PUCRS

ESCOLA DE CIÊNCIAS
PROGRAMA DE PÓS-GRADUAÇÃO EM ZOOLOGIA
DOUTORADO EM ZOOLOGIA

FIDÉLIS JÚNIO MARRA SANTOS

# A REVISION OF THE SMALL SNAKES OF THE FAMILY ANOMALEPIDIDAE (REPTILIA: SQUAMATA: SERPENTES), USING HIGH RESOLUTION COMPUTERIZED TOMOGRAPHY

Porto Alegre
2018

PÓS-GRADUAÇÃO - *STRICTO SENSU*

AD VERVM DVCIT

Pontifícia Universidade Católica do Rio Grande do Sul

**PONTIFÍCIA UNIVERSIDADE CATÓLICA DO RIO GRANDE DO SUL**
**ESCOLA DE CIÊNCIAS**
**PROGRAMA DE PÓS-GRADUAÇÃO EM ZOOLOGIA**

# A REVISION OF THE SMALL SNAKES OF THE FAMILY ANOMALEPIDIDAE (REPTILIA: SQUAMATA: SERPENTES), USING HIGH RESOLUTION COMPUTERIZED TOMOGRAPHY

**Fidélis Júnio Marra Santos**

**TESE DE DOUTORADO**
**PONTIFÍCIA UNIVERSIDADE CATÓLICA DO RIO GRANDE DO SUL**
**Brasil**

**2018**

PONTIFÍCIA UNIVERSIDADE CATÓLICA DO RIO GRANDE DO SUL
ESCOLA DE CIÊNCIAS
PROGRAMA DE PÓS-GRADUAÇÃO EM ZOOLOGIA

# A REVISION OF THE SMALL SNAKES OF THE FAMILY ANOMALEPIDIDAE (REPTILIA: SQUAMATA: SERPENTES), USING HIGH RESOLUTION COMPUTERIZED TOMOGRAPHY

**Fidélis Júnio Marra Santos**
**Orientador: Roberto E. Reis**

**TESE DE DOUTORADO**
**PORTO ALEGRE - RS - BRASIL**

“*A onisciência é negada ao homem*”.

Ludwig von Mises

## AVISO

Esta tese é parte dos requisitos necessários para obtenção do título de doutor, área de Zoologia, e como tal, não deve ser vista como uma publicação no senso do Código Internacional de Nomenclatura Zoológica (capítulo 3 – artigo 9) (apesar de disponível publicamente sem restrições). Desta forma, quaisquer informações inéditas, opiniões e hipóteses, assim como nomes novos, não estão disponíveis na literatura zoológica. Pessoas interessadas devem estar cientes de que referências públicas ao conteúdo desse estudo, na sua presente forma, somente devem ser feitas com aprovação prévia do autor.

## NOTICE

This thesis is a partial requirement for the PhD degree in Zoology and, as such, should not be considered as a publication in the sense of the International Code of Zoological Nomenclature (chapter 3 – article 9) (although it is available without restrictions). Therefore, any new information, opinions, and hypotheses, as well as new names are unavailable in the zoological literature. Interested people are advised that any public reference to this study, in its current form, should only be done after previous acceptance of the author.

**Sumário**

Eu dedico esta tese à minha Mãezinha Linda e ao meu Saudoso Pai (*in memoriam*).

## Agradecimentos

Primeiramente, eu agradeço a Jesus Cristo e à minha Família, de onde me inspiro e me fortaleço.

Ao meu Orientador, Professor Dr. Roberto Esser dos Reis, não de agora, mas desde que ele me aceitou como seu orientando no mestrado tempos atrás. Muito obrigado por tudo!! Pela orientação, por todos os ensinamentos, pela paciência e pelo exemplo a ser seguido.

Ao Professor Dr. Nelson Ferreira Fontoura pelo importante apoio inicial no desenvolvimento do trabalho com CT Scan.

Ao Professor Dr. Arno Antônio Lise pela avaliação inicial do projeto de tese.

Aos Professores, Dr. Carlos Alberto Santos de Lucena e Dr. Eduardo Eizirik pelas sugestões durante o exame de qualificação.

Aos Professores que formaram a banca durante a defesa da minha tese: Dra. Sonia Zanini Cechin, Dr. Francisco Luís Franco, Dr. Márcio Borges Martins e Dr. Roberto Esser dos Reis.

À Dra. Bárbara Borges Calegari e Dr. Héctor Samuel Vera-Alcaraz por toda a bibliografia que me foi repassada durante o exame de qualificação.

Aos Doutorandos Andres Felipe Jaramillo e Steven Alejandro Valencia Zuleta pelas informações de espécimes depositados em coleções da Colômbia.

Ao Mestrando Jayme Massim Marques por toda a sua dedicação e esforço nas diversas etapas do trabalho com CT Scan.

Ao Geólogo M.Sc. Adolpho Herbert Augustin pelo escaneamento dos espécimes e instrução sobre a utilização dos programas utilizados no processamento dos modelos 3D.

Ao Professor Dr. Gervásio Silva Carvalho pelos ensinamentos a respeito das bases de Nomenclatura Zoológica.

*A Big Thanks to Dr. Christopher J. Bell for receiving me in his laboratory, and for all the support in the acquisition of specimens and scanning during the time I worked at the University of Texas at Austin. Chris, Thank You Very Much*!!

*Dr. Jessica Anderson Maisano and Patrick Stafford, thank you very much for your support on the scanning of specimens.*

*Teresita Gonzalez, thank you very much for the support with all documentation. Your support was essential for the development of my work. Thank you!*

*I thank also to Erin Brown for his support in organization of documents. My thanks also to Dr. William Gelnaw, M.S. Joshua Lively, and M.S. Rachel Wallace of the Jackson School of Geosciences.*

*Special thanks to Rachael Rawlins. Thank you very much for all your attention and support since I arrived in Austin.*

Ao Biólogo Juliano Romanzini do MCT-PUCRS pelas fotografias dos espécimes representantes de novos táxons.

Agradeço aos professores do Programa de Pós-Graduação em Zoologia da PUCRS pelo aprendizado, não somente durante o doutorado, mas desde o mestrado. Obrigado!

Em relação ao suporte na resolução de questões relacionadas a defesa da minha tese, eu agradeço muito o Coordenador do Programa de Pós-Graduação em Zoologia, Professor Dr. Sandro Luis Bonatto, aos integrantes da Comissão Coordenadora do PPG-Zoo-PUCRS no período 2017/1 e ao Coordenador de Programas Stricto Sensu da PUCRS, Professor Dr. Christian Haag Kristensen.

