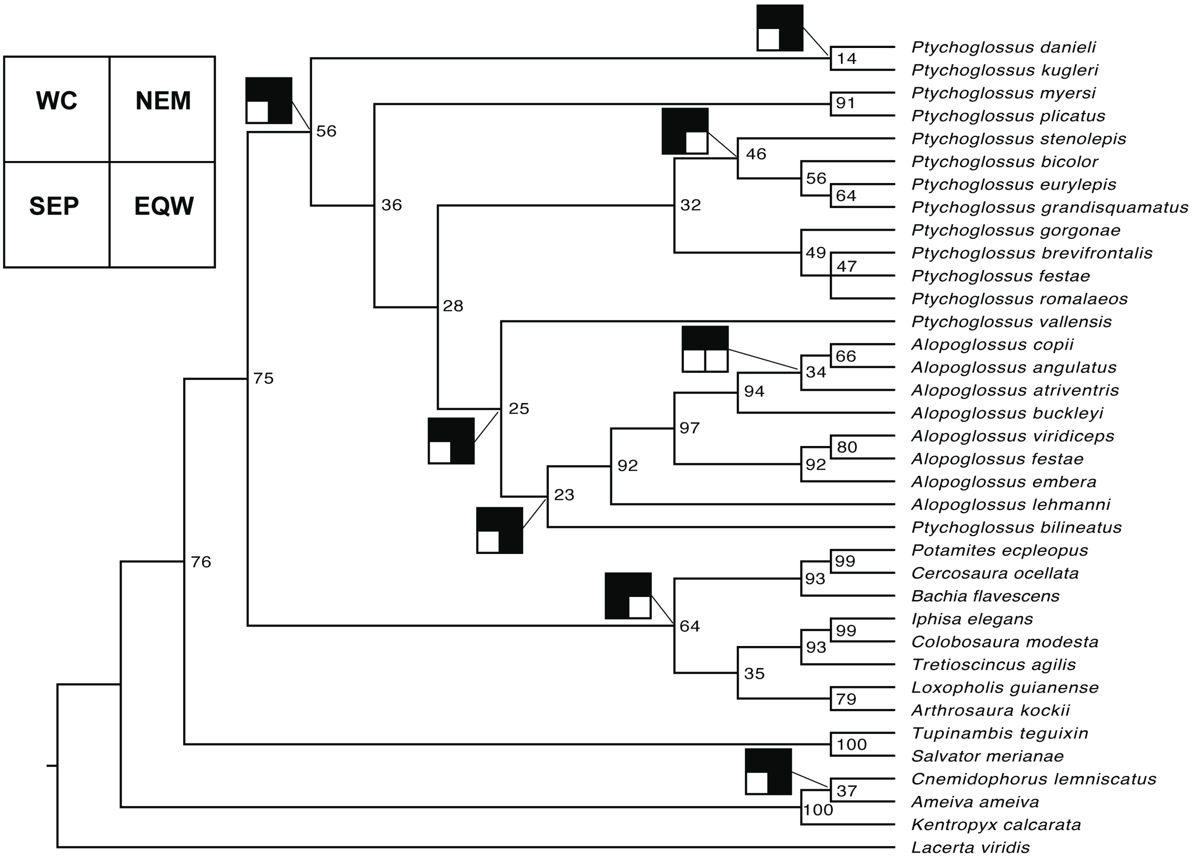

Figure 1. The phylogenetic relationship within Alopoglossidae, based on molecular and morphological data, showed by preferred topology (WC scheme). Navajo Rug plots indicate incongruence with respect the alternative weighting schemes.

Phylogenetic relationships of Alopoglossidae

Our preferred tree was the generated by the WC scheme (see methods for justification). In this tree *Alopoglossus* is recovered as monophyletic (albeit nested in a paraphyletic *Ptychoglossus*). *Alopoglossus angulatus*, *A. copii* and its sister taxon *A. atriventris* form the sister clade of *A. festae*, *A. viridiceps* and *A. embera. Alopoglossus lehmanni* is the sister taxon of all other *Alopoglossus* (Fig. 1). On the other hand, *Ptychoglossus* is recovered as paraphyletic. *Ptychoglossus bilineatus* is the sister taxon of the *Alopoglossus* genera and in turn *P. vallensis* is the sister taxon of *Alopoglossus* + *P. bilineatus.* The majority of *Ptychoglossus* (*P. bicolor*, *P. brevifrontalis*, *P. eurylepis*, *P. festae*, *P. gorgonae*, *P. grandisquamatus*, *P. romaleos,* and *P. stenolepis*) form the sister group of the clade described before (Fig. 1). *Ptychoglossus myersi* and

P. plicatus are grouped in another clade. And finally, *P. danieli* and *P. kugleri* are the sister group of all others alopoglossids.

As mentioned above, SEP scheme was the most divergent (Fig. 2). In this, *Ptychoglossus kugleri* is recovered as the sister group of Gymnophthalmidae+Alopoglossidae. Moreover *Ptychoglossus vallensis* and *Ptychoglossus bilineatus* are not nearly related with *Alopoglossus* but with *Ptychoglossus.* In all schemes Teiidae is recovered as non-monophyletic.

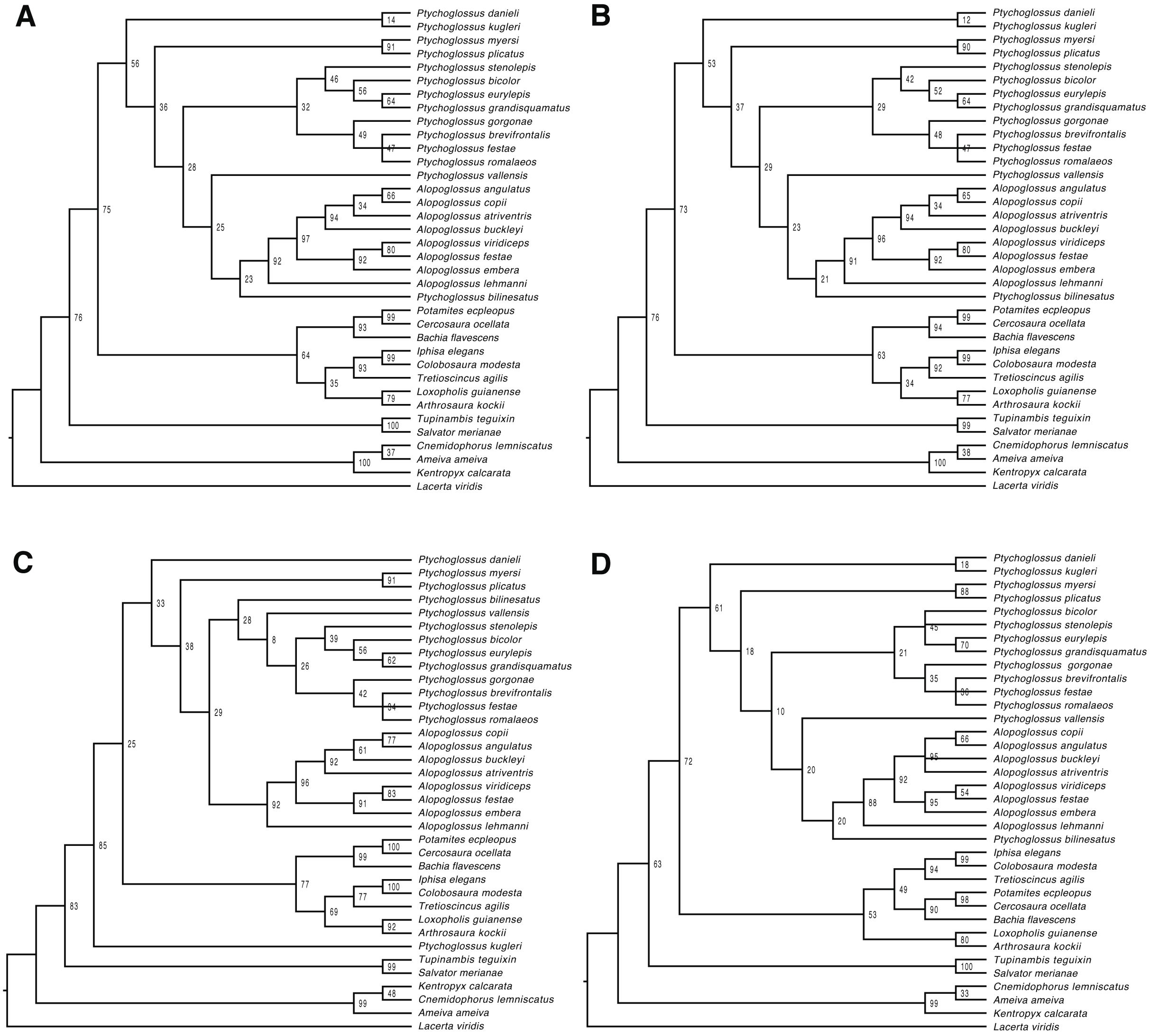

Figure 2. Selected trees generated by the four weighting schemes: (A) WC, (B) NEM, (C) SEP and (D) EQ.

Discussion

Teiidae was recovered as paraphyletic in all of the analyses, with Teiinae (*Ameiva ameiva*, *Cnemidophorus lemiscatus* and *Kentropyx calcarata*) and Tupinambinae (*Tupinambis teguixin* and *Salvator merianae*) recovered as monophyletic with high support, whereas the two subfamilies are not related to each other. These results differ from previews studies, that recovered this family as monophyletic (Goicoechea *et al.*, 2016). Our sampling is smaller than previous studies and the study was not designed to test the monophyly of Teiidae. We, therefore, refrain from commenting further on the taxonomy of the outgroup beyond a brief note that if these are to be recognized as separate taxa, the names Teiidae Gray, 1827 and Tupinambidae Gray, 1825 are applicable to the aforementioned clades.

The need for an updates taxonomy of Alopoglossidae

Our results strongly support the paraphyly of *Ptychoglossus*. Species of the genus are distributed in four different clades, with monophyletic *Alopoglossus* nested within a clade containing *P. vallensis* and *P. bilineatus* (Fig. 1). Given this context, there is a necessity of a reappraisal of the taxonomic arrangement in Alopoglossidae. Given the position of *Alopoglossus* with respect to *Ptychoglossus*, few options are available—most of which would result in a complete overhaul of the taxonomy and the creation of several small new genera. We do not favor such drastic changes and, therefore, opted for a simpler solution to the problem. We consider *Ptychoglossus* Boulenger, 1890 as a junior synonym of *Alopoglossus* Boulenger, 1885, and transfer all nominal *Ptychoglossus* species to *Alopoglossus.* We preferred this conservative arrangement instead of, for example, the alternative option of splitting *Ptychoglossus* in multiple genera and transferring *P. bilineatus* and *P. vallensis* to *Alopoglossus.* If we decided to split *Ptychoglossus*, will be necessary to create two new genera, one to include *P. myersi* and *P. plicatus*, and another for *P. danieli* and *P. kugleri* (Fig. 1). This option is inconvenient for a series of reasons. Collectively, *Alopoglossus* + *Ptychoglossus* are easily diagnosable, whereas splitting this clade into multiple genera would result in smaller but undiagnosable group.

This arrangement produces a secondary homonymy between *Ptychoglossus festae* (Peracca 1896) (senior homonym) and *Alopoglossus festae* Peracca 1904 (junior homonym). To solve this situation, a new name must be given for the junior synonym—we propose the name *Alopolossus [[harrisi]] nom. nov.* Etymology—the name is given in honor of Dennis Harris, for his outstanding contribution to the taxonomy of Alopoglossidae. Harris was an author in the descriptions of almost one third of the known alopoglossid species (seven out of 22; Ayala and Harris, 1984; Harris and Rueda, 1985; Harris, 1994)

In light of the new proposed generic arrangement for the family, below we provide an updated diagnosis for Alopoglossidae. A summary of the new taxonomy is given in the Table 4.

Alopoglossus Boulenger, 1885

Type species: *Alopoglossus angulatus* (Linnaeus, 1758)

Diagnosis: *Alopoglossus* (=Alopoglossidae) can be distinguished from other gymnophthalmoids by having: (i) the tongue entirely covered of oblique plicae (only partially covered of oblique plicae or covered with papillae like scales in other gymnophthalmoids); (ii) *cristae cranii* of the frontal forming a tubular structure (flanged in Gymnophthalmus and Heterodactylus); (iii) presence of postorbitofrontal (also present in *Calyptommatus*, *Dryadosaura*, *Anotosaura*, *Colobosauroides*, *Ameiva*, *Cnemidophorus*, *Dicrodon*, *Dracaena*, *Kentropyx* and *Teius*); (iv) borders of the palatine process are curved divergently and its distal tip is truncated—in other Gymnophthalmoidea, this process has convergent or parallel borders (Hernández-Morales *et al.*, In press); and hemipenis without mineralized structures (Teiidae shows the same condition but most gymnophthalmid have mineralized structures in its hemipenis).

Table 4. Taxonomic updates resulting from the new generic arrangement of Alopoglossidae.

Alopoglosus angulatus (Linnaeus, 1758)
Alopoglossus atriventris Duellman, 1973
Alopoglossus bicolor (Werner, 1916), **new comb.**
Alopoglossus bilineatus (Boulenger, 1890), **new comb.**
Alopoglossus brevifrontalis (Boulenger, 1912) , **new comb.**
Alopoglossus buckleyi (O'Shaughnessy, 1881)
Alopoglossus copii Boulenger, 1885
Alopoglossus danieli (Harris, 1994), **new comb.**
Alopoglossus embera Peloso and Hernandez-Morales, 2017
Alopoglossus eurylepis (Harris and Rueda, 1985), **new comb.**
Alopoglossus festae (Peracca, 1896)
Alopoglossus gorgonae (Harris, 1994), **new comb.**
Alopoglossus grandisquamatus (Rueda, 1985), **new comb.**
Alopoglossus kugleri (Roux, 1927), **new comb.**
Alopoglossus lehmanni Ayala and Harris, 1984
Alopoglossus myersi (Harris, 1994), **new comb.**
Alopoglossus harrisi nom. nov.
Alopoglossus plicatus (Taylor, 1949), **new comb.**
Alopoglossus romaleos (Harris, 1994), **new comb.**
Alopoglossus stenolepis (Boulenger, 1908), **new comb.**
Alopoglossus vallensis (Harris, 1994), **new comb.**
Alopoglossus viridiceps Torres-Carvajal and Lobos, 2014

Biogeographic Comments

Very little is known about the biogeography of Alopoglossidae, and our objective here is to provide comments on the most striking biogeographic patterns that can be inferred from our analyses. We do not intend to provide a definitive account of the biogeography of the group, but limit our observations to obvious geographic patterns.

The vast majority of the known species in Alopoglossidae are found west of the Andes (Trans-Andean), with a few noteworthy exceptions. *Alopoglossus brevifrontalis* is exclusively Cis-Andean and is found across most of the Amazon Basin (Peloso and Avila-Pires, 2014). *Alopoglossus bicolor* is restricted to the eastern slope of the Andes, in the upper Rio Magdalena valley. Alopoglossus (*Ptychoglossus festae*) is found both on the western and eastern slopes of the Andes—Harris (1994) did mention some minor morphological differences among these two populations, but nonetheless considered them to be conspecific.

Torres-Carvajal and Lobos (2014) suggested a phylogenetic split between Cis-Andean and Trans-Andean taxa—their work considered only species then assigned to *Alopoglossus*, and did not include the Trans-Andean *A. lehmani*. Morales and Peloso (2017) named *A. embera* from the western slopes of the Andes but did not test its phylogenetic position. The authors, however, speculated a close relationship between *A. embera, A. harrisi* (as *A, festae*) and *A. viridiceps* (Morales and Peloso, 2017)—our phylogenetic analysis support this relationship. Our analyses do not fully support a split between Cis-Andean and Trans-Andean, even if only the species formerly included in *Alopoglossus* are included. Although the Cis-Andean clade including (*A. embera, A. harrisi and A. viridiceps* is monophyletic, and sister of the Trans-Andean clade including *A. angulatus, A. atriventris, A. buckleyi* and *A. copii,* collectively these two clades are the sister species of *A. lehmani* (Trans-Andean).