À Patricia Costa Baptista e Zíngara Leal Lubaszewski por toda atenção às minhas requisições junto ao Programa de Pós-Graduação em Zoologia da PUCRS.

Agradeço à Secretaria do Museu de Ciências e Tecnologia da PUCRS por toda assistência com os assuntos relacionados ao desenvolvimento do meu trabalho no museu e, da mesma maneira, aos funcionários do MCT-PUCRS pela solicitude em resolver as demandas que eu precisei no laboratório.

Agradeço muito à Ariane Nunes de Oliveira, Gizela Vieira Scartazzini e Joyce Ferrari Pinheiro da Biblioteca Central Irmão José Otão-PUCRS, pela aquisição de todas as bibliografias que eu precisei e solicitei à Biblioteca. Muito Obrigado!

Agradeço à Policia Militar do estado de São Paulo e à Equipe de Segurança do Parque Estadual de Ilhabela durante a campanha na ilha de São Sebastião.

Ao Programa de Pós-Graduação em Zoologia da PUCRS pelo suporte financeiro na execução da campanha no Parque Estadual de Ilhabela.

Agradeço ao Programa de Pós-Graduação em Zoologia da PUCRS e à CAPES pela bolsa de estudos durante o doutorado e também pela bolsa PDSE, que foi essencial para eu examinar espécimes tipo de Anomalepididae e conhecer técnicas avançadas de escaneamento e processamento digital de vertebrados, o que, infelizmente, não seria possível aqui no Brasil, e neste agradecimento à CAPES, eu faço um agradecimento especial à Valdete Lopes, responsável pelo meu processo durante o período do sanduíche. Muito obrigado Valdete por sua atenção e agilidade na resolução das burocracias!

Agradeço às gerações passadas de Zoólogos, que em épocas atrás, se dedicaram à anatomia, à morfologia das cobras cegas, especialmente das Anomalepididae, que foi em seu tempo um grande desafio (e continua sendo), mas o resultado dos seus esforços nos ajuda hoje a compreender um pouco mais a biologia deste incrível grupo de serpentes.

E finalizando, agradeço muito às tantas pessoas que surgiram ao longo desses cinco anos, por vários lugares onde eu passei e, de uma maneira ou de outra, contribuíram para o fechamento desta desafiadora jornada lidando com as cobras-cegas. Obrigado!

Por fim, um agradecimento especial aos pagadores de impostos Brasileiros, que produzem riquezas e trabalho, e agregam valor ao Brasil. Aos pagadores de impostos Brasileiros, o meu especial Muito Obrigado pelo dinheiro que custeou o meu doutorado.

**Resumo**

A família Anomalepididae atualmente é constituída por 18 espécies de cobras, conhecidas como "cobras-cegas", fossoriais e de distribuição geográfica restrita à região Neotropical. Praticamente, não há informações a respeito da história de vida dos Anomalepididae, pois são animais de difícil coleta e a manutenção em cativeiro para estudos com biologia é bastante difícil. As informações disponíveis a respeito de cobras Anomalepididae estão concentradas em estudos anatômicos, principalmente osteologia do crânio, taxonomia e filogenia a nível de famílias dentro de Serpentes. Mas, desde a descrição de Anomalepididae por Taylor em 1939, não houve uma revisão taxonômica abrangente dentro da família ou alguma inferência filogenética com novos arranjos taxonômicos. Em relação à taxonomia do grupo, a literatura é restrita à descrição de novas espécies e revisões taxonômicas de dois gêneros (*Anomalepis* e *Liotyphlops*). O objetivo primário deste estudo foi a revisão taxonômica da família Anomalepididae e, para isto, foi utilizado toda a amostragem possível de espécies e espécimes na aquisição de dados morfológicos, além do emprego da técnica High-Resolution X-ray Computed Tomography (HRXCT). O objetivo secundário foi inferir uma hipótese filogenética para as espécies dentro de Anomalepididae com base nos caracteres anatômicos obtidos do exame de espécimes. Este trabalho resultou em um novo arranjo taxonômico para Anomalepididae, com 19 espécies válidas, descrição de duas novas espécies de *Liotyphlops* para o Brasil, sendo uma para o estado de Mato Grosso e outra para o estado de Santa Catarina e a recondução de *Liotyphlops beui* para a sinonímia de *Liotyphlops ternetzii*. Além disto, a análise de parcimônia com base em caracteres do crânio e da morfologia externa recuperou Anomalepididae como um táxon monofilético dentro de Scolecophidia.

**Palavras-chave**: Taxonomia, Filogenia, CT scan, Neotropical, Biodiversidade.

## Abstract

The family Anomalepididae currently consists of 18 species known as "blind snakes", fossorial in habit and with geographical distribution restricted to the Neotropical region. Practically, there is no information about the life history of the Anomalepididae, because they are difficult to collect and the maintenance in captivity for biology studies is quite difficult. The information available regarding Anomalepididae snakes is concentrated on anatomical studies, mainly osteology of the skull, taxonomy, and phylogeny at the level of families within Serpentes. But since the description of Anomalepididae by Taylor in 1939, there has been no comprehensive taxonomic review within the family or some phylogenetic inference with new taxonomic arrangements. In relation to the taxonomy of the group, the literature is restricted to the description of new species and taxonomic revisions of two genera (*Anomalepis* and *Liotyphlops*). The primary objective of this study was the taxonomic revision of the Anomalepididae and, for this, all possible sampling of species and specimens were used in the acquisition of morphological data, besides the use of the High-resolution X-Ray Computed Tomography (HRXCT) technique. The secondary objective was to infer a phylogenetic hypothesis for the species within Anomalepididae based on the anatomical characters obtained from the specimen examination. This work resulted in a new taxonomic arrangment for Anomalepididae, with 19 valid species, description of two new species of *Liotyphlops* from Brazil, being one for the state of Mato Grosso and the other for the state of Santa Catarina, and the re-conduction of *Liotyphlops beui* to the synonymy of *Liotyphlops ternetzii*. In addition, the parsimony analysis based on characters from the skull and external morphology recovered Anomalepididae as a monophyletic taxon within Scolecophidia.



**Keywords**: Taxonomy, Phylogeny, CT scan, Neotropical, Biodiversity.

## Apresentação

Conhecer a história natural das serpentes fossoriais, conhecidas como "cobras cegas" é, talvez, um dos grandes desafios da Ofiologia e, igualmente desafiador, é o trabalho com objetivo taxonômico e sistemático. Em se tratando especificamente da família Anomalepididae, o trabalho se torna ainda mais desafiador pois, num primeiro momento, a distribuição geográfica restrita a Região Neotropical pode parecer algo favorável, principalmente em se tratando da aquisição de espécimes. Ocorre que os espécimes desta família depositados nas coleções não são abundantes (com exceção de poucas espécies) e há uma série de restrições quanto às técnicas invasivas. Além de ser muito difícil a coleta desses animais na Natureza em condições ambientais normais, pois, em condições em que o habitat passa por alguma alteração, como uma enchente, por exemplo, as possibilidades de contato com essas serpentes são maiores.

Dito isto, o objetivo desta tese de doutorado é contribuir para o conhecimento taxonômico e sistemático da família Anomalepididae. A tese esta estruturada em forma de artigo científico, de acordo com o item 10 da Norma de Apresentação de Dissertações e Teses do Programa de Pós-Graduação em Zoologia da PUCRS, disponível em: http://www.pucrs.br/fabio/programa-de-pos-graduacao-em-zoologia/informacoes-adicionais/formularios/. O artigo segue as normas da revista Zoologia: an international journal for Zoology ISSN 1984-4689 (https://zoologia.pensoft.net/about#Author-Guidelines).

O artigo, intitulado **A revision of the small snakes of the family Anomalepididae (Reptilia: Squamata: Serpentes), using high resolution computerized tomography** tem por resultados a revisão taxonômica de Anomalepididae, a recondução de *Liotyphlops beui* (Amaral, 1924) para a sinonímia de *Liotyphlops ternetzii* (Boulenger, 1896) após o estudo de caracteres ósseos do crânio e morfologia externa, a descrição de duas espécies novas de *Liotyphlops* para o Brasil e uma hipótese filogenética para as espécies de Anomalepididae.

# A revision of the small snakes of the family Anomalepididae (Reptilia: Squamata: Serpentes), using high resolution computerized tomography

Fidélis Júnio Marra Santos[1] & Roberto E. Reis[1]

[1]PUCRS, Laboratório de Sistemática de Vertebrados. Av. Ipiranga, 6681 Partenon. 90619-900 Porto Alegre, Rio Grande do Sul, Brasil. E-mail: fidelismarra@gmail.com and reis@pucrs.br.

**Abstract**. The family Anomalepididae was proposed by Taylor in 1939, and currently consists of 18 species known as "blind snakes", fossorial in habit, with geographical distribution restricted to the Neotropical region, and containing four genera: *Anomalepis* Jan, 1860 (four species), *Helminthophis* Peters, 1860 (three species), *Liotyphlops* Peters, 1881 (10 species) and *Typhlophis* Fitzinger, 1843 (one species). Since the description of the family, no taxonomic review or phylogenetic hypothesis for the species of Anomalepididae were published, so the objective of this study is the taxonomic revision and the inference of a phylogenetic hypothesis for the species of this family based on skull characters using the High-resolution X-Ray Computed Tomography (HRXCT) technique and external morphology. This work resulted in a new taxonomic arrangement for the Anomalepididae, with 19 valid species, description of two new species of *Liotyphlops* from Brazil, being one from the state of Mato Grosso and the other from the state of Santa Catarina, and the re-conduction of *Liotyphlops beui* to the synonymy of *Liotyphlops ternetzii*. In addition, the parsimony analysis based on characters from the skull and external morphology recovered Anomalepididae as a monophyletic taxon within Scolecophidia.

**Key works.** Taxonomy, Phylogeny, CT scan, Neotropical, Biodiversity.

## Introduction

Blind snakes are divided into five families: Anomalepididae Taylor, 1939 (four genera and 18 species), Leptotyphlopidae Stejneger, 1892 (13 genera and 139 species), Typhlopidae Merrem, 1820 (11 genera and 260 species), Gerrhopilidae Vidal, Wynn, Donnellan & Hedges, 2010 (one genus and 15 species), and Xenotyphlopidae Vidal, Vences, Branch & Hedges, 2010 (one genus and two species) (Vidal et al. 2010, Van Wallach et al. 2014, Vitt & Caldwell 2014, Uetz & Hošek 2017). The Anomalepididae consists of snakes known popularly as "blind snakes" and contains four genera: *Anomalepis* Jan, 1860 (four species), *Helminthophis* Peters, 1860 (three species), *Liotyphlops* Peters, 1881 (10 species) and *Typhlophis* Fitzinger, 1843 (one species). These genera have geographical distribution restricted to the Neotropical region, presenting a disjunct distribution in Central America and South America (Fig. 1; McDiarmid et al. 1999, Van Wallach et al. 2014, Vitt & Caldwell 2014, Uetz & Hošek 2017). Anomalepidid snakes are mainly diagnosed by the pattern of the head scales, especially the form and contact between the rostral, prefrontal, and frontal scales (Fig. 2; Dixon & Kofron 1984, Peters et al. 1986). Among the Anomalepididae, *Typhlophis squamosus* (Schlegel, 1839) is monotypic, and unlike other genera within the family, the scales of the head are undifferentiated.

According to Taylor (1939), the snake genus which Jan (1861) named *Anomalepis*, was regarded by him as belonging in the family Typhlopidae. Still according Taylor, Garman (1883), who allocated the genus in the subfamily Stenostominae rather than Typhlopinae of the family Typhlopidae, did so through an error. In 1939, in the proposition of the family Anomalepididae, Taylor wrote the following: “this small group of snakes associated in the genus *Anomalepis* differs from both the families Typhlopidae and Leptotyphlopidae in such a way as to preclude their inclusion in either of these families.” Still according to him, the squamation of the head is so very different that it may be considered unique in serpents, and he diagnosed Anomalepididae as follows: “small wormlike snakes, the eye largely concealed under a shield; teeth present in maxilla and mandible. Body covered with smooth cycloid scales, bearing single pits.”

After the proposition of the Anomalepididae by Taylor (1939), four genera were included in the family: *Anomalepis*, described by Jan in 1860; *Helminthophis*, described by Peters in 1860; *Liotyphlops*, described by Peters in 1881 and; *Typhlophis*, described by Fitzinger in 1843. Hahn (1980) provided a brief review of the Anomalepididae, and until today is the only work related to a taxonomic review of this family. Detailed taxonomic revisions were made by Dixon & Kofron (1984) for the species of *Liotyphlops*, and by Kofron (1988) for the species of *Anomalepis*. The species of *Helminthophis* and *Typhlophis* have not yet been reviewed. The most recent works on the taxonomy of Anomalepididae were restricted to the description of new species of *Liotyphlops* (Freire et al. 2007, Haad et al. 2008, Centeno et al. 2010).