Concluding remarks

This study is a big progress in our understanding of phylogenetic relationships within Alopoglossidae—it is the first phylogenetic study to include all valid species of this family. However, we also detected important gaps that will need to be addressed in the future. The position of Alopoglossidae within Gymnophthalmoidea remains contentious—and so does the monophyly of Tupinambinae, as currently defined. Moreover, future studies should improve on the sampling used here. It will be important to collect tissue samples for the species for which we do not have genomic data available, and further complete the morphological partition. Our morphological matrix of 143 characters was constructed based in previous data, but a large number of new characters were proposed. This matrix has the potential to be a baseline for future phylogenetic studies that incorporate morphological data not only on Alopoglossidae, but for the entire Gymnophthalmoidea.

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References

Arevalo, E.S., Davis, S.K., Sites, J.W. 1994. Mitochondrial DNA sequence divergence and phylogenetic relationships among eight chromosome races of the *Sceloporus grammicus* complex (Phrynosomatidae) in central Mexico. Systematic Biology. 43, 387–418.

Arteaga, A., Pyron, R.A., Pe, N., Romero-barreto, P., Culebras, J., Bustamante, L., Yanez-Munuz, M., Guayasamin, J.M. 2016. Comparative phylogeography reveals cryptic diversity and repeated patterns of cladogenesis for amphibians and reptiles in northwestern Ecuador. PloS one. 11, e0151746.

Ayala, S.C., Harris, D.M. 1984. A new microteiid lizard (*Alopoglossus*) from the pacific rainforest Of Colombia. Herpetologica. 40, 154–158.

Benson, D.A., Cavanaugh, M., Clark, K., Karsch-Mizrachi, I., Lipman, D.J., Ostell, J., Sayers, E.W. 2013. GenBank. Nucleic Acids Research. 41, 36–42.

Boulenger, G.A. 1912. Descriptions of new batrachians from the Andes of South America, preserved in the British Museum.. The Annals and Magazine of Natural History. ser. 8, 185–191.

Boulenger, G.A. 1908. Descriptions of new batrachians and reptiles discovered by Mr. M. G. Palmer in south-western Colombia. The Annals and Magazine of Natural History. ser. 8, 515–522.

Boulenger, G.A. 1890. First report on additions to the lizard collection in the British Museum (Natural History). Proceedings of the Zoological society of london. 1890, 77–86.

Boulenger, G.A. 1885. Catalogue of the Lizards in the British Museum (Natural History). II. Iguanidae, Xenosauridae, Zonuridae, Anguidae, Anniellidae, Helodermatidae, Varanidae, Xantusiidae, Teiidae, Amphisbaenidae. Taylor & Francis, London, United Kingdon.

Castoe, T., Doan, T., Parkinson, C. 2004. Data partitions and complex models in bayesian analysis: the phylogeny of gymnophthalmid lizards. Systematic Biology. 53, 448–469.

Colli, G.R., Hoogmoed, M.S., Cannatella, D.C., Cassimiro, J., Oliveira, J.G., Ghellere, J.M., Nunes, P.M.S., Pellegrino, K., Salerno, P., Marques, S. de S., Rodrigues, M.T. 2015. Description and phylogenetic relationships of a new genus and two new species of lizards from Brazilian Amazonia , with nomenclatural comments on the taxonomy of Gymnophthalmidae (Reptilia: Squamata). Zootaxa. 4000, 401–427.

Conrad, J.L. 2008. Phylogeny and systematics of Squamata (Reptilia) based on morphology.

Bulletin of the American Museum of Natural History. 310, 1–182.

Duellman, W.E. 1973. Descriptions of New Lizards from the Upper Amazon Basin. Herpetologica. 29, 228–231.

Gauthier, J.A., Kearney, M., Maisano, J.A., Rieppel, O., Behlke, A.D.B. 2012. Assembling the Squamate tree of life : perspectives from the phenotype and the fossil record. Peabody Museum of Natural History at Yale University. 53, 3–308.

Goicoechea, N., Frost, D.R., De la Riva, I., Pellegrino, K.C.M., Sites, J., Rodrigues, M.T., Padial. 2016. Molecular systematics of teioid lizards (Teioidea: Gymnophthalmoidea: Squamata) based on the analysis of 48 loci under tree-alignment and similatity. Cladistics. 32, 1–48.

Goloboff, P.A. 2014. Extended implied weighting. Cladistics. 30, 260–272.

Goloboff, P.A. 2008. Calculating SPR distances between trees. Cladistics. 24, 591–597.

Goloboff, P.A. 1993. Estimating character weights during tree search. Cladistics. 9, 83–91.

Goloboff, P.A., Farris, J.S., Nixon, K.C. 2008. TNT, a free program for phylogenetic analysis.. Cladistics. 24, 774–786.

Gray, J.E. 1827. Synopsis of the genera of saurian reptiles, in which some new genera are indicated, and the others reviewed by actual examination. Philadelphia Magazine. 2, 54–58.

Gray, J.E. 1825. A synopsis of the genera of reptiles and amphibians, with a description of some new species. Annals of Philosophy (Thompson). 10, 193–217.

Harris, D.M. 1994. Review of the teiid lizard genus *Ptychoglossus*. Herpetological Monographs. 8, 226–275.

Harris, D.M. 1985. Infralingual plicae: support for Boulenger's Teiidae (Sauria). Copeia. 1985, 560–565.

Harris, D.M., Rueda, J. V. 1985. A new microteiid lizard (Sauria: *Ptychoglossus*) with exceptionally wide scales from southwestern Colombia.. Lozania. Acta Zoologica Colombiana. 48, 1–6.

Hernandez-Morales, C., Peloso, P.L. V., Bolivar-G, W., Daza, J.D. n.d. Cranial anatomy of the colombian endemic lizard *Ptychoglossus vallensis* (Alopoglossidae), a comparative treatise within Gymnophthalmoidea, a megadiverse Neotropical clade. The Anatomical Record.

Hoyos, J.M. 1998. A reapraisal of the phylogeny of lizards of the family Gymnophthalmidae (Sauria, Scincomorpha). Revista Espeñola de Herpetologia. 12, 27–43.

Katoh, K., Kuma, K., Toh, H., Miyata, T. 2005. MAFFT, a novel method for rapid multiple sequence alignment based on fast Fourier transform. Nucleic Acids Research. 30, 3059–3066.

Kearse, M., Moir, R., Wilson, A., Stones-Havas, S., Cheung, M., Sturrock, S., Buxton, S., Cooper, A., Markowitz, S., Duran, C., Thierer, T., Ashton, B., Meintjes, P., Drummond, A. 2012. Geneious Basic: An integrated and extendable desktop software platform for the organization and analysis of sequence data. Bioinformatics. 28, 1647–1649. doi:10.1093/bioinformatics/bts199

Kocher, T.D., Thomas, W.K., Meyer, A., Edwars, S. V., Paabo, S., Villablanca, F.X., Wilson, A.C. 1989. Dynamics of mitochondrial DNA evolution in animals: Amplification and sequencing with conserved primers. Proceedings of the National Academy of Sciences. 86, 6196– 6200.

Köhler, G., Diethert, H.-H., Veselý, M. 2012. A contribution to the knowledge of the lizard genus *Alopoglossus* (Squamata: Gymnophthalmidae). Herpetological Monographs. 26, 173–188.

Laurenti, J.N. 1768. Specimen medicum, exhibens synopsin reptilium emendatam cum experimentis circa venena et antidota reptilium austracorum, quod authoritate et consensu, Thomae, 2. ed. Vienna, Joan.

Linnaeus, C. 1758. Systema Naturae per Regna Tria Naturae, Secundum Classes, Ordines, Genera, Species, cum Characteribus, Differentiis, Synonymis, Locis. Ed. 10, Vol. 1. Laurentii Salvii, Sweden.

Machado, D.J. 2015. YBYRÁ facilitates comparison of large phylogenetic trees. BMC Bioinformatics. 16.

MacLean, R.R. 1974. Feeding and locomotor mechanisms of teiid lizards: functional morphology and evolution. Papéis Avulsos de Zoologia. Museu de Zoologia da Universidade de Sao Paulo. 27, 179–213.

Maddison, W.P., Maddison, D.R. 2010. Mesquite: a modular system for evolutionary analysis, version 3.04. http://mesquite- project.org.

Maisano, J.A. 2008. A protocol for clearing and double-staining squamate specimenes. Herpetological Review. 39, 52–54.

Mirande, J. 2009. Weighted parsimony phylogeny of the family Characidae (Teleostei: Characiformes). Cladistics. 25, 574–613.

Nunes, P.M.S. 2011. Morfologia hemipenial dos lagartos microteídeos e suas implicações nas relações filogenéticas da familia Gymnophthalmidae (Teiioidea: Squamata) Volumes 1 and 2. Unpubl. PhD Thesis. Universidade de São Paulo.

O'Shaughnessy, A.W.E. 1881. An account of the collection of lizards made by Mr. Buckley in Ecuador, and now in the British Museum, with descriptions of the new species. Proceedings of the Zoological society of london. 227–245.

Pellegrino, K.C.M., Rodrigues, M.T., Yonenaga-Yassuda, Y., Sites, J.W.J. 2001. A molecular perspective on the evolution of microteiid lizards (Squamata, Gymnophthalmidae), and a new classification for the family. Biological Journal of the Linnean Society. 74, 315–338.

Peloso, P.L., Pellegrino, K.C.M., Rodrigues, M.T., Ávila-Pires, T.C.S. 2011. Description and phylogenetic relationships of a new genus and species of lizard (Squamata, Gymnophthalmidae) from the Amazonian rainforest of northern Brazil. American Museum Novitates. 3713, 1–24.

Peloso, P.L. V, Hernandez-Morales, C. 2017. Description of a new species of *Alopoglossus* Boulenger , 1885 from western Colombia (Gymnophthalmoidea). South American Journal of Herpetology. 12, 89–98.

Peracca, M.G. 1904. Rettili ed amfibii. Bollettino dei Musei di Zoologia ed Anatomia comparata della R. Universita´ di Torino 19:1–41.

Peracca, M.G. 1896. Descrizione di un nuevo genere e di una nuova specie di Teiidae raccolta nel Darien dal dott. E. Festa.. Boll. Mus. Zool. Anat. Comp. Univ. Torino. 11, 1–4.

Pesantes, O.S. 1994. A method for preparing the hemipenis of preserved snakes. Journal of Herpetology. 28, 93–95.

Presch, W. 1980. Evolutionary history of the south american microteiid lizards (Teiidae: Gymnophthalmidae). Copeia. 1980, 36–56.

Pyron, R.A., Burbrink, F.T., Wiens, J.J. 2013. A phylogeny and revised classification of Squamata, including 4161 species of lizards and snakes. BMC evolutionary biology. 13, 1–53. doi:10.1186/1471-2148-13-93

Reeder, T.W., Townsend, T.M., Mulcahy, D.G., Noonan, B.P., Wood, P.L., Sites, J.W., Wiens, J.J. 2015. Integrated analyses resolve conflicts over squamate reptile phylogeny and reveal unexpected placements for fossil taxa. PloS one. 10, 1–22. doi:10.1371/journal.pone.0118199

Reemer, M., Ståhls, G. 2013. Phylogenetic relationships of Microdontinae (Diptera: Syrphidae) based on molecular and morphological characters. Systematic Entomology. 38, 661–688. doi:10.1111/syen.12020

Ribeiro, M.A. 2018. A new species of *Alopoglossus* lizard (Squamata, Alopoglossidae) from the Southern Guiana Shield, northeastern Amazonia, with remarks on diagnostic characters to the genus. Zootaxa. 4422, 25–40. doi:10.11646/zootaxa.4422.1.2

Rieppel, O., Gauthier, J., Maisano, J. 2008. Comparative morphology of the dermal palate in squamate reptiles, with comments on phylogenetic implications. Zoological journal of the Linnean Society. 152, 131–152.

Rodrigues, M.T., Cassimiro, J., Pavan, D. 2009. A new genus of microteiid lizard from the Caparaó mountains, southeastern Brazil, with a discussion of relationships among Gymnophthalminae (Squamata). American Museum Novitates. 1–28.

Rodrigues, M.T., Freire, E.M.X., Pellegrino, K.C.M., Sites Jr., J.W. 2005. Phylogenetic relationships of a new genus and species of microteiid lizard from the Atlantic forest of north-eastern Brazil (Squamata, Gymnophthalmidae). Zoological Journal of the Linnean Society. 144, 543–557. doi:10.1111/j.1096-3642.2005.00177.x

Rodrigues, M.T., Machado, K.C., Dixo, M., Verdade, V.K., Sites, J.W. 2007. A new genus of microteiid lizard from the Atlantic Forests of state of Bahia, Brazil, with a new generic name for *Colobosaura mentalis*, and a discussion of relationships among the Heterodactylini (Squamata, Gymnophthalmidae). American Museum Novitates. 1–27.

Roscito, J.G., Nunes, P.M.S., Rodrigues, M.T. 2014. Digit evolution in gymnophthalmid lizards. The International Journal of Developmental Biology. 58, 895–908. doi:10.1387/ijdb.140255jg

Roscito, J.G., Rodrigues, M.T. 2010. Comparative cranial osteology of fossorial lizards from the tribe Gymnophthalmini (Squamata, Gymnophthalmidae). Journal of morphology. 271, 1352–65. doi:10.1002/jmor.10878

Roux, J. 1927. Contribution a l’erpetologie du Venezuela. Verhandl. Naturforsch. Ges. Basel. 38, 252–261.

Rueda, J. V. 1985. Acerca de las especies colombianas del genero *Ptychoglossus* (Sauria: Gymnophthalmidae) con la descripción de una nueva especie. Lozania. 51, 1–12.

Saint, K.M., Austin, C.C., Donnellan, S.C., Hutchinson, M.N. 1998. C-mos, a nuclear marker useful for Squamate phylogenetic analysis.. Molecular Phylogenetics and Evolution. 10, 259–263.

Taylor, E.H. 1949. Two new teiid lizards from Costa Rica. Univ. Kansas Sci. Bull. 33, 271–278.

Torres-Carvajal, O., Lobos, S.E. 2014. A new species of *Alopoglossus* lizard (Squamata, Gymnophthalmidae) from the tropical andes, with a molecular phylogeny of the genus. ZooKeys. 120, 105–120. doi:10.3897/zookeys.410.7401

Uetz, P., Hallerman, J. 2014. The reptile database. http:// www.reptile-database.org/. Accessed in September, 2008.

Vaidaya, G., Lohman, D.J., Meier, R. 2011. SequenceMatrix: concatenation software for the fast assembly of multi-gene datasets with character set and codon information. Cladistics. 27, 171–180.

Werner, F. 1916. Bemerkungen uiber einige niede- re Wirbeltiere der Anden von Kolumbien mit Beschreibungen neuer Arten. Arten. Zool. Anz. 47.

Wheeler, W.C. 1996. Optimization alignment: the end of multiple sequence alignment in phylogenetics?. Cladistics. 12, 1–9.

Zaher, H., Prudente, A. 2003. Hemipenes of *Siphlophis* (Serpentes, Xenodontinae) and techniques of hemipenial preparation in snakes: a Response to Dowling. Herpetological Review. 34, 302–307.

Appendix 1. Morphological Characters

Tongue (n = 5)

1. Morphology of the dorsal surface of the tongue: (0) entirely covered by oblique plicae; (1) covered by oblique plicae proximally and by papillae like scales distally; (2) entirely covered by papillae like scales (Boulenger, 1885).