There are several papers analyzing the phylogeny of snakes within the Squamata or the relationships among snake families, based on anatomical, morphological, ecological, molecular, or combining anatomical and molecular data (e.g. Lee et al. 2002, 2007, Vidal & Hedges 2002, Townsend et al. 2004, Conrad 2008, Vidal et al. 2010, Wiens et al. 2010, 2012, Gauthier et al. 2012, Pyron et al. 2013, Hsiang et al. 2015, Reeder et al. 2015). However, the authors who included Scolecophidia snakes in their analyses, specifically Anomalepididae, worked with small samples, possibly due to the limitations of material for more evasive morphological studies and/or, mainly, limitations on acquisition of material for molecular analyses. Most of the works on phylogeny of snakes that included Anomalepididae, present information on two species, *Liotyphlops albirostris* and *Typhlophis squamosus* (e.g. Vidal et al. 2010, Gauthier et al. 2012, Pyron et al. 2013, Figueroa et al. 2016), and others show information regarding a single species, *L. albirostris* (e.g. Vidal & Hedges 2002, Conrad 2008, Wiens et al. 2012). Since the description of the family Anomalepididae by Taylor (1939), except for the brief review of Hahn (1980), there was no paper published dealing with phylogenetic hypothesis within Anomalepididae and proposing new taxonomic arrangements. For this reason, the main objetive of this work is the taxonomic revision of the family Anomalepididae and, in addition, the phylogeny of species of Anomalepididae employing a cladistics analysis based on external morphology and osteology of the skull of 16 of the 19 valid species.

## Material and methods

We adopted the definition of the Unified Species Concept (Queiroz 2007), in which species are equated with independently evolving metapopulation lineages. In the absence of autapomorphy for species, consistent morphological difference among separate populations is used as a proxy for lineage independence (Reis 2017). The matrix used for the parsimony analysis was constructed with characters taken from the osteology of the skull and external morphology (Table 1). For the osteology 29 specimens of Anomalepididae were examined, including representatives of the four genera and 16 valid species. The specimens were obtained from loans and studied by means of scanning using High-Resolution X-ray Computed Tomography. Specimens of the following institutions were examined: AMNH (Department of Herpetology, American Museum of Natural History, New York), BMNH (The Natural History Museum, London), CEPB (Centro de Estudos e Pesquisas Biológicas da Pontifícia Universidade Católica de Goiás, Goiânia), CM (Carnegie Museum of Natural History, Pittsburgh), INPA (Instituto Nacional de Pesquisas da Amazônia, Manaus), MCP (Museu de Ciências e Tecnologia da Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre), MCZ (Museum of Comparative Zoology, Harvard University, Cambridge), MHNLS (Museo de Historia Natural La Salle, Caracas), MNRJ (Museu Nacional da Universidade Federal do Rio de Janeiro, Rio de Janeiro), MVZ (Museum of Vertebrate Zoology, Berkeley), MZUSP (Museu de Zoologia da Universidade de São Paulo, São Paulo), UFRGS (Universidade Federal do Rio Grande do Sul, Porto Alegre), ZUEC (Museu de Zoologia da Universidade Estadual de Campinas, Campinas), and ZUFSM (Coleção de Répteis da Universidade Federal de Santa Maria, Santa Maria). *Anilius scytale* (Linnaeus, 1758) and *Acrochordus* sp. were included in the outgroup based on the work of Lee & Scalon (2002) (the four specimens of *A. scytale* MCP 4454, MCP 14069, MCP 14070 e MCP 19066 were examined for the acquisition of external morphology characters). In addition, six specimens of three species of Leptotyphlopidae Stejneger 1892, and three specimens of two species of Typhlopidae Merrem, 1820 were scanned for the composition of the outgroup. All specimens of Leptotyphlopidae and Typhlopidae are part of the herpetological collection of MCP (Appendix II). In this study, the outgroup was formed by eight terminal taxa, including *Lanthanotus borneensis* (Steindachner 1878) as the root. The selection of taxa for the outgroup is based on the work of Lee & Scanlon (2002) where the sister group of Anomalepididae is Typhlopidae with Leptotyphlopidae constituting the sister group of the branch Anomalepididae + Typhlopidae. The characters follow the original descriptions of Lee & Scanlon (2002), and some characters follow the description of Gauthier et al. (2012). The source of each character is presented at the end of the description. New characters or new character states proposed in this study are marked with a superscript "[N]". Characters reinterpreted were marked as "modified".

The study of external morphology occurred by examining specimens preserved in alcohol under stereomicroscope. The terminology used for the head squamation and scale counts follows Dixon & Kofron (1984), Peters et al. (1986), Kofron (1988), and Centeno et al. (2010). Regarding the character described by Taylor as "the eye largely concealed under a shield", this means the character named in the present work as "eye spot", due to the presence of vestigial eyes that can be seen (or not) (Fig. 3) in the form of a tiny stain, which conventionally is called "eye spot". The terminology used for the bones of the skull follows Haas (1968), Lee & Scanlon (2002), Rieppel et al. (2009), and Gauthier et al. (2012). The set of characters of skull osteology were grouped into neurocranium (characters 1-48), mandible (49-54), dentition (55-59), and external morphology (60-68). All illustrations of the skull are derived from three-dimensional reconstructions of the CT scans acquired for this study. All specimens examined in this study are listed in Appendix II.

For the morphometric and meristic analyses two numeric analytical tools were used: Univariate, with range of variation, mean (average value), mode (most frequent value), and standard deviation; and Bivariate, for body proportions. For these analyses were used the software Past 3.14 (Hammer et al. 2001), and DATAX 4.1 (Reis & Fontoura 1991). The result of numeric analytical tools is presented in all descriptions. For species that were represented by one specimen or the original description there is no range of variation, mean, mode, and standard deviation. The photographs were obtained using a digital camera Nikon D5100 coupled to a lens Micro AF-S VR 105mm F/2.8G IF-ED. Also, two desktop digital stereomicroscopes were used, a COSMOS LCD and a Leica DMC 2900. For the preparation of the drawings a Wacom Intuos Draw CTL490DW digital tablet was used with the desktop digital stereomicroscope COSMOS LCD.