2. Tongue papillae relationship: (0) juxtaposed; (1) imbricated.

3. Sublingual plicae: (0) absent: (1) present (Harris, 1985).

4. Longitudinal sulcus on the middle part of the tongue: (0) absent; (1) present.

5. Pigmentation of the tongue: (0) entirely light; (1) entirely dark; (2) light proximally and dark distally.

Scutellation (n = 68)

6. Eyelid: (0) absent; (1) present.

7. Proportion of the frontonasal: (0) wider than larger; (1) larger than wider or approximately equal sides.

8. Prefrontal scales: (0) absent; (1) present.

9. Contact between prefrontals: (0) absent; (1) present.

10. Nasal divided: (0) absent; (1) present.

11. Nasal scales division: (0) two scales; (1) three scales.

12. Nasal scales relationship: (0) in contact; (1) separated from each other by the rostral and frontonasal scales.

13. Nostril position: (0) lateral; (1) lateroposterior (Köhler *et al.* 2012).

14. Frontoparietal scales: (0) absent; (1) present.

15. Supraoculars count: (0) three; (1) four; (2) two.

16. Size of second supraocular: (0) similar in size to third supraocular; (1) twice the size of third supraocular.

17. Posterior border of the parietal and interparietal scales: (0) form a nearly straight suture across the back of the head; (1) form an irregular suture across de back of the head; (2) form a rounded suture across de back of the head.

18. Interparietal: (0) absent; (1) present.

19. Interparietal divided: (0) entire; (1) divided.

20. Size of interpariertal: (0) similar in size to the parietal; (1) smaller than parietals; (2) larger than parietals.

21. Exceptionally broad scales forming occipital scale rows: (0) absent; (1) present (Harris 1994).

22. Two enlarged longitudinal rows of scales on the nape: (0) absent; (1) present.

23. Ornamentation of the parietal scales: (0) absent; (1) present.

24. Type of ornamentation of the parietal: (0) ridged; (1) irregular surface.

25. Ornamentation of the frontoparietal scales: (0) absent; (1) present.

26. Type of ornamentation of the frontoparietal: (0) ridged; (1) irregular surface.

27. Ornamentation on the frontal scales: (0) absent; (1) present.

28. Type of ornamentation of the frontal: (0) ridged; (1) irregular surface.

29. Tympanic recess: (0) absent; (1) present.

30. Ornamentation of temporal scales: (0) smooth; (1) keeled.

31. Loreals: (0) unique; (1) divided, more than one.

32. Frenocular in contact with the nasal anteriorly: (0) absent; (1) present.

33. Pairs of enlarged chin shields: (0) three; (1) two; (2) one; (3) six (4) five; (5) four.

34. Number of infralabials in contact with chin shields: (0) 4; (1) 5; (2) 6; (3) 3.

35. Third chinshields separated from infralabials: (0) absent; (1) present.

36. Third chinshields separated from infralabials by: (0) one sublabial; (1) two sublabials, (2) granular scales.

37. Third pair of chinshields in contact medially: (0) absent; (1) present.

38. Second pair of chinshields in contact medially: (0) absent; (1) present.

39. Gular crease: (0) absent; (1) present.

40. Gutural fold: (0) absent, (1) present.

41. Pregulars differentiated from the gulars: (0) absent; (1) present.

42. Pregular scales shape: (0) plate-like; (1) granular; (2) granular medially and like plates laterally; (3) with a pair of enlarged scales medially.

43. Pregulars scales relationship: (0) justaposed; (1) imbricated.

44. Widened paramedian plates: (0) absent; (1) present.

45. Lateral neck scales: (0) plate-like; (1) granular; (2) granular anteriorly and plate-like posteriorly; (3) longitudinal rows of granular scales between rows of enlarged scales.

46. When plates-like, lateral neck scales: (0) round; (1) quadrangular; (2) lanceolate, (3) cicloid.

47. Ornamentation of the lateral neck scales: (0) smooth; (1) keeled; (2) only keeled at the posterior part of the neck.

48. Dorsal scales rows: (0) more evidently disposed in transversal rows; (1) disposed in transversal and oblique rows.

49. Relationship between dorsal scales with its antero-posterior relatives: (0) juxtaposed; (1) imbricated; (3) longitudinal rows of juxtaposed scales between rows of imbricated scales.

50. Relationship between dorsal scales with its lateral relatives: (0) juxtaposed; (1) imbricated.

51. Dorsal scales shape: (0) rectangular; (1) squared; (2) mucronate; (3) granular; (4) pentagonal; (5) cicloid (6) rows of mucronate and rows of granular.

52. Ornamentation of dorsal scales: (0) smooth; (1) keeled; (2) rows of smooth and rows of keeled.

53. Well-defined para-vertebral rows scales: (0) absent; (1) present.

54. Posterior border of the ventral scales: (0) truncated; (1) mucronate; (2) angulated; (3) rounded.

55. Posterior border of infracaudals: (0) truncated; (1) angulated; (2) rounded; (3) mucronate.

56. Relationship of ventral scales with its lateral relatives: (0) juxtaposed; (1) imbricate.

57. Ornamentation of ventral scales: (0) smooth; (1) keeled.

58. Lateral fold: (0) absent; (1) present.

59. Transversal rows of scales on lateral fold: (0) absent; (1) present.

60. Precloacal pores in males: (0) absent; (1) present.

61. Precloacal pores in females: (0) absent; (1) present.

62. When precloacal pores series present: (0) at the same level where they come together; (1) staggered behind the femoral pore series.

63. Femoral pores in males: (0) absent; (1) present.

64. Femoral pores in females: (0) absent; (1) present.

65. Scales bearing femoral pores: (0) entire; (1) divided.

66. Scales bearing pre-cloacal pores: (0) entire; (1) divided.

67. Thenar scales size: (0) small; (1) enlarged (Harris, 1994).

68. Ornamentation of dorsal scales of the arm: (0) smooth; (1) keeled.

69. Ornamentation of anterior scales of the thigh: (0) smooth; (1) keeled.

70. Ornamentation of the posterior part of the thigh scales: (0) smooth; (1) keeled.

71. Ornamentation of the anterior part of the bobbin: (0) smooth; (1) keeled.

72. Ornamentation of tail ventral scales: (0) smooth; (1) keeled.

73. Ornamentation of tail dorsal scales: (0) smooth (1) keeled.

Hemipenis (n = 10)

74. Hemipenis with mineralized spines: (0) absent; (1) present.

75. Hemipenis with comb-like spicules: (0) absent; (1) present.

76. Hemipenis shape: (0) cylindrical; (1) the proximal part narrow that turns wider gradually in distal direction (Nunes, 2011).

77. Hemipenis distally forked: (0) absent; (1) present.

78. Hemipenial capitulo: (0) absent; (1) present.

79. Hemipenis with odd projections on the distal tip of the capitule: (0) absent (1) present.

80. Ornamentation of the distal region of the hemipenis: (0) symmetrical; (1) asymmetrical (Harris, 1994; Nunes, 2011).

81. Flounces of the hemipenis: (0) absent; (1) present.

82. Direction of the hemipenial flounces of the asulcated face: (0) perpendicular in relation with the longitulinal axis of the hemipenis; (1) oblique in relation with the longitudinal axis of the hemipenis.

83. Spermatic sulcus obliterated distally: (0) absent; (1) present (Nunes, 2011).

Cranium (n = 39)

84. Relation among neurocranium and dermatocranium: (0) dermatocranium and neurocranium located at different levels, with a larger postemporal fenestrae (1) dermatocranium and neurocranium located at the same level, obliterating the fenestrae postemporal (Rieppel, 1984).

85. Maximum number of dental cuspids in maxillary teeth: (0) 1; (1) 2; (2) 3.

86. Like molar teeth: (0) absent; (1) present.

87. Pterygoid teeth: (0) absent; (1) present (Harris, 1994).

88. Lateral borders of the dorsal process of the premaxilla: (0) parallel; (1) convergent distally.

89. Basal part of the dorsal process of the premaxilla: (0) with basal constriction, that constriction is strong and abrupt; (1) without basal constriction.

90. Contact between the nasals: (0) absent; (1) present.

91. The contact between the dorsal surface of the posterior process of the maxilla and the suborbital process of the jugal visible laterally: (0) absent, covered by the posterior part of the facial process of the maxilla; (1) present.

92. The relation between the palatal shelf and the vomer: (0) palaeochoanate condition; (1) incomplete neochoanate condition; (2) neochoanate condition, (3) duplicipalatine (Rieppel *et al.*, 2008)

93. In the maxilla, width of the palatal shelf: (0) relatively de same through all palatal shelf; (1) abrupt reduction of the palatal shelf at its mid-point; (2) palatal shelf disappears after the midpoint of the dental row.

94. Interorbital constriction of the frontal: (0) half wide than the posterior part of the frontal; (1) a third part than posterior part of the frontal; (2) only slightly smaller than the posterior part of the frontal.

95. Frontoparietal tabs: (0) with the same or less length of the parietal processes of the frontal; (1) taller than the parietal processes of the frontal; (2) without frontoparietal tabs (MacLean, 1974; Presch, 1980).

96. *Cristae cranii*: (0) forming lateral descending ridges; (1) forming a tubular structure (MacLean, 1974; Presch, 1980).

97. Parietal proportions, this considering the length since the posterior part of the posteromedial slit to the contact border with the frontal, and the width between the dorsal edges of the supratemporal fenestras: (0) wider than longer (1) longer than width.

98. Lateral borders of the body of parietal: (0) straight; (1) slightly curved medially; (2) strongly curved medially.

99. Lateral shelf of the parietal: (0) absent; (1) present.

100. Sagital crest on the parietal: (0) absent; (1) present.

101. Parietal flat: (0) absent, dorsally convex; (1) present.

102. The descending ventral process of the parietal: (0) small, occuping only the superior part of the infratemporal fenestra; (1) hyperthrophied (Roscito and Rodrigues, 2010).

103. The posterolateral processes of the parietal proportions: (0) the length is similar to the lateral edge of the parietal body; (1) longer than the lateral edges of the parietal body; (2) reduced.

104. Posterolateral process of the parietal shape: (0) laterally flat; (1) vertically flat.

105. Foramen pineal: (0) absent; (1) present.

106. The prefrontal articulated with the palatine: (0) absent; (1) present.

107. Lacrimal bone in the adult forms: (0) absent; (1) present.

108. Postorbitofrontal: (0) absent; (1) present (MacLean, 1974; Presch, 1980).

109. Posfrontal shape: (0) triradiated; (1) tretaradiated.

110. Jugal proportions: (0) dorsal process and suborbital process of the jugal with similar length; (1) subornital process of the jugal conspicuity reduced.

111. Contact between the jugal and the postorbital or postorbitofrontal: 0) the tip of the dorsal process of the jugal articulates with the ventral tip of the ventral process of the postorbital (postorbitofrantal; (1) the medial suface of the dorsal process of the jugal contacts with the lateral surface of the ventral process of the postorbital (postorbitofrontal) (2) the anterior border of the dorsal process of the jugal contacts with the posterior border of the ventral process of the post ocular.

112. Proportion of dorsal and ventral rami pterygoid facet of the ectopterigoid: (0) dorsal and another ventral rami with similar lenght; (1) without ventral rami.

113. Quadrate reduced: (0) absent; (1) present.

114. Dorsoanterior part of the tympanic crest of the quadrate: (0) convex, doing a continuous curved outline with rest of the tympanic crest; (1) from flatter to slightly concave generating a discontinuity with the curve middle part of the tympanic crest.

115. Posterolateral process of the vomer: (0) absent; (1) present.

116. Contact between the palatine and the *Cristae cranii* of the frontal: (0) absent; (1) present.

117. Palatines contact each another: (0) absent; (1) present.

118. Lateral border of the palatine with a shelf that projects medially: (0) absent; (1) present.

119. Shape of the palatine process of the pterygoid: (0) borders are curved divergently with the distal tip truncated and broad; (1) convergent or parallel borders with a distal narrow tip; (2) bifurcated.

120. Little conic tubercle that surge of the anterior border of the palatine process of the pterygoid: (0) absent; (1) present.

121. Pterygoid flange bifurcated: (0) absent; (1) present.

122. Basipterygoid process size: (0) small; (1) consciously projected.

123. Basipterygoid process direction: (0) directed lateroventrally; (1) directed anteriorly.

Mandible (n = 5)

124. Meckels groove: (0) open only anteriorly; (1) open from the middle to the anterior part of the dentary; (2) encased in a tubular section of the dentary (MacLean, 1974; Presch, 1980).

125. Posterodorsal process of the dentary: (0) absent; (1) present.

126. Length of the anterior part of the splenial: (0) strongly projected anteriorly; (1) non or only slightly projected anteriorly.

127. Posterior process of the splenial: (0) truncated, (1) projected posteriorly.

128. Angular process of the mandible orientation: (0) ventromedially projected, (1) ventrally projected.

Hyoid apparatus (n = 5)

129. Hyoid cornu shape: (0) slender with parallel borders; (1) wide with rounded shape.

130. Lateral border of the hyoid cornu: (0) medialy curved; (1) laterally curved.

131. Medial process of the hyoid cornu: (0) absent; (1) present.

132. Second ceratobranchial size: (0) goes posteriorly beyond the first ceratobranchial; (1) do not goes beyond the first ceratobranchial; (2) absent.

133. First epibranchial with proximal expansion: (0) absent; (1) present.

Post-cranium (n = 10)

134. *Processus lingualis* with posterior expansion: (0) absent; (1) present.

135. Free epibranchial: (0) absent; (1) present.

136. Scapular fenestra: (0) absent; (1) present.

137. Interclavicle shape: (0) rod shaped without lateral processes; (1) rhomboidal shaped with little lateral processes that go up the first coracoid fenestrae; (2) cross shaped with large lateral processes that can be go beyond the second coracoid fenestra (Presch, 1980).

138. Phalanges of the first finger of the hand: (0) 2; (1) 1; (2) 0 (Roscito *et al.*, 2014).

139. Size of fourth finger in relation to the third finger: (0) fourth finger longer than third finger; (1) fourth finger shorter or similar than third finger.

140. Ventral metacarpophalangeal sesamoids: (0) absent; (1) present.

141. Ventral distal phalangeal sesamoid: (0) absent; (1) present.

142. Dorsal distal phalangeal sesamoid: (0) absent; (1) present.

143. Position of the first caudal vertebrae with autotomy axis: (0) fifth vertebrae; (1) fourth vertebrae; (2) sixth vertebrae.

Appendix 2. Specimens examined

Institutions acronyms

AMNH, American Museum of Natural History, New York, USA; **CD-UV**, Colección Zoologica de Docencia de la Universidad de Valle, Cali, Colombia; **CEPB**, Centro de Estudos e Pesquisas Biológicas da Pontifícia Universidade Católica de Goiás, Goiânia, Brasil; **DHMECN**, División de Herpetología del Museo Ecuatoriano de Ciencias Naturales, Quito, Ecuador; **ICMN**, Museo de Ciencias Naturales Federico Carlos Lehmann Valencia, Cali, Valle del Cauca, Colombia; **MHUA**, Museo de Herpetologia de la Universidad de Antioquia, Medellin, Antioquia, Colombia; **MPEG**, Museu Paraense Emílio Goeldi, Pará, Brazil; **USNM**, Smithsonian Institution's National Museum of Natural History, District of Columbia, USA; **UV-C**, Colección de Herpetologia de la Universidad del Valle, Cali, Colombia; **UF-FLMNH**, Florida Museum of Natural History, Gainsville, Florida, USA; **ULABG,** Laboratorio de Biogeografia, Universidad de los Andes, Merida, Venezuela; **UMMZ**, University of Michigan Museum of Zoology, Ann Arbor, Michigan, USA; **YPM**, Yale Peabody Museum of Natural History, New Haven, Connecticut, USA.

CT Scans

Alopoglossus angulatus: AMNH 119395 (Brownsberg Nature Park, Estate Brokopongo, Surinam, 125 m). *Alopoglossus buckleyi*: AMNH 113762 (Río Cusuime, Cusuime, Provincia Morona Santiago, Ecuador, 2° 40' 12" S, 77° 42' 0" W, 320 m). *Alopoglossus embera*: AMNH 109682 (Holotype, Quebrada Guanguí, upper Río Saijá drainage, Departamento Cauca, Colombia, 100-200 m). *Alopoglossus festae*: AMNH 110610 (Municipio Naranjal, Provincia Guayas, Ecuador, 30 m). *Alopoglossus lehmanni*: FMNH 165199 (Holotype, Km 22 on the road from Buenaventura to San Isidro on the lower Calima River, Departamento Valle del Cauca, Colombia). *Lacerta viridis*: YPM 12858 (pet trade originated). *Ptychoglossus danieli*: AMNH 32774 (Paratype, Municipio Medellin, Departamento Antioquia, Colombia 1538 m). *Ptychoglossus plicatus*: AMNH 114307 (Fortuna Research Station, Rio Chiriquí, Provincia de Chiriquí, Panama, 1000 m). *Ptychoglossus vallensis*: AMNH 119239 (Paratype, Lago Calima, Departamento Valle del Cauca, Colombia, 3° 53' 30" N, 76° 29' 30" W, 1450 m). *Lacerta viridis*: YPM 12858 (pet trade originated).