The head of the specimens were scanned at the High-Resolution X-ray Computed Tomography Facility at Pontifícia Universidade Católica do Rio Grande do Sul on a Skyscan 1173 microfocus X-ray CT, and in at the High-Resolution X-ray CT Facility at the University of Texas at Austin using a Xradia microXCT Scanner. The dataset was rendered in three dimensions using a laptop with CTvox 3.2 (Bruker 2016) for Windows 64 bits with Intel Core i7-5500U 2.40GHz, 16 GB DDR3L-1600 RAM, and GPU NVIDIA GeForce 920M with 2 GB. All specimens scanned in both institutions had skulls with less than 6.0 mm in length. Scanning parameters were adjusted to each individual specimen, and the Appendix III summarises three basic parameters (source voltage, source current, and voxels) for each scanned specimen.

The data matrix was constructed in the software Mesquite 3.04 (Maddison & Maddison 2015). The parsimony analysis was conducted with the software WinClada 1.00.08 (Nixon 2002) in conjunction with the software NONA 2.0 (Goloboff 1999). The most parsimonious trees were obtained through a heuristic search with 10,000 replications, keeping a maximum of 100,000 trees (hold), and branch swapping by Tree Bissection and Reconnection (Multiple TBR + TBR). All characters are of equal weights and unordered. Node support was presented as Bremer support (Bremer 1994), calculated in TNT 1.5 (Goloboff & Catalano 2016) by searching suboptimal trees.

The locality of each specimen of Anomalepididae examined in this study were plotted using the software Google Earth Pro version 7.1.5.1557, and maps with locality points were built using the software ArcMap (ArcGis) version 10.4.1 for desktop. The geographical coordinates use the cartographic system WGS 1984 in all maps. There is overlap of locality points on some maps.

The family distribution map was constructed based on the collection information from two databases: VertNet (http://portal.vertnet.org/search) and SpeciesLink (http://www.splink.org.br/index?lang=pt). All specimens with at least information on the country, state/or province, and municipality were included in Figure 1.

## Results

### Taxonomic accounts

### Anomalepididae Taylor, 1939

Anomalepidae Taylor, 1939, Proceedings of the New England Zoölogical Club 17: 87-96 [95].

Anomalepidinae Amaral, 1954, Memórias do Instituto Butantan 26: 197-202 [198].

Anomalepididae Robb and H. M. Smith, 1966, Natural History Miscellanea 184: 1-8 [1].

**Type-genus.** *Anomalepis* Jan, 1860.

**Diagnosis.** Anomalepididae is diagnosed by two synapomorphies: (1) the nasal bone fused (character 7, state 1), and (2) cephalic scales covering the "eye spot", making it invisible or poorly visible (character 60, state 3). In addition, Anomalepididae is also distinguished from all other families of Scolecophidia snakes by lacking ocular scales (vs. ocular scales present), by laking the lateral maxillary foramina (Fig. 4A) (vs. foramina present, Fig. 4B), by laking a prefrontal-nasal contact (Fig. 5A) (vs. contact present, Fig. 5B), by having one discrete ossification, conventionally termed postorbitofrontal (Fig. 6A) (vs. postorbitofrontal absent, Fig. 6B), and by having an ectopterygoid (Fig. 7A) (vs. ectopterygoid absent, Fig. 7B).

**Genera included.** *Anomalepis* Jan, 1860, *Helminthophis* Peters, 1860, *Liotyphlops* Peters, 1881, and *Typhlophis* Fitzinger, 1843 (Table 1).

**Distribution.** The family is restricted to the Neotropical region, with disjunct distribution in Central and South America, extending from Honduras to Argentina. A single species, *Liotyphlops caissara* Centeno, Sawaya & Germano, 2010, has insular distribution restricted to the island of São Sebastião, São Paulo State, Brazil.

**Popular names.** Blind Snakes (English), cobra-cega (Portuguese).

**Table 1**. New classification of snakes of the family Anomalepididae. The taxonomic arrangement used in this study is compared to previous classifications (e.g., McDiarmid et al. 1999, Wallach et al. 2014, Uetz et al. 2017). New species described in this study are listed here.

| Previous classification | This study | Geographical distribution |
|---|---|---|
| Family Anomalepididae Taylor, 1939 | Anomalepididae | |
| Genus *Anomalepis* Jan, 1860 | *Anomalepis* | |
| *Anomalepis aspinosus* Taylor, 1939 | *Anomalepis aspinosus* | Peru |
| *Anomalepis colombia* Marx, 1953 | *Anomalepis colombia* | Colombia |
| *Anomalepis flavapices* Peters, 1957 | *Anomalepis flavapices* | Ecuador |
| *Anomalepis mexicanus* Jan, 1860 | *Anomalepis mexicanus* | Honduras, Costa Rica, Panama, Peru |
| Genus *Helminthophis* Peters, 1860 | *Helminthophis* | |
| *Helminthophis flavoterminatus* (Peters, 1858) | *Helminthophis flavoterminatus* | Colombia, Venezuela |
| *Helminthophis frontalis* (Peters, 1860) | *Helminthophis frontalis* | Costa Rica, Panama |
| *Helminthophis praeocularis* Amaral, 1924 | *Helminthophis praeocularis* | Colombia |
| Genus *Liotyphlops* Peters, 1881 | *Liotyphlops* | |
| *Liotyphlops albirostris* (Peters, 1858) | *Liotyphlops albirostris* | Costa Rica, Panama, Colombia, Ecuador, Venezuela, Curaçao |
| *Liotyphlops anops* (Cope, 1899) | *Liotyphlops anops* | Colombia |
| *Liotyphlops argaleus* Dixon & Kofron, 1984 | *Liotyphlops argaleus* | Colombia |
| *Liotyphlops caissara* Centeno, Sawaya & Germano, 2010 | *Liotyphlops caissara* | Brazil |
| *Liotyphlops haadi* Silva-Haad, Franco & Maldonado, 2008 | *Liotyphlops haadi* | Colombia |
| *Liotyphlops schubarti* Vanzolini, 1948 | *Liotyphlops schubarti* | Brazil |
| *Liotyphlops ternetzii* (Boulenger, 1896) | *Liotyphlops ternetzii* | Brazil, Paraguay, Uruguay, Argentina |
| *Liotyphlops beui* (Amaral, 1924) | *Liotyphlops ternetzii* | |
| *Liotyphlops trefauti* Freire, Caramaschi & Argôlo, 2007 | *Liotyphlops trefauti* | Brazil |
| *Liotyphlops wilderi* (Garman, 1883) | *Liotyphlops wilderi* | Brazil, Paraguay |
| | *Liotyphlops ss* new species | Brazil |
| | *Liotyphlops tt* new species | Brazil |
| Genus *Typhlophis* Fitzinger, 1843 | *Typhlophis* | |
| *Typhlophis squamosus* (Schlegel, 1839) | *Typhlophis squamosus* | Brazil, Venezuela, Guyana, Surinam, French Guiana |