Scutellation

Alopoglossus angulatus: ICN-R 8086-8088 (Surroundings of the Lago Taraira, Municipio Caparú, Departamento Caquetá, Colombia); ICN-R 8617, 8618, 8648 (Municipio Leticia, Deprtamento Amazonas, Colombia); USNM 158083 (Municipio Belém, Brazil, 1° 25‘ 48” S, 48° 28’ 47.99” W, 5 m); USNM 196064 (Río Pindo, Provincia Pastaza, Ecuador, 2° 7’ 0.01” S, 76° 2’ 59.99” W, 184 m); USNM 222340 (Reserva Tambopata, Municipio Puerto Maldonado, Departamento Madre de Dios, Perú, 12° 49’ 48” S, 69° 16’ 48” W, 280 m); USNM 288896, 288897 (Río Tapajos, Parque Nacional da Amazonia, Municipio Itaituba, 4° 16’ 59.98” S, 55° 58’ 59.87” W, 7 m); USNM 313958 (on Río Sucusari near its confluence with Río Napo, Municipio Iquitos, Departamento Loreto, Perú, 3° 15’ 34.92” S, 77° 55’ 12” W, 530 m); USNM 538369 (Municipio San Martin, Departamento Cuzco, Perú, 11° 47’ 8.16” S, 72° 41’ 57.12 W, 474 m); USNM 566400 (Municipality Kwakwani, Region East Berbice, Guyana, 5° 5’ 6” N, 58° 14’ 13.92” W, 61 m). *Alopoglossus atriventris*: AMNH 106634 (Paratype, Municipio Mocoa, Departamento Putumayo, Colombia, 700 m); ICN-R 8083, 8085 (Surroundings of the Lago Taraira, Municipio Caparú, Departamento Caquetá, Colombia); ICN-R 9024 (Serrania de Churrumbelos, Municipio Mocoa, Departamento Putumayo, Colombia); ICN-R 9036 (without data); USNM 195230 (Municipio Chichirota, Provincia Pastaza, Ecuador, 2° 22’ 59.98” S, 76° 39’ 0” W, 262 m), USNM 195231-195231 (Río Pindo, Provincia Pastaza, Ecuador, 2° 7’ 0.012” S, 76° 2’ 59.99” W, 184 m); USNM 195234 (Río Curaray, Municipio Paracachi, Ecuador, 1° 36’ 0” S, 76° 20’ 59.99” W, 232 m); USNM 196060 (Río Conambo, Provincia Pastaza, Ecuador, 1° 52’ 0.012” S, 76° 46’ 59.879” W, 246 m); USNM 321088, 321089, 321091 (Municipio Coca, Provincia Pastaza, Ecuador, 1° 7’ 12” S, 76° 57’ 0” W, 300 m); USMN 565887-565886 (Municipio Bellavista, Departamento Loreto, Perú, 1° 47’ 2.04” S, 75° 37’ 10.919” W, 224 m). *Alopoglossus buckleyi*: ICN-R 7135 (Finca Mariposa, Vereda Alto Campucana, Corregimiento San Antonio, Municipio Mocoa, Departamento Putumayo, Colombia, 10°12’ N, 76°38’ W, 1385 m); ICN-R 8246 (Serrania de Churumbelos, Departamento Cauca, 1250 m); ICN-R 8247 (Villa Iguana, Serrania de Churumbelos, Departamento Cauca, 1450 m); USNM 195235 (Río Pindo, Provincia Pastaza, Ecuador, 2° 7’ 0.01” S, 76° 2’ 59.99” W, 184 m); USNM 195236 (Municipio Chiguaza, Provincia Morona Santiago, Ecuador, 2° 1’ 0.012” S 77° 58’ 0.12” W, 942 m); USNM 195237 (Municipio Taisha, Provincia Morona Santiago, Ecuador, 2° 22’ 59.99” S, 77° 30’ 0” W, 446 m); USNM 195238 (Río Huiyayacu, Provincia Pastaza, Ecuador); USNM 196059

(Municipio Loreto, Provincia Orellana, Ecuador); USNM 316768 (vicinity of Pais, on the lower Río Alto Cenepa, Departamento Amazonas, Perú, 4° 25’ 12” S, 78° 12’ 0” W, 838 m); USNM 316769 (vicinity of Kagka, , on the lower Río Alto Cenepa, Departamento Amazonas, Perú, 4° 22’ 12” S, 78° 13’ 11.99” W, 316 m); USNM 316770 (vicinity of Huampami, Río Cenepa, Departamento Amazonas, Perú, 4° 28’ 12” S, 78° 10’ 12” W, 210 m); USNM 538374, 538375 (Río Camisea, Departamento Cuzco, Perú, 11° 42’ 23.04” S, 72° 54’ 11.16” W, 465 m); USNM 568707 (vicinity of Galilea, Río Santiago, Departamento Amazonas, Perú, 4° 0’ 52.92” S, 77° 46’ 42.96” W, 200 m); USNM 568708 (vicinity of Shiringa, Río Yutupis, Departamento Amazonas, Perú, 4° 1’ 26.04” S, 77° 46’ 42.96” W, 190 m). *Alopoglossus copii*: USNM 196061 (Río Pindo, Provincia Pastaza, Ecuador, 2° 7’ 0.012” S, 76° 2’ 59.99”, 184 m); USNM 196062 (Río Bobonaza, Municipio Montalvo, Provincia Pastaza, Ecuador, 2° 4’ 0.012” S, 76° 58’ 0.12” W, 314 m); USNM 196063, 196067, 518295 (Municipio Sarayacu, Provincia Pastaza, Ecuador, 1° 43’ 59.988” S, 77° 28’ 59.88” W, 402 m); USNM 196065 (Municipio Loreto, Provincia Orellana, Ecuador, 0° 41’ 32.64” S, 77° 18’ 39.959” W, 396 m); USNM 196066 (Río Pucuyacu, Provincia Pastaza, Ecuador, 1° 57’ S, 77° 0’ W, 345 m); USNM 568709 (vicinity of Galilea, Río Santiago, Departamento Amazonas, Perú, 4° 0’ 52.92” S, 77° 46’ 42.96” W, 200 m). *Alopoglossus embera*: AMNH 107910, 109682 (Quebrada Guanguí, upper Río Saijá drainage, Departamento Cauca, Colombia, 150 m); CD-UV2457 (Corregimento Pianguita, Municipio Buenaventura, Departamento del Valle del Cauca, Colombia (03°27′ 35.42″ N, 77°11′ 17.88″ W; 0 m); UV-C 7231, 7232 (Paratype, Vereda Camancito, Río Cajambre, Municipio Buenaventura, Departamento del Valle del Cauca, Colombia (03°27′ 26.58″ N, 77°10′ 16.58″ W; 75 m). *Alopoglossus festae*: ICN-R 5486(Río Mira, Centro de Invetigación El Mira, Municipio Tumaco, Departamento Nariño, Colombia); ICN-R 12669 (Corregimiento Salahonda, Minicipio Francisco Pizarro, Departamento Nariño, Colombia); USNM 20613 (Río Santiago, Municipio Plaza de Oro, Provincia Esmeraldas, Ecuador); USM 142600 (Duran - Tambo Road, Provincia Cañar, Ecuador); USNM 196078 (Municipio Palma Real, Provincia Imbabura, Ecuador, 0° 19’ 59.99” N, 78° 55’ 59.88” W, 654 m); USNM 196080, 196084 (Municipio Quevedo, Provincia Los Ríos, Ecuador, 1° 1’ 59.88” S, 79° 27’ 0” W, 54 m); USNM 196086 (Municipio Negal Grande, Provincia Pichincha, Ecuador, 0° 7’ 0.12” N, 78° 40’ 0.12” W, 1530 m); USNM 286279 (Municipio Pinas, Provincia El Oro, Ecuador, 3° 39’ 20.016” S, 79° 46’ 44.039” W, 406 m). *Alopoglossus lehmanni*: FMNH 165199 (Holotype, lower Río Calima, Municipio Buenaventura, Departamento Valle del Cauca, Colombia, 4°00’ N, 76°59’ W, 27 m). *Alopogossus viridiceps*: QCAZ 10670 (Reserva de Bosque Nublado Santa Lucia, Municipio Nanegal Provincia Pichincha, Ecuador, 0° 6’ 48.70” N, 78° 36’ 48.6” W, 1729 m). *Ameiva ameiva*: MPEG 25061(Parque estadual Paulo Cesar Vinha, Municipio Guarapari, Estado Espírito Santo, Brasil, 20° 36’ 27,68" S, 40° 25’ 0,62" W, 10 m). *Arthrosaura kocki*: MPEG 7463, 27464 (Reserva Biologica Maicuru, Municipio Almeirim, Estado Pará, Brasil, 0° 49’ 2,38" N, 53° 56’ 22,52" W, 320 m). *Bachia flavescens*: USNM 566423-566426 (confluence of Berbice River and Kurudini River, Municipality Kwakwani, East Berbice Region, Guyana, 5° 5’ 6” N, 58° 14’ 13.92” W, 33 m), USNM 566427 (Konawaruk River, Municipatity Mabura Hill, Mazaruni-Potar Region, Guyana, 5° 13’ 6.96” N, 59° 2’ 43.079” W, 68 m). *Colobosaura modesta*: MPEG 30999, 31012 (Parque Serra das Andorinhas, Municipio São Geraldo de Araguaia, Estado Pará, Brasil, 6° 13’ 25,45" S, 48° 27’ 19,09" W, 208 m). *Cercosaura ocellata* MPEG 22989, 23004 (Monte Dourado, Municipio Almerin, Estado Pará, Brasil, 0° 41’ 45" S, 52° 48’ 32" W, 152 m). *Cnemidophorus lemniscatus*: MPEG 17843 (Tafelberg, Estate Brokopondo. Suriname), 29454 (Municipio Itaituba, Estado Pará, Brasil, 4° 28’ 21" S, 56° 14’ 46" W). *Iphisa elegans* MPEG PLVP 365, 366 (Municipio Oiapoque, Estado Amapá, Brasil). *Kentropyx calcarata* MPEG 26733, 26734 (Floresta Estadual de Paru, Municipio Almerín, Estado Pará, Brasil, 0° 56’ 0" S, 53° 14’ 29" W). *Lacerta viridis* USNM 58342 (State Tirol, Austria); USNM 7344, 7399 (Europe). *Loxopholis guianense*: USNM 288921, 288922 (Río Tapajos, Parque Nacional da Amazonia, Municipio Itaituba, Estado Pará, Brasil, 4° 16’ 59.99” S, 55° 58’ 59.879” W, 7 m); USNM 289087, 289088 (Reserva Ecologia Río Trombetas, Estado Pará, Brasil, 1° 11’ 18.96” S, 56° 40’ 14.879” W, 19 m). *Potamites ecpleopus*: USNM 196122-196124 (Río Misahualli, Municipio Tena, Provincia Napo, Ecuador, 0° 59’ 26.00” S, 77° 47’ 48.84” W, 571 m); USNM 196126 (Municipio Veracruz, Provincia Pastaza, Ecuador, 1° 30’ 0” S, 77° 55’ 59.88” W, 974 m). *Ptychoglossus bicolor*: ICN-R 11712 (Vereda Rosa blanca, Municipio Floridablanca, Departamento Santander, Colombia); ICN-R 12180 (Vereda La Bodega, Parque Nacional Natural Yariguíes, Municipio El Carmen de Chucerí, Departamento Santander, Colombia); ICN-R 2163 (Municipio Icononzo, Departamento Tolima, Colombia, 1640 m); UIS-R 1540, 1579, 2586, 2588 (Hacienda El Roble, Municipio Los Santos, Departamento Santander, Colombia, 06° 52′ N; 73° 03′ W, 1631 m). *Ptychoglossus bilineatus*: ICN-R 12011 (Reserva Natural Río Ñambí, Vereda El Barro, Corregimiento Altaquer, Municipio Barbacoas, Departamento Nariño, Colombia, 01°17’ 86” N, 78° 4’ 17,7” W, 1420 m). *Ptychoglossus breviforntalis*: USNM 196258 (Río Pucayacu, Provincia Pastaza, Ecuador, 1° 57’ 0” S, 77° 0’ 0” W, 367 m); USNM 196259, 248258 (Río Corrientes, Provincia Pastaza, Ecuador, 2° 7’ 0.01” S, 76° 2’ 59.99 W, 184 m); USNM 196260 (upper Río Oglan, Provincia Pastaza, Ecuador, 1° 18’ 0” S, 77° 37’ 59.88” W, 506 m); USNM 196261 (Río Arajuno, Provincia Pastaza, Ecuador, 1° 23’ 60” S, 77° 52’ 59.88” W, 969 m). *Ptychoglossus danieli*: AMNH 32774 (Paratype, Municipio Medellin, Departamento Antioquia, Colombia 1538 m); AMNH 38819 (Paratype, Quebrada La Clara, Municipio Angelopolis, 1955 m). *Ptychoglossus eurylepis* ICN-R4460 (Holotype, Quebrada Sopladero, Municipio La Uribe, Departamento Cauca, Colombia, 2° 37’ N, 76° 54’ W, 2190 m). *Ptychoglossus festae*: ICN-R 11320 (Cerro Murrucucú, Parque Nacional Natural Paramillo, Departamento Córdoba, Colombia); ICN-R 11435 (Vereda Miramar, Municipio San Alberto, Departamento Cesar, Colombia, 715 m); ICN-R 7230 (Vereda Barbascales, Municipio Yacopi, Departamento Cundinamarca, Colombia, 720 m); ICN-R 7916 (Municipio Puerto Romero, Departamento Boyacá, Colombia); MHUA 11394 (Hacienda Las Brisas, Municipio Maceo, Departamento Antioquia, Colombia); USNM 150124, 150125 (Municipio Armila, Archipielago de San Blas, Comarca Guna Yala, Panamá). *Ptychoglossus gorgonae*: ICN-R6544 (Isla Gorgona, Municipio Guapi, Departamento Cauca, Colombia); USNM 196263 (Paratype, Finca La Esperanza, Municipio Santo Domingo de los Colorados, Provincia Pichincha, Ecuador, 0° 15’ 0” S, 79° 9’ 0” W, 576 m). *Ptychoglossus grandisquamtus*: ICN-R 5937 (Holotype, Campamento Ingeominas, Río Amparradó, Municipio Dabeiba, Departamento Antioquia, Colombia, 6° 42’ S, 76° 27’ W, 805 m). *Ptychoglossus kugleri*: MCZ 48739, 48912 (Municipio Paují, Estado Bolívar, Venezuela, 11° 01’ N, 68° 38’ W. 400 m). *Ptychoglossus myersi*: UK 96911- 96914 (Cerro Pirre, Serrania de Pirre, Provincia Darien, Panama, 7° 50’ N, 77° 43’ W, 1000 m). *Ptychoglossus plicatus*: ICN-R 12002 (Vereda Montebello, Municipio Pueblo Rico, Departamento Risaralda, Colombia, 5° 14’ 32” N, 76° 5’ 33” W, 1800 m); ICN-R 5939 (Campamento Ingeominas, Río Amparradó, Municipio Dabeiba, Departamento Antioquia, Colombia, 6°42’ N, 76°27’ W, 805 m); UF 52496 (Municipio Puntarenas, Costa Rica); USNM 151085 (Cerro Mali, Provincia de Darien, Panamá, 1433 m); USNM 151121, 151123 (Cerro Tacarcuna, Provincia de Darien, Panamá, 1250 m); USNM 219724 (Municipio Almirante, Provincia Bocas del Toro, Panamá); USNM 219980 (Rio Claro, Provincia San José, Panamá, 10° 3’ 29.88” N, 83° 58’ 29.999” W, 1000 m); USNM 339801, 339802 (Municipio Los Planes, Provincia Chiriquí, Panamá, 1100 m).