**Key to genera.**

1. Scales on head undifferentiated (Fig. 8) …………………..…...…...…… ***Typhlophis***

1'. Scales on head differentiated …………………...………………..………………… 2

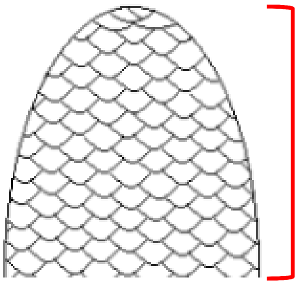


**Figure 8**. Dorsal view of head in *Typhlophis*.

2. Prefrontals separated behind rostral; rostral in contact
with frontal (Fig. 9) ……………………………………………......……….. ***Liotyphlops***

2'. Prefrontals in contact behind rostral; rostral not in contact with
frontal ……………...…………………………………….……...……………………. 3

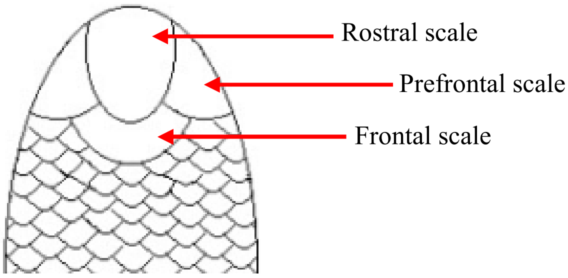


**Figure 9**. Dorsal view of head in *Liotyphlops*.

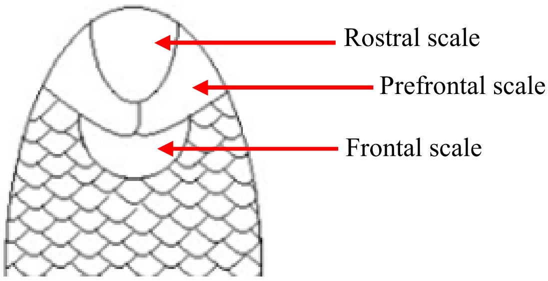


**Figure 10**. Dorsal view of head in *Helminthophis*.

3. Elongate, triangular prefrontals followed by
frontal (Fig. 10) ……………………….……………………...……………..… ***Helminthophis***

3'. Short, pentagonal prefrontals followed by
frontal (Fig. 11) .......……………………....………………………….…….. ***Anomalepis***

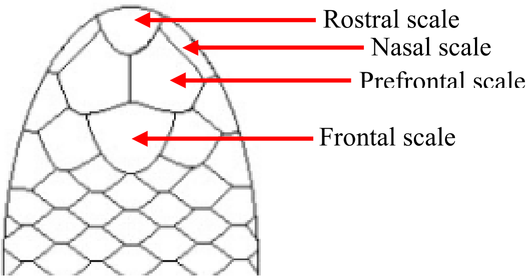


**Figure 11**. Dorsal view of head in *Anomalepis*.

**Remarks.** Robb and Smith (1966) discussed the name of the family "Anomalepidae" proposed by Taylor in 1939 where they argued that in conformity with Article 29 (and Appendix D, p. 135) of the 1961 Code of Zoological Nomenclature, the proper orthography of the family name is the Anomalepididae, since the genitive plural of -*lepis*, from the stem of which the name must be formed, is -*lepidis*. They also argued that the revised orthographic form of the name, first noted by Amaral (1954) although for the subfamily instead of family level, retains the date and authorship of the original orthography. Since then, the name of this family is properly Anomalepididae Taylor, 1939.

***Anomalepis* Jan, 1860**

*Anomalepis* Jan *in* Jan and Sordelli, 1860, Iconographie Générale des Ophidiens I, livr.1: [index to pl. 5 (fig. 1), pl. 6 (fig. 1)]; Type species: *Anomalepis mexicanus* Jan, 1860.

*Anomalolepis* Günther, 1885, Biologia Centrali-Americana. Reptilia and Batrachia 326 Pp. [87]; Type species: *Anomalolepis mexicanus*.

**Diagnosis.** *Anomalepis* is diagnosed by one exclusive synapomorphy: a pentagonal frontal (character 68, state 1). It is also clearly distinguished from all other Anomalepididae by having the nasal-frontal boundary approximately straight and transverse (Fig. 12A) (vs. convex posteriorly in a shallow W-shaped suture, Fig. 12B), by having a fused, single parietal (Fig. 13A) (vs. paired parietal, Fig. 13B), by lacking a supratemporal (Fig. 14A) (vs. supratemporal present, Fig. 14B), and by the supraoccipital participating in internal sidewall of neurocranium (Fig. 15A) (vs. the supraoccipital not participating in internal sidewall of neurocranium, Fig. 15B). In addition, it is also distinguished from *Typhlophis* by having differentiated scales of the head (Fig. 16A) (vs. undifferentiated scales of the head, Fig. 16B). It is further distinguished from *Liotyphlops* by having prefrontals in contact behind the rostral (Fig. 17A) (vs. prefrontals separated behind the rostral, Fig. 17B); and from *Helminthophis* by having short, pentagonal prefrontals (Fig. 18A) (vs. elongate, triangular prefrontals, Fig. 18B).

**Species included.** Four species, *Anomalepis aspinosus* Taylor, 1939, *Anomalepis colombia* Marx, 1953, *Anomalepis flavapices* Peters, 1957, and *Anomalepis mexicanus* Jan, 1860.

**Distribution.** Lower Central America and northwestern South America: Honduras, Costa Rica, Panama, Colombia, Ecuador, and Peru.