Ptychoglossus romalaeos: UMMZ 171655, 171656 (Cuchilla Hierbabuena, Sierra Nevada de Santa Marta, Municipio San Pedro de la Sierra, Departamento Magdalena, Colombia, 10° 54’ N, 74° 01’ W, 1900 m). *Ptychoglossus stenlepis*: IMCN 136 (Vereda Betania, Municipio Bolívar, Departamento Valle del Cauca, Colombia); CD-UV 3039, UV-C 11856, 12012, 12475, 13217 (Hacienda San Pedro, Corregimiento El Queremal, Municipio Dagua, Departamento Valle del Cauca, Colombia, 3° 30’ 40.86” N, 76° 43’ 30.43” W, 1774 m). *Ptychoglossus vallensis*: AMNH 119239 (Paratype, Lago Calima, Departamento Valle del Cauca, Colombia, 3° 53′ 30″ N, 76° 29′ 30″ W, 1450 m); CD-UV2032; CD-UV2144; CD-UV2147; CD-UV3056 (Parque de las Heliconias, Municipio Caicedonia, Departamento Valle del Cauca, Colombia); CD-UV3077 (Municipio Santander de Quilicháo, Departmento Cauca, Colombia, 3°00′30″N 76°29′02″W, 1067m); *Salvator merianae*: MPEG14631 (x); *Tretioscincus agilis*: MPEG 22131 (Municipio Almeirim, Estado Pará, Brasil, 0° 35’ 27" S, 52° 44’ 9" W, 139 m); MPEG 24095 (Monte Dourado, Municipio Almeirim, Estado Pará, Brasil, 1° 11’ 32" S, 52° 54’ 17" W, 43 m). *Tupinambis teguixin* MPEG 3209 (Municipo Amapá, Estado Amapá, Brasil, 1° 40’ 46,1" N, 50° 52’ 35,3" W), MPEG 31890 (Parque do Utinga, Municipio Belém, Estado Pará, Brasil).

Dry preparations

Ameiva ameiva: MPEG 25061(Parque estadual Paulo Cesar Vinha, Municipio Guarapari, Estado Espírito Santo, Brasil, 20° 36’ 27,68" S, 40° 25’ 0,62" W, 10 m); *Salvator merianae*: CEPB 1088 (unavailable data). *Kentropyx calcarata*: MPEG 22298 (Rio Tapajos, Parque Nacional Natural da Amazônia, Municipio Itaituba, Estado Pará, Brasil, 4° 40' 27" S, 56° 32' 52" W). *Tupinambis teguixin*: MPEG 18484 (Taperinha, Municipio Santarem, Estado Pará, Brasil, 2° 31' 6,4" S, 54° 17' 2,27" W).

Tongue

Alopoglossus angulatus: ICN-R 8086-8088 (Surroundings of the Lago Taraira, Municipio Caparú, Departamento Caquetá, Colombia). *Alopoglossus atriventris*: AMNH 106634 (Paratype, Municipio Mocoa, Departamento Putumayo, Colombia, 700 m). *Alopoglossus buckleyi*: ICN-R 7135 (Finca Mariposa, Vereda Alto Campucana, Corregimiento San Antonio, Municipio Mocoa, Departamento Putumayo, Colombia, 10°12’ N, 76°38’ W, 1385 m). *Alopoglossus copii*: USNM 196061 (Río Pindo, Provincia Pastaza, Ecuador, 2° 7’ 0.012” S, 76° 2’ 59.99”, 184 m).

Alopoglossus embera: UV-C 7231 (Paratype, Vereda Camancito, Río Cajambre, Municipio Buenaventura, Departamento del Valle del Cauca, Colombia (03°27′ 26.58″ N, 77°10′ 16.58″ W; 75 m). *Alopoglossus festae*: USNM 142600 (Duran - Tambo Road, Provincia Cañar, Ecuador). *Alopoglossus lehmanii*: FMNH 165199 (Holotype, lower Río Calima, Municipio Buenaventura, Departamento Valle del Cauca, Colombia, 4°00’ N, 76°59’ W, 27 m). *Ameiva ameiva*: MPEG 32080 (MPEG Campus, Municipio Belém, Estado Pará, Brasil). *Arthrosaura kocki*: PLVP 388 (Municipio Oiapoque, Estado Amapá, Brasil). *Cercosaura ocellata*: MPEG 29372 (Monte Dourado, Municipio Almerin, Estado Pará, Brasil, 0° 41’ 45" S, 52° 48’ 32" W, 152 m). *Cnemidophorus lemniscatus*: MPEG 17396 (Municipio Santarem, Estado Pará, Brasil, 2° 30' 10" S, 54° 57' 18" W). *Colobosaura modesta*: MPEG 31012 (Parque Serra das Andorinhas, Municipio São Geraldo de Araguaia, Estado Pará, Brasil, 6° 13’ 25,45" S, 48° 27’ 19,09" W, 208 m). *Kentropyx calcarata*: MPEG 22298 (Rio Tapajos, Parque Nacional Natural da Amazônia, Municipio Itaituba, Estado Pará, Brasil, 4° 40' 27" S, 56° 32' 52" W). *Lacerta viridis*: USNM 7344 (Europe). *Loxopholis guianense*: USNM 288921 (Río Tapajos, Parque Nacional da Amazonia, Municipio Itaituba, Estado Pará, Brasil, 4° 16’ 59.99” S, 55° 58’ 59.879” W, 7 m). *Potamites ecpleopus*: MPEG 13092 (Río Azul, Serra dos Carajás, Municipio Parauapebas, Estado Pará, Brasil, 6° 1’ 13" S, 50° 17’ 42" W, 684 m). *Ptychoglossus bicolor*: ICN-R 11712 (Vereda Rosa blanca, Municipio Floridablanca, Departamento Santander, Colombia). *Ptychoglossus biliniatus*: ICN-R 12011 (Reserva Natural Río Ñambí, Vereda El Barro, Corregimiento Altaquer, Municipio Barbacoas, Departamento Nariño, Colombia, 01°17’ 86” N, 78° 4’ 17,7” W, 1420 m). *Ptychoglossus breviforntalis*: USNM 196258 (Río Pucayacu, Provincia Pastaza, Ecuador, 1° 57’ 0” S, 77° 0’ 0” W, 367 m). *Ptychoglossus danieli*: AMNH 32774 (Paratype, Municipio Medellin, Departamento Antioquia, Colombia 1538 m). *Ptychoglossus eurylepis*: ICN-R 4460 (Holotype, Quebrada Sopladero, Municipio La Uribe, Departamento Cauca, Colombia, 2° 37’ N, 76° 54’ W, 2190 m). *Ptychoglossus festae*: ICN-R 11435 (Vereda Miramar, Municipio San Alberto, Departamento Cesar, Colombia, 715 m). *Ptychoglossus gorgonae*: ICN-R 6544 (Isla Gorgona, Municipio Guapi, Departamento Cauca, Colombia). *Ptychoglossus grandisquamatus*: ICN-R 5937 (Holotype, Campamento Ingeominas, Río Amparradó, Municipio Dabeiba, Departamento Antioquia, Colombia, 6° 42’ S, 76° 27’ W, 805 m). *Ptychoglossus myersi*: UK 96914 (Cerro Pirre, Serrania de Pirre, Provincia Darien, Panama, 7° 50’ N, 77° 43’ W, 1000 m). *Ptychoglossus plicatus*: USNM 151123 (Cerro Tacarcuna, Provincia de Darien, Panamá, 1250 m).

Ptychoglossus stenlepis: IMCN 136 (Vereda Betania, Municipio Bolívar, Departamento Valle del Cauca, Colombia). *Ptychoglossus vallensis*: AMNH 119239 (Paratype, Lago Calima, Departamento Valle del Cauca, Colombia, 3° 53’ 30” N, 76° 29‘ 30” W, 1450 m). *Salvator merianae*: CEPB 1088 (unavailable data). *Tupinambis teguixin* MPEG 15675 (Rio Arari, Fazenda Tuyuyu, Ilha do Marajó, Estado Pará, Brasil, 0° 49' 0,59" S, 49° 8' 1,41" W).

Hemipenis

Alopoglossus festae: DHMECN 2573 (Reserva Ecologica Buenaventura, Municipio Piñas, Provincia El Oro, Ecuador). *Ameiva ameiva*: MPEG 25061 (Parque Estadual Paulo Cesar Vinha, Municipio Guarapari, Estado Espírito Santo, Brasil, 20° 36’ 27,68" S, 40° 25’ 0,62" W, 10 m). *Bachia flavescens*: AMNH 140925 (Dubulay Ranch House, Warniabo Creek Stream, Upper Demerara-Berbice Region, Guyana). *Colobosaura modesta*: MZUSP 80080 (Serra da Mesa, Estado Goías, Brasil). *Loxopholis guianense*: MZUSP 77483 (Igarapé Camaipi, Río Maracá, Municipio Poção, Estado Pará). *Ptychoglossus brevifrantalis*: MPEG 25943 (Floresta Nacional de Faro, Municipio Faro, Estado Para, Brasil). ULABG 4149 (Venezuela). *Ptychoglossus myersi*: UK 113648 (Cerro Cituro, Serrania de Pirre, Provincia Darien, Panama, 1000 m). *Salvator merianae*: ERN 189 (x). *Tretioscincus agilis*: MUZSP 72950 (Municipio São Luis do Aruá, Estado Roraima, Brasil).

Clear and double stained

Alopoglossus angulatus MPEG 27542 (Floresta Estadual do Paru, Municipio Almeirim, Estado Pará, Brasil, 0° 56’ 29,91" S, 53° 13’ 55,71" W, 73 m). *Alopoglossus atriventris*: MPEG 28137 (Reserva de Desenvolvimento Sustentável Cujubim, Municipio Juatí, Estado Amazonas, Brasil, 5° 5’ 18" S, 69° 12’ 59" W, 132 m). *Bachia flavencens* MPEG 27586 (Estação Ecologica Geão, Municipio Óbidos, Estado Pará, Brasil, 0° 9’ 55,76" S, 55° 11’ 11,04" W, 376 m). *Cnemidophorus lemniscatus*: MPEG 17393 (Municipio Santarem, Estado Pará, Brasil, 2° 29’ 16" S, 54° 57’ 53" W, 20 m) *Colobosaura mosdeta*: MPEG 31004 (Parque Serra das Andorinhas, Municipio São Geraldo de Araguaia, Estado Pará, Brasil, 6° 13’ 15" S, 48° 27’ 54" W, 236 m). *Loxopholis guianense*: MPEG 29800 (Municipio Laranjal do Jari, Estado Amapá, Brasil, 0° 42’ 37" S, 52° 23’ 53" W, 147 m). *Potamites ecpleopus*: MPEG 13092 (Río Azul, Serra dos Carajás, Municipio Parauapebas, Estado Pará, Brasil, 6° 1’ 13" S, 50° 17’ 42" W, 684 m). *Ptychoglossus* *brevifrantalis*: MPEG 29389 (Municipio Urucará, Estado Amazonas, Brasil, 2° 24’ 53" S, 57° 38’ 20" W, 18 m). *Ptychoglossus stenolepis*: CD-UV 3603 (Vereda Chicoral, CorregiVeremiento Bitaco, Muncipio Dagua, Departamento Valle del Cauca, Colombia, 3°35.162’ N, 76° 34.813’ W, 1849m). *Tretioscincus agilis*: MPEG 24109 (Monte Dourado, Municipio Almeirim, Estado Pará, Brasil, 1° 1’ 33" S, 52° 34’ 3" W, 54 m); *Iphisa elegans*: PLVP 305 (Municipio Oiapoque, Estado Amapá, Brasil). *Arthrosaura kocki*: PLVP 388 (Municipio Oiapoque, Estado Amapá, Brasil). *Colobosaura mosdeta*: MPEG 31004 (Parque Serra das Andorinhas, Municipio São Geraldo de Araguaia, Estado Pará, Brasil, 6° 13’ 15" S, 48° 27’ 54" W, 236 m).

Appendix 3. Taxonomic sampling

For the molecular data when an unpublished sequence was used the collection number of the voucher is reported and in the case of Genbank sequences the accession number is presented. Available morphological data is marked with "x". Unavailable data is marked by "--".

Taxa	12S	16S	ND4	C-mos	Scallation	Hemipenis	Cranium	Post-Cranium	Hyoid
Alopoglossus angulatus	LSUMNSH-17798	LSUMNSH-17798	LSUMNSH-17798	LSUMNSH-17798	x	x	x	x	--
Alopoglossus. atriventris	MPEG 28120	MPEG 28120	MPEG 28120	MPEG 28120	x	x	x	x	--
Alopoglossus. buckleyi	--	KU999143	KU999132	--	x	x	--	--	--
Alopoglossus. copii	LSUMZ H12692	LSUMZ H12692	LSUMZ H12692	LSUMZ H12692	x	x	--	--	--
Alopoglossus embera	--	--	--	--	x	--	x	x	--
Alopoglossus. festae	--	KU999144	KU999128	--	x	x	x	x	--
Alopoglossus lehmanni	--	--	--	--	x	x	x	--	--
Alopoglossus. viridiceps	--	KU999159	KU999140	--	x	x	x	x	x
Ameiva ameiva	KF742700	KF742716	KC109625	AF151206	x	x	x	x	--
Arthrosaura kockii	AF420680	AF420721	AF420866	KT254396	x	x	x	x	x
Bachia flavescens	AF420705	AF420753	AF420869	AF420859	x	x	x	x	x
Cnemidophorus lemniscatus	AY046438	AY046480	AF026171	KC109629	x	x	x	x	x
Cercosaura ocellata	KY555177	KY555249	KY555405	KY555332	x	x	x	x	x
Colobosaura modesta	AF420666.1	AF420733.1	AF420887.1	AF420845.1	x		x	x	x
Iphisa elegans	AF420668.1	AF420714.1	AF420889.1	AF420843.1	x	x	x	x	x
Kentropix calcarata	AF420707	AF420760	AF420913	AF420864	x	x	x	x	
Loxopholis guianansis	JN588623.1	VUB3594	JN588741.1	JN588711.1	x	x	x	x	x
Potamites ecpleopus	AF420668.1	AF420714.1	AF420889.1	AF420843.1	x	x	x	x	x
Ptychoglossus bicolor	ICN-R12180	ICN-R12180	--	ICN-R12180	x	x	x	x	x
Ptychoglossus	--	--	--	--	x	x	--	--	--

bilineatus									
Ptychoglossus brevifrontalis	ICN-R12518	MPEG25905	MPEG 29389	MPEG 29388	x	x	x	x	x
Ptychoglossus danieli	--	--	--	--	x	--	x	x	--
Ptychoglossus. eurylepis	--	--	--	--	x	--	--	--	--
Ptychoglossus festae	CD-UV 2272	CD-UV 2272	MHCH 3113	CD-UV 2272	x	x	--	--	--
Ptychoglossus. gorgonae	--	ICN-R12670	ICN-R12670	ICN-R12670	x	--	--	--	--
Ptychoglossus. grandisquamatus	--	--	--	--	x	--	--	--	--
Ptychoglossus kugleri	--	--	--	--	x	x	--	--	--
Ptychoglossus myersi	MHCH 3118	--	--	SMF 97562	x	x	--	--	--
Ptychoglossus plicatus	SMF 91573	SMF 91576	MHCH 2361	SMF 91576	x	x	x	x	
Ptychoglossus romaleos	--	--	--	--	x	--	--	--	--
Ptychoglossus stenolepis	--	--	--	--	x	x	x	x	x
Ptychoglossus vallensis	CD-UV 2274	CD-UV 2274	CD-UV 2269	CD-UV 2274	x	x	x	x	--
Salvator merianae	KU894499.1	KU894537.1	AF151210	KC109634	x	x	x	--	--
Tretioscincus agilis	AF420681	AF420732	AF420891	AF420837	x	x	x	x	--

Capítulo 2

Uma nova espécie de *Alopoglossus* Boulenger, 1885 (Gymnophthalmoidea) do oeste da Colombia

O capítulo II desta dissertação foi elaborado e formatado conforme as normas da publicação científica *South American Journal of Herpetology (Qualis B2)*, as quais se encontram em anexo (Anexo XX). Artigo publicado no volume 12 da revista mencionada.

Description of a New Species of *Alopoglossus* Boulenger, 1885 from Western Colombia (Gymnophthalmoidea)

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Abstract

We describe and name a new species of *Alopoglossus* (Gymnophthalmoidea: Alopoglossidae) from western Colombia (Departamentos Cauca and Valle del Cauca: Chocó biodiversity hotspot). The new taxon is morphologically similar to *Alopoglossus festae* and *A. viridis*, from which it differs, among other things: in having strongly keeled imbricated temporal scales; strongly keeled scales on dorsum of hand; rhomboid, keeled, ventral scales; and color pattern. Specimens from this new taxon have been sitting in museum shelves for several decades (holotype collected over 40 years ago)—thus, we discuss the relevance of biological specimen collection and the importance of reexamination of old museum records, in search of unnamed biodiversity.

Keywords: Alopoglossidae; Biodiversity; Chocó; Emberá; Gymnophthalmidae; Systematics; Taxonomy

INTRODUCTION

A recent study recognized the morphologically distinct clade composed of *Alopoglossus* Boulenger 1885 and *Ptychoglossus* Boulenger 1890 as a full family (Alopoglossidae) instead of a subfamily (Alopoglossinae) of a larger Gymnophthalmidae (Goicoechea et al., 2016). Regardless of the taxonomic rank adopted (family or subfamily), the two genera that compose this clade are collectively recognized as a monophyletic group, with a few morphological synapomorphies supporting their relationship (Presch, 1980; Goicoechea et al., 2016). Few morphological characters allow the unambiguous distinction between the two genera, and there has been scattered suggestions that some species may need reallocation to render both genera as monophyletic (Ayala and Harris, 1984; Harris, 1994). At any rate, according to Harris (1994), most species can be allocated in one of the two genera on the basis of organization of dorsal scales (laterally imbricated in *Alopoglossus*, parallel sided in *Ptychoglossus*), and in ornamentation forelimb scales (strongly keeled in *Alopoglossus*, smooth in *Ptychoglossus*). *Alopoglossus* is a relatively small genus, including seven formally recognized species—*A. angulatus* (Linnaeus, 1758)*, A. atriventris* Duellman, 1973, *A. buckleyi* (O'Shaughnessy, 1881), *A. copii* Boulenger, 1885, *A. festae* Peracca, 1904, *A. lehmanni* Ayala & Harris, 1984, *A. viridiceps* Torres-Carvajal & Lobos, 2014. The genus is distributed through Cis- and Trans-Andean northern South America. Inasmuch as a recent review of the taxonomic status of several populations of *Alopoglossus* is available (Köhler et al., 2012), the diversity of the genus is likely underestimated (Torres-Carvajal and Lobos, 2014). During a morphological study of alopoglossids, we stumbled across a few specimens from western (Trans-Andean) Colombia that we could not promptly identify. Examination of additional museum specimens, including most type specimens, and the relevant taxonomic literature of the genus, revealed these specimens represent an unnamed species of *Alopoglossus*.

Herein, we provide a description of known specimens and formalize its recognition as a new species. The majority of the type specimens of the new taxon was collected over 30 years ago—we, therefore, discuss the importance of natural history collections and of revising old museum records in search of hidden biodiversity.

MATERIAL AND METHODS

Specimens used in the description or examined for comparisons are deposited in the following institutions: **AMNH** (American Museum of Natural History, New York, USA); **CD-UV** (Colección Zoológica de Docencia, Universidad del Valle, Cali, Colombia), **KU** (University of Kansas, Lawrence, USA); **MPEG** (Museu Paraense Emilio Goeldi, Belém, Brazil); **UMMZ** (University of Michigan Museum of Zoology, Ann Harbor, USA); **UV-C** (Colección de Anfibios y Reptiles, Universidad del Valle, Cali, Colombia).

Scale counts and measurements were taken with the aid of a stereoscope. Measurements were taken with an electronic caliper and were recorded to the nearest 0.1 mm. Scale nomenclature follow Harris (1994) with a few observations, as follows. The first chinshield is referred to as postmental whereas postparietals are referred as occipitals. It is worth noting that scale nomenclature may differ from other authors and thus difference in scale counts must be evaluated with care.

RESULTS

Alopoglossus embera sp. nov.

Alopoglossus festae Peracca, 1904. Two of the paratypes (UV-C 7230, 7231) of *A. embera* have been referred in the literature as *A. festae:* Castaño-Mora et al. (2004); Castro-Herrera and Vargas-Salinas (2008); Cardona-Botero et al. (2013).

Holotype (Figs. 1, 2A-D, 3A, 4)

AMNH-R 109682 (field number CWM 11931), and adult female, in very good preservation state. Collected by Charles W. Myers and John W. Daly, on 09 February 1973, at Quebrada Guanguí, Upper Río Saija Drainage, Departamento Cauca, Colombia.

Paratypes

AMNH-R 1096780–109681, **AMNH-R 109683-109684**, collected by Charles W. Myers and John W. Daly, between February 09–20 1973, at the type locality. **UV-C 7231–7232**, collected by Bladimir Vasquez and Yesid Solarte, on August 12–13 1983, at Camancito, Rio Cajambre, Municipality of Buenaventura, Departamento Valle del Cauca, Colombia (03°27’26.58"N, 77°10’16.58"W; 75 m.a.s.l.). **UV-C 7270,** collected by Yesid Solarte, on August 18 1983, Piñuetal, Rio Cajambre, Municipality of Buenaventura, Departamento Valle del Cauca, Colombia (03°27'35.42"N, 77°11'17.88"W; 500 m.a.s.l.). **CD-UV 2457**, collected by Jefferson Panche, on 11–13 April 2013, at Pianguita, Municipality of Buenaventura, Departamento Valle del Cauca, Valle del Cauca Colombia (03°27'35.42"N, 77°11'17.88"W; 0 m.a.s.l.).

Type locality

The holotype (AMNH-R 109682), along with six of the paratypes were collected at Quebrada Guanguí (= Guanguí stream), 0.5 km, above its junction with Río Patia (= Patia River), at approx. 100-200 meters above seal level. This is the same locality where the famous Golden Poison Frog (*Phyllobates terribilis* Myers, Daly and Malkin, 1978) was originally described (i.e., type locality). In the description of *P. terribilis* Myers et al. (1978) commented on the locality and mentioned that although it is rarely shown in any maps it does have permanence. We consider the locality as given in Myers et al. (1978), and in the entry into AMNH collection catalog, to be the type locality of *A. embera.* We could not obtain precise geographic coordinates for the Quebrada Guanguí locality, and its placement in our map (Fig. 5) is tentative. We based the placement of the locality on the observations of Myers et al. (1978)—according to them, this locality is the same shown in Myers and Daly (1976: Map 1, Locality E).

Etymology

The specific name *embera* is used as a noun in apposition and is given in homage of the Emberá People. Emberá is an indigenous ethnicity inhabiting an important hotspot of biodiversity: the Chocó-Derién ecoregion, which extends from southwest Panama to northwest Ecuador, running along the entire Colombian Pacific coast. The Emberá composed of several subgroups that can be readily identified by conspicuous differences in their dialects and culture, as well as their geographic distribution (Hernandéz, 2001). Human settlements, agriculture and deforestation are major threats to the Colombian Chocó region. Habitat destruction and degradation in the region and endanger not only the Emberá and their cultural heritage, but also a host of animal and plant species, many of which are endemic to that part of the World.

Characterization and diagnosis

A member of Alopoglossidae based on the presence of oblique plicae (folds), instead of scale-like papillae, on the surface of the tongue (Harris, 1985). Allocated to *Alopoglossus* based on: (1) the presence of keeled scales on forelimb; (2) and laterally imbricated, keeled, dorsal scales.
The combination of the following characters can be used as a diagnosis for the new taxon: (1) Parietal and interparietals with a pair of well developed ridges on each scale; (2) Chinshields in direct contact with gulars, not separated by rows of pregulars; (3) Third pair of chinshiels always in medial contact (separated by small granules only posteriorly); (4) Two longitudinal rows of widened gular scales; (5) Dorsals laterally imbricated, lanceolate, strongly keeled; (6) Ventrals rhomboid and keeled; (7) Temporal scales strongly keeled; (8) Scales on dorsal surface of hand strongly keeled; (9) Two femoral pores in males; (10) Eight femoral pores in male, 0 –2 pores in females; (11) Pre-cloacal pores absent in both sexes; (12) Ventral scales usually heavily pigmented.

Comparisons with other taxa

Alopoglossus embera differs from *Alopoglossus angulatus* by the presence of two longitudinal rows of widened gular scales (absent in *A. angulatus*); temporals strongly keeled (smooth or only slightly keeled in *A. angulatus*); precloacal pores absent (one pore present in male *A. angulatus*); eight femoral pores in males (over 10 pores in *A. angulatus*). *Alopoglossus embera* differs from *A. atriventris* by the absence of enlarged pregular scales (present in *A. atriventris*); third pair of chinshield in contact medially (separated by small granular scales in *A. atriventris*); the presence of two longitudinal rows of widened gular scales (absent in *A. atriventris*). *Alopoglossus embera* differs from *A. buckleyi* in having larger, pointed, slightly imbricated, keeled scales on side of neck (small, granular, juxtaposed and generally smooth in *A. buckleyi*); strongly keeled temporals (smooth in *A. buckleyi*); ventrals keeled and usually rhomboidal (smooth and usually round in *A. buckleyi*); by the absence of enlarged pregular scales (present in *A. buckleyi*); third pair of chinshield in broad contact medially (separated by small granular scales in *A. buckleyi*); precloacal pores absent (one pore present in males of *A. buckleyi*). *Alopoglossus embera* differs from *A. copii* in having rhomboid or lanceolate, tightly juxtaposed scales on side of neck (conical with free skin between scales in *A. copii*); third pair of chinshield in contact medially (separated by small granular scales in *A. copii*); by the presence of two longitudinal rows of widened gular scales (absent in *A. copii*); eight femoral pores in males (over 10 pores in *A. copii*). *Alopoglossus* *embera* differs from *A. festae* in having more strongly keeled temporals (Fig. 2C, D) (smooth or weakly keeled temporals in *A. festae*: Fig. 2G, H); ventrals keeled (smooth in *A. festae*); rhomboid posterior margins of ventrals (round or semicircular in *A. festae*: Fig. 3); scale on dorsum of hand sharply keeled (smooth or lightly keeled in *A. festae*); venter usually heavily pigmented (venter usually pale). *Alopoglossus embera* differs from *A. lehmanni* by the absence of a well defined collar fold (present in *A. lehmanni*); third pair of chinshelds in contact medially (separated by gulars in *A. lehmanni*); dorsals lanceolate and imbricated (hexagonal and parallel in *A. lehmanni*); scales in lateral of trunk similar to dorsals (discrete zone of granular scales in *A. lehmanni*); absence of enlarged postparietals (present in *A. lehmanni*); four transverse rows of ventrals (10 in *A. lehmanni*); ventrals rhomboid (rectangular in *A. lehmanni*); precloacal pores absent (one pore present in *A. lehmanni*). *Alopoglossus embera* differs from *A. viridiceps* by the absence of enlarged pregular scales (present in *A. viridiceps*); longitudinal stripe from mouth commissure to shoulder absent (present and distinct in *A. viridiceps*); two femoral pores on each side of males (single femoral pore in *A. viridiceps*).

Description of holotype

Rostral hexagonal, much wider than long; visible from above; in broad contact with frontonasal, anterior margin of nasal, and first supralabial. Frontonasal pentagonal, wider than long; in contact with nasals laterally, and with prefrontals posteiorly. Two prefontals; each irregularly pentagonal; in contact with first two supraocularls laterally, and with frontal posteriorly. Frontal irregularly hexagonal, much longer than wide, wider anteriorly and narrower posteriorly; in contact with second and third supraoculars laterally, and frontoparietals posteriorly. Two frontoparietals; each irregularly pentagonal; in contact with third and fourth supraoculars laterally, and with interparietal and parietals posteriorly. Interparietal nearly pentagonal, with parallel lateral margins. Parietals hexagonal, as long as interparietal; in broad lateral contact with interparietal (inner side) and with a postocular and an enlarged temporal (outer side); in broad contact with posterior margins of frontoparietals and fourth supraocular anteriorly. Interparietal and parietals forming an undulated margin posteriorly, followed by a small row of lanceolate scales (postparietals). All scales on dorsal head juxtaposed. Interparietal and parietals with a pair of well developed ridges each; ridges extend through frontoparietals and prefrontals, although they are much less developed than thos in parietals; postparietals keeled; all other dorsal head scales smooth.

Four supraoculars, first the smallest, followed by fourth, third and second. Five superciliars. Nasal divided; longer than wide; irregularly pentagonal (trapezoid); in contact with rostral anteriorly, frontonasal and prefrontal dorsally, first and second supralabials ventrally, loreal and frenocular posteriorly; nostril opening on lower portion of nasal, touching adjacent first supralabial. Loreal rectangular, slightly taller than wide. Frenocular irregularly pentagonal, in point contact with nasal (not in contact with any supralabial). Four suboculars, the second very elongated (nearly four times the length of the others). Posterior subocular in contact with a single postocular. Lower eyelid semitransparent, with four lower palpebrals; upper border of eyelid is pigmented. Six supralabials; third the longest (at least three times longer than any other); one postsupralabial. Temporals irregularly polygonal and with variable size; the ones more anteriorly smaller than those posteriorly; distinctly keeled; almost entirely juxtaposed, with minor imbrication on larger posterior scales. Tympanum recessed, tympanic membrane not pigmented. Except temporals, all lateral head scales juxtaposed and smooth.

Mental trapezoidal, with a round anterior margin; postmental heptagonal, in contact with first two infralabials laterally, and first pair of chinshields posteriorly. Five infralabials, third the longest. Three pairs of chinshields; first two in ample contact medially and in contact with infralabials; second in point contact with the sublabial in its lateroposterior margin; third pair of chinshield in medial contact anteriorly, not in contact posteriorely, where it is separated by small granules; chinshields in direct contact with gulars. All scales on ventral head juxtaposed and smooth.

Gulars strongly imbricated; roughly organized in six rows; first row formed by scales approximately equal in size, followed by four rows where two medial scales are conspicuously broader than others. Gulars mostly smooth with round or mucronate (slightly pointed) posterior edges; ones on the flanks lanceolate and keeled. Collar with five scales; medial three enlarged, smooth and with round posterior margin; flanking scales lanceolate and keeled.

Scales on nape similar to dorsals; lanceolate, strongly imbricated, and distinctly keeled. Scales on side of neck irregularly shaped, generally granular and juxtaposed anteriorly slightly pointed and imbricated posteriorly; mostly keeled, except those on anteroventral region, which may be keeled or smooth.

Scales on dorsal and lateral parts of midbody equal; lanceolate, strongly keeled and imbricated; organized in transversal rows; 29 rows counted from first after the postparietal to posterior margin of the cloacae. Ventrals mucronate; lightly keeled and imbricated; organized in transversal rows; 17 londitudinal rows counted from collar to cloacal plate; four transversal rows. Cloacal plate formed by four scales, all longer than wide. Cloacal and femoral pores absent. Scales on tail mucronate, imbricated, keeled (more sharply on dorsal than ventral scales), organized in longitudinal and transversal rows.

Scales on forelimbs mostly rhomboidal or lanceolate, mucronate, imbricated, strongly keeled; granular and smooth on posterior surface of arm; scales on dorsal surface of hands rhomboidal, imbricate, mucronate and keeled (Fig. 4) , on dorsal surface of fingers rectangular, smooth; scales on undersurface of hand granular, juxtaposed, not smooth. Subdigital lamellae of fingers single, rectangular, smooth. 14 subdigital lamellae under fourth finger (on both sides).