**Key to species of *Anomalepis*.**

**1**. Three infralabials ……………………………………………………………….… **2**

**1'**. Four infralabials …………………………………...…… *Anomalepis flavapices*

**2**. Number of scale rows around the midbody 22-24; dorsals 277-312;
ventrals 261-293 …………………………………………………………………….. **3**

**2'**. Number of scale rows around the midbody 29; dorsals 387;
ventrals 354 ……………………..…………………………...… *Anomalepis colombia*

**3**. Subcaudal scales nine …………………….……………...…… *Anomalepis aspinosus*

**3'**. Subcaudal scales 10-11 ……………………………...…. *Anomalepis mexicanus*

**Remarks.** Kofron (1988) revised the genus *Anomalepis* and noted that all four species of *Anomalepis* are characterized by the same arrangement of head scales. He also explained that the number of dorsal scales and the number of scale rows around the body are the only characteristics by which the species can be diagnosed from each other. Based on the examination of specimens of *Anomalepis* in this study, it is concluded that the observation made by Kofron was correct, because the arrangement of scales on the head of the four species of *Anomalepis* is identical and the only diagnostic characters are the scales around the body, the number of dorsal scale rows and, in addition, the number of ventral scale rows. *Anomalepis aspinosus* and *Anomalepis mexicanus*, except for the subcaudal scales (9 and 10-11, respectively) are inseparable by morphology, with overlapping in all observable characters. It is possible that *A. aspinosus* be eventually discovered to be a junior synonym of *A. mexicanus*, and this synonymy is not proposed here due to the need of the examination of more numerous specimens of the two species.

***Anomalepis aspinosus* Taylor, 1939**

*Anomalepis aspinosus* Taylor, 1939, Proceedings of the New England Zoölogical Club 17: 87-96 [92, pl. 5 (figs. 5-7)]. Type-locality: Perico, Peru.

**Holotype.** MCZ-R 14782, total length 126 mm. Type-locality: Perico, Peru, collected by G. K. Noble.

**Paratypes.** MCZ-R 14781, 14783, 14785, 14701; USNM 76295, all topotypes, collected by G. K. Noble.

**Diagnosis.** *Anomalepis aspinosus* is distinguished from its congeners, except *A. mexicanus*, by having 26/ 24/ 22 scales in rows around body, and 283 scales on dorsal middle row (vs. 31/ 29/ 27 scales in rows around body, and 387 scales on dorsal middle row in *A. colombia*, and 26 scales in midbody scale rows, 24 scales in posterior scale rows, and 304-308 scales on dorsal middle row in *A. flavapices*). It is distinguished from *A. mexicanus* by having nine subcaudal scales (vs. 10-11 subcaudal scales).

**Redescription.** Meristic data in Table 2. Standard length 122.6 mm, head length 3.2% of standard length, head width 2.2% of standard length, head height 1.4% of standard length, snout-vent length 97.4% of standard length, tail length 2.6% of standard length, head width 69.2% of head length, and head height 43.6% of head length. Body covered with cycloid scales. Snout rounded, rostral short, longer than wide, contacting nasals anterolaterally, and prefrontals posteriorly. Pair of pentagonal prefrontals with acute angle posteriorly, bordered anteriorly by rostral, laterally by large divided nasal, and posteriorly by single frontal. Single polygonal frontal bordered anteriorly by prefrontals, laterally by two small scales on each side, and posteriorly by first scale on dorsal middle row. Divided nasal scale bordered anteriorly by rostral, dorsally by prefrontal, ventrally by first supralabial, and posteriorly by two scales that lie between prefrontal and second supralabial. Eye spot poorly visible. Mental extremely reduced, divided, contacting first infralabials. Supralabials 4, infralabials 3. Scales around body 26/ 24/ 22. Dorsal scales 283, 271 ventrals, and nine subcaudal scales.

**Coloration in alcohol.** Dorsal and ventral body coloration pale cream. Scales close to opening of cloaca and subcaudal scales lighter than rest of body.

**Distribution.** Know only from the Northwestern Peru, in the transandean region of Cajamarca (Fig. 19).

**Remarks.** Except for specimen LSUMZ-H 32591 (not examined here) collected in Amazonas, Peru, *Anomalepis aspinosus* apparently seems to be completely transandean, endemic in the region of Cajamarca, Peru.

***Anomalepis colombia* Marx, 1953**

*Anomalepis colombia* Marx, 1953, Fieldiana: Zoology 34: 197-198 [197].

**Holotype.** FMNH 54986, total length 176.9 mm. Type-locality: La Selva, Pueblo Rico, Caldas, Colombia, collected by Kjell von Sneidern in January 1946.

**Diagnosis.** *Anomalepis colombia* is distinguished from its congeners by having 31/ 29/ 27 scales in rows around body, and 387 scales on dorsal middle row (vs. 26/ 24/ 22 scales in rows around body, and 283 scales on dorsal middle row in *A. aspinosus*; 26/ 26/ 24 scales in rows around the body, and 304-308 scales on dorsal middle row in *A. flavapices*; and 25-26/ 22-24/ 21-23 scales in rows around body, and 277-312 scales on dorsal middle row in *A. mexicanus*).

**Redescription.** Meristic data in Table 2. Standard length 176.9 mm, head length 2.4% of standard length, head width 1.8% of standard length, head height 1.1% of standard length, snout-vent length 98.4% of standard length, tail length 1.6% of standard length, head width 72.1% of head length, and head height 44.2% of head length. Body covered with cycloid scales. Snout rounded, rostral short, longer than wide, contacting nasals anterolaterally, and prefrontals posteriorly. Pair of pentagonal prefrontals with acute angle posteriorly, bordered anteriorly by rostral, laterally by large divided nasal, and posteriorly by single frontal. Single polygonal frontal bordered anteriorly by prefrontals, laterally by two small scales on each side, and posteriorly by first scale on dorsal middle row. Divided nasal scale bordered anteriorly by rostral, dorsally by prefrontal, ventrally by first supralabial, and posteriorly by two scales that lie between prefrontal and second supralabial. Eye spot not visible. Mental extremely reduced, divided, contacting first infralabials. Supralabials 4, infralabials three left side and two right side. Scales around body 31/ 29/ 27. Dorsal scales 387, 354 ventrals, and 11 subcaudal scales.

**Coloration in alcohol.** Dorsal and ventral body coloration pale cream. Scales close to opening of cloaca and subcaudal scales lighter than rest of body.

**Distribution.** Known only from the type locality in the transandean locality of La Selva, Pueblo Rico, Caldas, Colombia (Fig. 20).

**Remarks.** *Anomalepis colombia* was described based on a single specimen, and since this specimen was collected by Kjell von Sneidern in January 1946, no other specimen has been collected.

### *Anomalepis flavapices* Peters, 1957

*Anomalepis flavapices* Peters, 1957, American Museum Novitates 1851: 1-13 [3].

**Holotype.** USNM 196349, total length 140 mm. Type-locality: near Esmeraldas, Esmeraldas Province, Ecuador, collected by by "Mr. Gray".