Scales on hindlimbs mostly rhomboidal or lanceolate, mucronate, imbricated, strongly keeled; granular and smooth on posterior surface thigh; scales on dorsal surface of feet rhomboidal, imbricate, mucronate and keeled, on dorsal surface of fingers rectangular, smooth; scales on undersurface of hand granular, juxtaposed, not smooth. Subdigital lamellae of toes like those of feet. 17 subdigital lamellae under fourth toe (left side).

Measurements and scale counts of the holotype are given in Tables 1.

Color of the holotype in preservative

Dorsum of head, body, limbs, and tail brown, with pale dorsolateral stripes extending from loreal region, running over the eyes (superciliar scales and lateral margins of supraoculars), towards midbody (does not reach forelimb). Lateral of head, body and tail brown. Undersurface of head cream, with dark pigmentation on most parts of mental, infralabials, posterolateral portion of second chinshields, lateral of third chinshields and all of the sublabial. Pigmentation is more scattered on postmental, first pair of chinshields, and medial portions of second and third chinshields. Gular region heavily pigmented (pigments concentrated on anterior margin of gular scales. Ventrals pale, with dark brown pigmentation concentrated on anterolateral region of scales. Cloacal plate pale with scattered dark brown pigments. Undersurface of forelimb brown; undersurface of hindlimb and tail heavily pigmented.

Variation in type series

Only one confirmed adult male is present in the type series (CD-UV 2457). This specimen has eight femoral pores on the right side (left side is damaged) and lack pre-cloacal pores. Another specimen (UV-C 7270, female) does have two femoral pores on each side and also lack pre-cloacal pores. All remaining specimens are female or juvenile and all lack femoral and pre-cloacal pores.

Most specimens have either three or four supraoculars, whereas a single specimen (UV-C 7231) has only two supraoculars on one the left side (three on the right).

The density of pigmentation on ventral surfaces of the body varies conspicuously. Most paratypes have a pattern very similar to that of holotype but some specimens have a cream venter, almost lacking pigments or are only slightly pigmented (AMNH-R 109684; CD-UV 2457).

Additional variations in scale counts and measurements among type specimens are given in Table 1.

Distribution (Fig. 5)

Alopoglossus embera is known only from the Colombian Chocó region, with a few scattered records in Departamentos Cauca (type locality) and Valle del Cauca. Given that the region is extremely poorly sampled with respect to its biodiversity, it is likely that this species occur more widely.

DISCUSSION

Alopoglossus embera is the eighth species of the genus *Alopoglossus*, as currently defined. Given its shared characters with *A. festae* and *A. viridis* we speculate a close phylogenetic relationship between *A. embera* and those two taxa. At least one potential morphological synapomorphy supporting the relationship of the three taxa can be immediately identified—the presence of a double longitudinal row of widened gular scales (absent in all other *Alopoglossus* and *Ptychoglossus*). Torres-Carvajal and Lobos (2014) suggested phylogenetic split between Cis-Andean and Trans-Andean taxa, which would be corroborated in case of a relationship between *A. embera* and *A. festae* + *A. viridiceps* is confirmed. This relationship is, however still at the speculative stage and need to pass an explicit phylogenetic test. Moreover, *A. lehmanni*, also found in the Pacific side of the Andes, was never included in any phylogenetic analysis and has a strikingly different morphology than the other three Trans-Andean taxa.

A number of additional species and subspecies have been historically recognized in *Alopoglossus*—at least four names are currently recognized as junior synonyms of *A. angulatus* (*Leposoma carinicaudatum* Cope, 1876; *Alopoglossus amazonius* Ruthven, 1924; *Alopoglossus copii surinamensis* Brongersma, 1946; *Alopoglossus andeanus* Ruibal, 1952). A recent systematic review of the genus (Köhler et al., 2012) did not find enough evidence to recognize any of those as valid species. On the other hand, the recent discovery of *A. viridiceps* (Torres-Carvajal and Lobos, 2014) and *A. embera* (reported herein) suggests that the diversity in the genus might be underestimated. The use of refined morphological analyses, hemipenis characters, and of genetic data, have revealed astonishing numbers of cryptic species across many Gymnophthamoidea clades (Nunes et al., 2012; Recoder et al., 2014; Torres-Carvajal et al., 2016)—perhaps the addition of data from alternative sources (in addition to pholidosis and morphometrics) will prove useful in unraveling additional diversity within *Alopoglossus.* Torres-Carvajal and Lobos (2014) indicated that more detailed systematic studies of *A. festae*, as well as species of *Alopoglossus* east of the Andes in Ecuador with extensive sampling are underway. Additional studies including a broader sampling of the widespread species *A. angulatus* and *A. atriventris* might also prove to be fruitful in revealing hidden species.

The importance of natural history collections for long-term biodiversity assessments

A lot of the attention is recent taxonomic studies have shifted towards barcode initiatives and phylogenetic species delimitation methods, both of which rely heavily on the use of DNA sequences and on the collection of fresh specimens and tissue samples. This effort has produced extremely relevant contributions and accelerated the discovery of unnamed diversity throughout the globe. However, it is also extremely important that our historical collections (many of them predating the practice of tissue samples collection) are surveyed, and the morphological features of specimens for which recent taxonomic revisions are available be reexamined. As pointed out in Peloso (2010) a lot of the unnamed global biodiversity is not cryptic “they are strikingly distinct and easily diagnosable; all we need is to find them, whether in the field or in old jars sitting in museum shelves”—this is an accurate description of what happened in the case of *Alopoglossus embera.* The species was discovered during the study of museum specimens collected over four decades ago. A large fraction of the preserved specimens that now compose the type series of *A. embera* have been sitting on the shelves of the American Museum of Natural History ever since they were collected, by Drs. Charles Myers and John Daly, in 1973. Further examination of specimens at the collections of Universidad del Valle, in Colombia, revealed additional specimens of the new species, some of them collected over 30 years ago. These finding further stress the importance of scientific collections in documenting species diversity in the long term.

Taxonomy is a continuous science and our ability to recognize (or better yet, define) the limits between species is ever evolving, either by the appearance of additional evidence (e.g., more specimens, additional characters) or by the appearance of new techniques (e.g., CT-scanning, electronic microscopy, refined statistical analyses). Therefore, the reevaluation of collections specimens is constantly revealing unexpected novelties from specimens previously thought to be members of more common taxa.

The increase in awareness about biological conservation, stricter permitting regulations, and recent advocates for the general avoidance of collection, continue to generate healthy debates over the importance and relevance of lethal collecting of specimens. We argue that even common species should always be collected in reasonable amounts, especially when surveys are conducted in remote sites, because we never know if one will ever be able to return to a locality. Even if one does go back to a locality it may look quite different and biodiversity may be all gone by then (Coloma et al., 2007; Coloma et al., 2010). Recent claims by some colleagues that biological collection should be avoided, or minimized beyond reasonable, is extremely prejudicial to taxonomy (Minteer et al., 2014; Pape, 2016; Gutiérrez and Pine, 2017). As an example, the majority of the specimens of *A. embera* were labeled as *Alopoglossus festae*, a common species in Colombia and Ecuador, and potentially sympatric with *A. embera*. Hence, some of these specimens (UV-C 7231, 7270) have been already referenced in scientific papers as *A. festae* (Castaño-Mora et al., 2004; Castro-Herrera and Vargas-Salinas, 2008; Cardona-Botero et al., 2013). Had the collectors of the new taxon dismissed these specimens as “simply additional records of *A. festae*” released the animals, the species would still be unknown to science and, maybe, we would have never known of its existence at all. In another, rather extreme, example Coloma et al. (2010) named five new species of Harlequin toads (Bufonidae: *Atelopus*) and suggested that four of them might already be extinct—*Atelopus ardila* (holotype from 1984,

oldest reported specimens from 1965); *At. orcesi* (all known specimens collected in 1988); *At. pastuso* (holotype 1980; oldest reported specimens from 1968); *At. podocarpus* (holotype from 1994, oldest reported specimens from 1977). The recognition of these species (our new *Alopoglossus* and the aforementioned *Atelopus*) were only possible due to the availability of well preserved museum specimens collected several decades before their actual "discoveries".
We agree that it may be impossible to define a general policy or guideline as to what defines reasonable collecting, i.e., collecting 10 adult specimens of any given population of *Alopoglossus* may seem reasonable, but collecting 10 mature specimens of *Eunectes murinus* will likely impact the population (and cause a massive headache to any curator in charge of storing these specimens). Nonetheless, we generally concur with several colleagues that have explicitly expressed that the collection of biological specimens is, and will continue to be, an essential tool for most areas of biology, especially taxonomy (Culley, 2013; Krell and Wheeler, 2016; Rocha et al., 2016).

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REFERENCES

Avila-Pires T.C.S. 1995. Lizards of Brazilian Amazonia (Reptilia: Squamata). *Zoologische Mededelingen Leiden* 299: 1–315.

Ayala S.C., Harris D.M. 1984. A new microteiid lizard (*Alopoglossus*) from the Pacific rainforest of Colombia. *Herpetologica* 40: 154–158.

Boulenger G.A. 1885. Catalogue of the lizards in the British Museum (Natural History). Trustees of the British Museum, London.

Boulenger G.A. 1890. First report on additions to the lizard collection in the British Museum (Natural History). *Proceedings of the Zoological Society of London* 1890: 77–86 (Plates VIII-XI).

Brongersma L.D. 1946. On an *Alopoglossus* from Surinam. *Zoologische Mededeelingen* 14: 231–236.

Cardona-Botero V.E., Viáfara-Vega R.A., Valencia-Zuleta A.V., Echeverry-Bocanegra A., Hernández-Córdoba O.D., Jaramillo-Martínez A.F. ..., Castro-Herrera F. 2013. Diversidad de la herpetofauna en el Valle del Cauca (Colombia): un enfoque basado en la distribución por ecorregiones, altura y zonas de vida. *Biota Colombiana* 14: 156–233.

Castaño-Mora O.V., Cardenas-A. G., Hernandez-R. E.J., Castro-Herrera F. 2004. Catalogo de reptiles en el Chocó biogeografico. pp. 615–631), in J. O. Rangel (Ed)^(Eds), Colombia. Diversidad Biotica IV. El Chocó Biogeografico / Costa Pacifica. Universidad Nacional de Colombia, Bogotá, D.C., Colombia.

Castro-Herrera F., Vargas-Salinas F. 2008. Anfibios y reptiles en el departamento del Valle del Cauca, Colombia. *Biota Colombiana* 9: 251–277.

Coloma L.A., Duellman W.E., Almendáriz C.A., Ron R.S., Terán-Valdez A., Guayasamin J.M. 2010. Five new (extinct?) species of Atelopus (Anura: Bufonidae) from Andean Colombia, Ecuador, and Peru. *Zootaxa* 2574: 1–54.

Coloma L.A., Lötters S., Duellman W.E., Miranda-Leiva A. 2007. A taxonomic revision of *Atelopus pachydermus*, and description of two new (extinct?) species of *Atelopus* from Ecuador (Anura: Bufonidae). *Zootaxa* 1557: 1–32.

Cope E.D. 1876. Report on the reptiles brought by Professor James Orton from the middle and upper Amazon, and western Peru. *Journal of the Academy of Natural Sciences of Philadelphia* 2: 159–183.

Culley T. 2013. Why vouchers matter in botanical research. *Applications in Plant Sciences* 1: e1300076. doi: 10.3732/apps.1300076

Duellman W.E. 1973. Descriptions of new lizards from the upper Amazon Basin. *Herpetologica* 29: 228-321.

Goicoechea N., Frost D.R., De la Riva I., Pellegrino K.C.M., Sites J., Rodrigues M.T., Padial J.M. 2016. Molecular systematics of teioid lizards (Teioidea/Gymnophthalmoidea: Squamata) based on the analysis of 48 loci under tree-alignment and similarity-alignment. *Cladistics* 32: 624–671. doi: 10.1111/cla.12150

Gutiérrez E.E., Pine R.H. 2017. Specimen collection crucial to taxonomy. *Science* 355: 1275. doi: 10.1126/science.aan0926

Harris D.M. 1985. Infralingual plicae: support for Boulenger's Teiidae (Sauria). *Copeia* 1985: 560–565.

Harris D.M. 1994. Review of the teiid lizard genus *Ptychoglossus*. *Herpetological Monographs* 8: 226–275.

Hernandéz C. 2001. Emberas: territorio y biodiversidad. Estrategias de control en escenarios de conflicto. Programa Semillas & Fundación Swissaid, Bogotá, Colombia.

Köhler G., Diethert H.H., Vesely M. 2012. A contribution to the knowledge of the lizard genus *Alopoglossus* (Squamata: Gymnophthalmidae). *Herpetological Monographs* 26: 173–188. doi: 10.1655/herpmonographs-d-10-00011.1

Krell F., Wheeler Q.D. 2016. Specimen collection: Plan for the future. *Science* 344: 815–816. doi: 10.1126/science.344.6186.815

Linnaeus C. 1758. Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Stockholm, Sweeden.

Minteer B.A., Collins J.P., Love K.E., Puchendorf R. 2014. Avoiding (Re)extinction. *Science* 344: 260–261. doi: 10.1126/science.1250953

Myers C.W., Daly J.W. 1976. Preliminary evaluation of skin toxins and vocalizations in taxonomic and evolutionary studies of poison-dart frogs (Dendrobatidae). *Bulletin American Museum of Natural History* 157: 173–262.

Myers C.W., Daly J.W., Malkin B. 1978. A dangerously toxic new frog used by emberá indias of western Colombia, with discussion of blowgun fabrication and dart poisoning. *Bulletin American Museum of Natural History* 161: 307–366.

Nunes P.M.S., Fouquet A., Curcio F.F., Kok P., Rodrigues M.T.R. 2012. Cryptic species in *Iphisa elegans* Gray, 1851 (Squamata: Gymnophthalmidae) revealed by hemipenial morphology and molecular data. *Zoological Journal of the Linnean Society* 166: 361–376. doi: 10.1111/j.1096-3642.2012.00846.x

O'Shaughnessy W.E. 1881. An account of the Collection of Lizards made by Mr. Buckley in Ecuador, and now in the British Museum, with description of the new species. *Proceedings of the Zoological Society of London* 1881: 227–245. doi:

Pape T. 2016. Taxonomy: species can be named from photos. *Nature* 537. doi: 10.1038/537307b

Peloso P.L.V. 2010. A safe place for amphibians? A cautionary tale on the taxonomy and conservation of frogs, caecilians, and salamanders in the Brazilian Amazonia. *Zoologia* 27: 667–673. doi: 10.1590/S1984-46702010000500001

Peracca M.G. 1904. Viaggio del Dr. Enrico Festa nell Ecuador e regioni vicine. Rettili ed anfibi. *Bollettino dei Musei di Zoologia e Anatomia Comparata della R. Universita di Torino* 19: 1–41.

Presch W. 1980. Evolutionary history of the South American microteiid lizards (Teiidae: Gymnophthalminae). *Copeia* 1980: 36–56.

Recoder R., Werneck F.P., Teixeira Jr M., Colli G.R., Sites Jr J.W., Rodrigues M.T. 2014. Geographic variation and systematic review of the lizard genus *Vanzosaura* (Squamata, Gymnophthalmidae), with the description of a new species. *Zoological Journal of the Linnean Society* 171: 206–225. doi: 10.1111/zoj.12128

Rocha L.A., Aleixo A., Allen G., Almeda F., Baldwin C.C., Barclay M.V.L. ..., Witt C.C. 2016. Specimen collection: An essential tool. *Science* 344: 814–815. doi: 10.1126/science.344.6186.814

Ruibal R. 1952. Revisionary studies of some South American Teiidae. *Bulletin of the Museum of Comparative Zoology* 106: 477–529.

Ruthven A.G. 1924. Description of a new lizard of the genus *Alopoglossus*. *Occasional Papers of the Museum of Zoology, University of Michigan* 153: 1–3.

Torres-Carvajal O., Lobos S.E. 2014. A new species of *Alopoglossus* lizard (Squamata, Gymnophthalmidae) from the tropical Andes, with a molecular phylogeny of the genus. *ZooKeys* 410: 105–120. doi: 10.3897/zookeys.410.7401

Torres-Carvajal O., Lobos S.E., Venegas P.J., Chávez G., Aguirre-Peñafiel V., Zurita D., Echeverría L.Y. 2016. Phylogeny and biogeography of the most diverse clade of South

American gymnophthalmid lizards (Squamata, Gymnophthalmidae, Cercosaurinae). *Molecular Phylogenetics and Evolution* 99: 63– 75. doi: 10.1016/j.ympev.2016.03.006

APPENDIX 1

Specimens examined for comparisons

Alopoglossus angulatus (*n = 2*). SURINAM: **Brokopondo**: Brownsberg Nature Park, AMNH-R 119395. BRAZIL: **Mato Grosso**: Vila Murtinho, UMMZ 56853 (*holotype* of *Alopoglossus amazonius*: examined from photographs).

Alopoglossus atriventris (*n = 2*). COLOMBIA: **Departamento Putumayo**: Aprox. 10 km (airline) south of Mocoa, AMNH-R 106634 (*paratype*). ECUADOR: **Provincia Napo**, Lago Agrio, KU 126783 (*holotype*: examined from photographs).

Alopoglossus buckleyi (*n = 4*). ECUADOR: **Provincia Morona-Santiago**: Cusuime, Río Cusuime, 60 km airline southeast of Macas, AMNH-R 113762–113764; **Provincia Canelos**, BMNH 1946.8.31.66 (*holotype*: examined from photographs in Avila-Pires (1995))

Alopoglossus copii (*n = 2*). ECUADOR: **0**, UMMZ177888. PERU: **Loreto**: 1.5 km north of Teniente Lopez, KU 222169.

Alopoglossus festae (*n = 9*). ECUADOR: **Provincia Pichincha**: Rio Baba, 5–10 km southwestern of Santo Domingo de los Colorados, AMNH-R 110608; **Provincia El Oro**: Santa Elena, AMNH-R 21855; Pasage, AMNH-R 21856; Santa Rosa, AMNH-R 21995; 3 km east of Pasaje, AMNH-R-110609; 10 km southeast of Machala, AMNH-R 112998–112999; **Provincia Guayas**: Bucay, AMNH-R 21956; 3 km north of Naranjal, AMNH-R 110610; Naranjal, AMNH-R 23429.

Alopoglossus lehmanni (*n = 1*). COLOMBIA: **Departamento Valle del Cauca**, Lower Rio Calima, FMNH 165199 (*holotype*)

Alopoglossus viridiceps (*n = 1*). ECUADOR: **Provincia Pichincha**: Nanegal, Santa Lucia Cloud Forest Reserve, QCAZ 10670 (*holotype*, examined from photographs in Torres-Carvajal and Lobos (2014)).

Table 1. Variation in measurements and selected scale counts in the type series of *Alopoglossus embera.* Holotype is marked in **bold**. **1.** From posterior end of last chinshields to snout; **2.** From anterior corner of eye to snout; **3,** From posterior corner of eye to tympanum; **4.** From first row of dorsals to the posterior margin of cloacal plate. **5.** From first row after gulars to last row before cloacal plate. Only adult specimens included.

	AMNH-R 109682	AMNH-R 109683	AMNH-R 109684	AMNH-R 109687	UV-CD 7270	UV-CD 2457	Range
Sex	**Female**	Female	Female	Female	Female	Male	
Snout to vent length	**51.5**	29.1	53.9	39.3	55.3	44.3	29.1–53.9
Head length[1]	**11.5**	7.8	11.3	9.3	11.2	9.4	7.8–11.5
Head width	**8.4**	5.3	7.2	6.6	8.1	7.1	5.3–8.4
Snout length[2]	**4.5**	2.9	4.6	3.6	4.9	3.8	2.9–4.6
Temporal region length[3]	**4.0**	2.1	4.2	3.1	4.6	3.5	2.1–4.2
Tympanum diameter	**1.8**	1.1	1.7	1.7	1.7	1.7	1.1–1.8
Fermoral pores	**0**	0	0	0	2	8	8 (M) / 0–2 (F)
Rows of dorsals[4]	**29**	25	29	27	32	32	23–32
Transversal rows of ventrals[5]	**17**	16	17	16	16	17	16–17
Infralabials	**6**	5	6	5	5	5	5–6
Subocular	**5**	4	4	5	5	4	4–5
Enlarged Palpebrals	**6**	6	5	7	3	7	3–7
Superciliars	**5**	5	5	5	6	5	5–5
Supraoculars	**4**	4	4	4	3	4	3–4
Scales on cloacal plate	**4**	4	4	4	3	3	3–4

Lamellae under finger IV	**14**	15	14	15	13	13	13–15
Lamellae under toe IV	**17**	18	18	19	19	17	17–19

Figure 1. Holotype of *Alopoglossus embera* AMNH-R 109682.

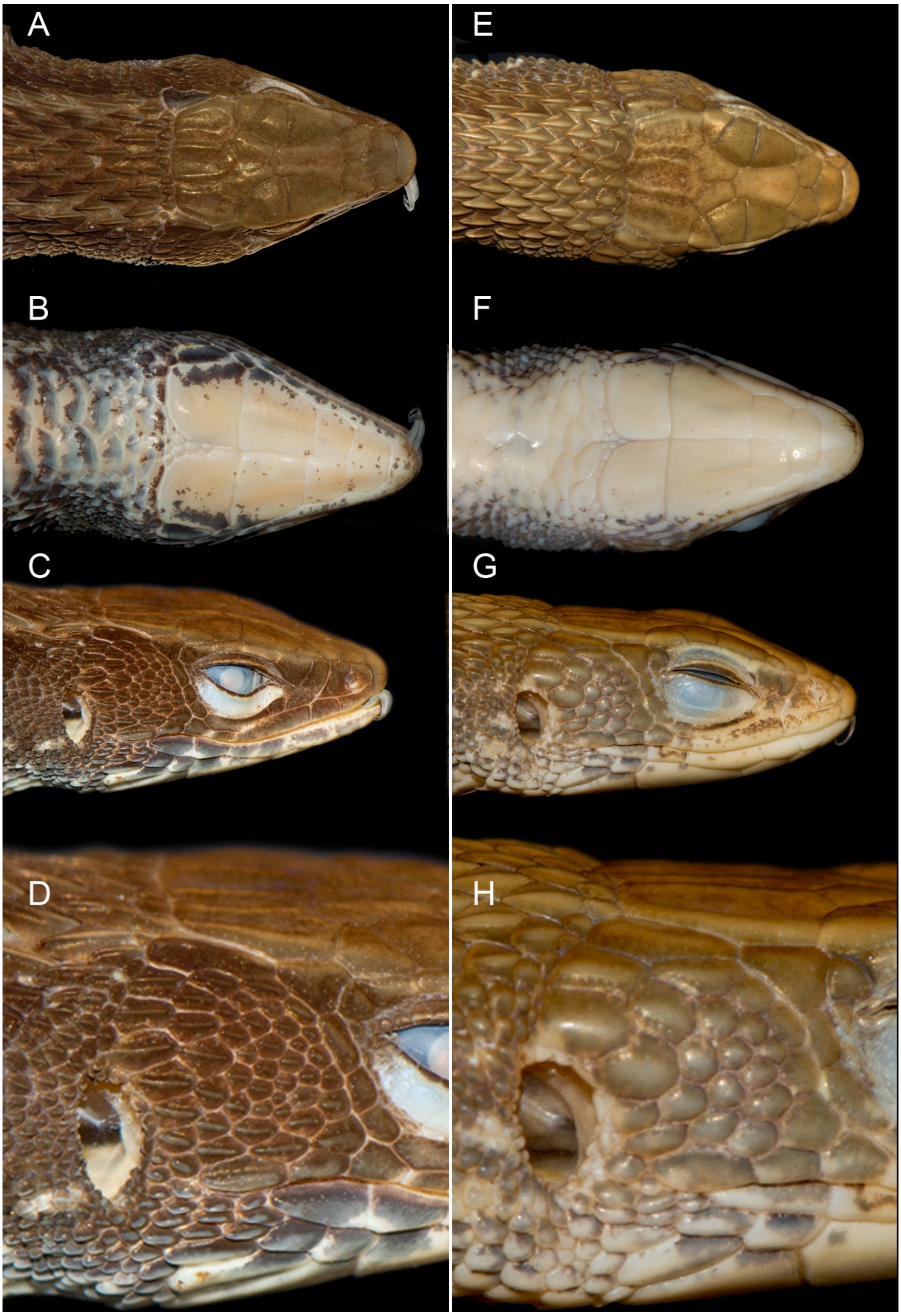

Figure 2. Heads of (**A–D**) *Alopoglossus embera* sp. nov. (AMNH-R 109682, holotype), and (**E–H**) *A. festae* (AMNH-R 110610). (**A, D**) Dorsal, (**B, E**) ventral, (**C, G**) and lateral views. (**D, H**) Close-ups of temporal region evidencing strong keels on temporal scales of *A. embera* (**D**), usually lacking in *A. festae* (**H**).

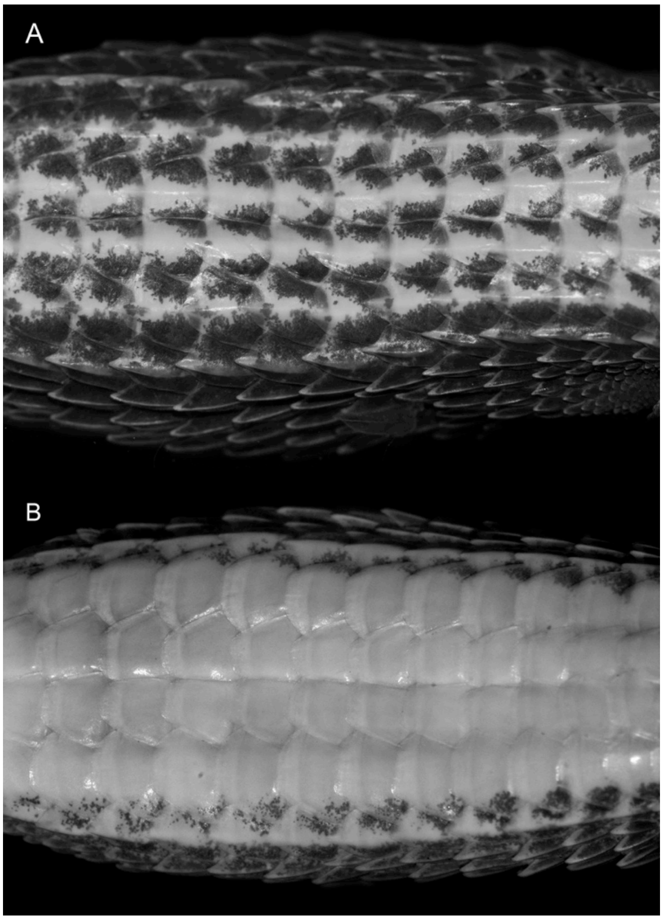

Figure 3. View of ventral scales, at midbody, of (**A**) *Alopoglossus embera* sp. nov. (AMNH-R 109682, holotype), and (**B**) *A. festae* (AMNH-R 110610). Note keels on scales of *A. embera*, lacking in *A. festae.*

Figure 4. Details of the dorsum of right hand of the holotype of *Alopoglossus embera* (AMNH-R 109682).

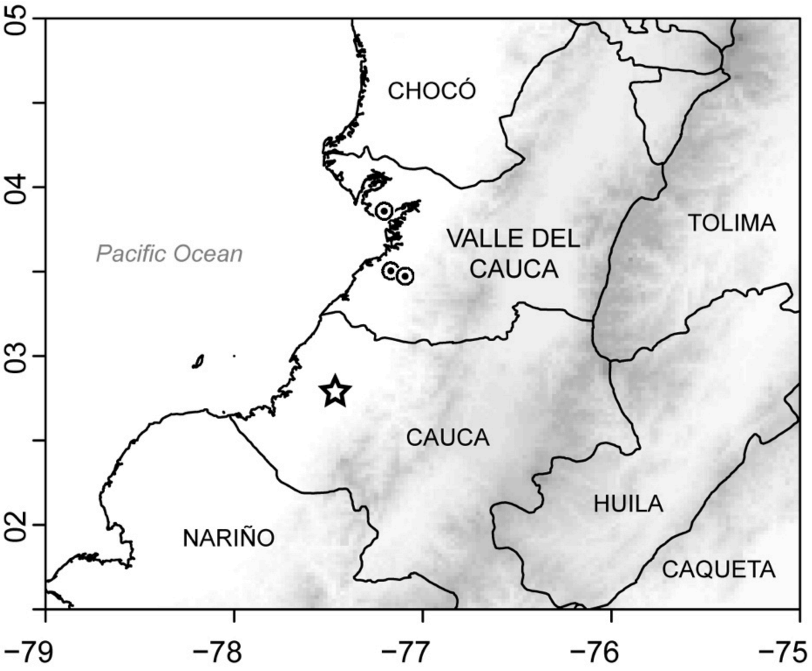

Figure 5. Known localities of *A. embera* sp. nov. Star = Quebrada Guanguí, Departamento Cauca (type locality). Dot = Two nearby localities at Departamento Valle del Cauca (see text for details).

CONCLUSÕES GERAIS

Este trabalho representa uma um avance considerável no conhecimento de Alopoglossidae em ralação com o feito ate agora. Antes deste trabalho somente tinham sido incluídas umas poucas espécies nas analises filogenéticas. A hipótese de relacionamento filogenético proposta aqui contem todas as validas de alopoglossideos. A topologia recuperada nesta analise mostrou que o género *Ptychoglossus* é parafiletico, assim foi necessário gerar um novo arranjo para Alopoglossidae, onde decideu-se sinonimizar *Ptychoglossus* (sinonimo junior) com *Alopoglossus* (sinonimo senior).

Embora neste trabalho foi feito um grande esforço para compilar toda a evidencia disponível, têm que se reconhecer as limitações na amostragem (sobre tudo na partição molecular). Assim futuros esforços têm que estar direcionados para ampliar a amostragem usada aqui e testar esta hipótese na luz de nova evidencia. Alem disso é importante ressaltar que a matriz morfológica gerada para este estudo, parte feita baseados na bibliografia e parte em caracteres novos, vai ser importante para futuros estudos filogenéticos não somente sobre Alopoglossidae mas também Gymnophthalmoidea.

A nova espécie descrita no segundo capitulo sugere a ocorrência de variação críptica dentro de Alopoglossidae. Por isto é importante avaliar detalhadamente as espécies descritas ate agora que talvez podem conter espécies ainda não descritas e incentivar a novas coletas em novas em novas localidades.

ANEXOS

Anexo I – As normas da revista *Cladistics* na qual vai ser encaminhado o Capitulo I desta dissertação para sua publicação podem ser conferidas no seguinte link:

https://onlinelibrary.wiley.com/page/journal/10960031/homepage/forauthors.html

Anexo II – As normas da revista *South American Journal of Herpetology* na qual vai ser encaminhado o Capitulo II desta dissertação para sua publicação podem ser conferidas no seguinte link:

http://sbherpetologia.org.br/publicacoes/south-american-journal-of-herpetology/instructions-to-authors/

ARTIGOS PUBLICADOS DURANTE O PERÍODO DO MESTRADO

Cordoba, DR., Vásquez, D., Arboleda, S., Hernández, C., Giraldo, A. (2016) Diversidad de peces en sistemas lóticos y lentícos asociada al bioma de bosque seco de Victoria, Caldas. Revista de Ciencias. 20 (2): 61– 78.

Hernandez-Morales, C., Peloso, P. L. V., Bolívar-G, W & Daza, J. D. (In press) Cranial anatomy of the colombian endemic lizard *Ptychoglossus vallensis* (Alopoglossidae), a comparative treatise within Gymnophthalmoidea, a megadiverse Neotropical clade. The Anatomical Record.

Peloso, P.L. V, Hernandez-Morales, C. 2017. Description of a new species of *Alopoglossus* Boulenger , 1885 from western Colombia (Gymnophthalmoidea). South American Journal of Herpetology. 12, 89–98.