**Paratypes.** AMNH R 6966, total length 146 mm. Collected at Manabi, Ecuador, by G. H. Pepper.

**Diagnosis.** *Anomalepis flavapices* is distinguished from its congeners by having four infralabial scales, and 304-308 scales on dorsal middle row (vs. three infralabial scales, and 283 scales on dorsal middle row in *A. aspinosus*, and three infralabial scales, and 387 scales on dorsal middle row in *A. colombia*). It is further distinguished from *A. mexicanus* by having four infralabial scales, and 26 scales in rows around midbody (vs. three infralabial scales, and 22-24 scales in rows around midbody).

**Redescription.** Meristic data in Table 2. Body covered with cycloid scales. Snout rounded, rostral short, longer than wide, contacting nasals anterolaterally, and prefrontals posteriorly. Pair of pentagonal prefrontals with acute angle posteriorly, bordered anteriorly by rostral, laterally by large divided nasal, and posteriorly by single frontal. Single polygonal frontal bordered anteriorly by prefrontals, laterally by two small scales on each side, and posteriorly by first scale on dorsal middle row. Divided nasal scale bordered anteriorly by rostral, dorsally by prefrontal, ventrally by first supralabial, and posteriorly by two scales that lie between prefrontal and second supralabial. Eye spot not visible. Mental extremely reduced, divided, contacting first infralabials. Supralabials 4, infralabials 4. Scales around body 26/ 26/ 24. Dorsal scales 304-308, and 7-10 subcaudal scales.

**Coloration in alcohol.** Dorsal and ventral body coloration pale cream. Holotype stained with dark tincture used to facilitate counting scales.

**Distribution.** In lowland forests of the transandean provinces of Esmeraldas and Manabi of northwestern Ecuador, and Amazonas, vicinity of Huampami (Aguaruna village), Rio Cenepa, Peru (Fig. 21).

**Remarks.** Because of the impossibility to examine specimens of *Anomalepis flavapices* during this study, the diagnosis and redescription presented here is based on the original description by James Peters, as well as our interpretation of data in the taxonomic literature on *Anomalepis*. Photos of the holotype USNM 196349 and of the specimen MVZ 163245 were used to obtain morphological characters. Because specimens of *A. flavapices* were not examined in this study, and the author of the original description had not reported on measurement data, morphometric information for this species is not available. Figure 21 represents the locality point of specimen MVZ 163245.

### *Anomalepis mexicanus* Jan, 1860

*Anomalepis mexicanus* Jan *in* Jan and Sordelli, 1860, Iconographie Générale des Ophidiens I, livr. 1: [index to pl. 5 (fig. 1), pl. 6 (fig. 1)]. Type-locality: "Mexico".

*Anomalolepis mexicanus*.−Günther, 1885, Biologia Centrali-Americana. Reptilia and Bathrachia, 326 Pp. [87].

*Anomalepis mexicana*.−Boulenger, 1893, Catalogue of the Snakes in the British Museum 1: 448 Pp. [59].

*Anomalepis dentatus* Taylor, 1939, Proceedings of the New England Zoölogical Club 17: 87-96 [90, pl. 5 (figs. 1-3)]. Type-locality: "Barro Colorado [Island], Canal Zone" Panama. Placed in synonymy by Dunn, 1941, Bulletin of the Museum of Comparative Zoology 87: 511-529 [517].

**Holotype.** Formerly MSNM, destroyed in 1943 during World War II, according Wallach et al. 2014. Type-locality: "Mexico".

**Diagnosis.** *Anomalepis mexicanus* is distinguished from its congeners, except *A. aspinosus*, by having 25-26/ 22-24/ 21-23 scales in rows around body, 277-312 scales on dorsal middle row. It is distinguished from *A. aspinosus* by having 10-11 subcaudal scales (vs. nine subcaudal scales in *A. aspinosus*). It is further distinguished from *A. colombia* by having 25-26/ 22-24/ 21-23 scales in rows around body, and 277-312 scales on dorsal middle row (vs. 31/ 29/ 27 scales in rows around body, and 387 scales on dorsal middle row), and from *A. flavapices* by having three infralabial scales, and 22-24 scales in rows around midbody (vs. four infralabial scales, and 26 scales in rows around midbody).

**Redescription.** Meristic data in Table 2. Standard length 78.7-119.6 mm (mean 98.1 ± 20.5), head length 3.3-5.6% of standard length (4.4 mean ± 1.1), head width 2.2-3.3% of standard length (2.7 mean ± 0.6), head height 1.6-2.2% of standard length (1.8 mean ± 0.3), snout-vent length 97.6-109.6% of standard length (101.6 mean ± 6.9), tail length 2.2-2.4% of standard length (2.3 mean ± 0.1), head width 59.1-65.0% of head length (61.7 mean ± 3.0), and head height 38.6-47.5% of head length (42.5 mean ± 4.5). Body covered with cycloid scales. Snout rounded, rostral short, longer than wide, contacting nasals anterolaterally, and prefrontals posteriorly. Pair of pentagonal prefrontals with acute angle posteriorly, bordered anteriorly by rostral, laterally by large divided nasal, and posteriorly by single frontal. Single polygonal frontal bordered anteriorly by prefrontals, laterally by two small scales on each side, and posteriorly by first scale on dorsal middle row. Divided nasal scale bordered anteriorly by rostral, dorsally by prefrontal, ventrally by first supralabial, and posteriorly by two scales that lie between prefrontal and second supralabial. Eye spot poorly visible. Mental extremely reduced, divided, contacting first infralabials. Supralabials 4, infralabials 3. Scales around body 25-26 / 22-24 / 21-23. Dorsal scales 277-312, 261-293 ventrals, and 10-11 subcaudal scales.

**Coloration in alcohol.** Body color brown with venter slightly lighter than dorsum. Scales close to opening of cloaca and subcaudal scales lighter than rest of body.

**Distribution.** Northeastern Honduras (Colón, Gracias a Dios), Northwest Costa Rica (Guanacaste), West Panama (Canal Zone: Barro Colorado Island) and Northwest Peru (Amazonas, Cajamarca) (Fig. 22).

**Remarks.** In his review of the genus *Anomalepis*, Kofron (1988) considered an error the indication of “Mexico” as the type locality of *A. mexicanus*. He explained that the holotype of *A. mexicanus* was illustrated by Jan & Sordelli (1860), who indicated that it has "22" scale rows and came from "Mexico". According to him, intensive collecting in Mexico during the past 100 years has failed to produce any specimens from that country, and it is obvious that Mexico is not the country of origin of the holotype, which is contrary to Peters & Orejas-Miranda (1970) who listed the species as "known only from Mexico and Panama". He cites Smith & Taylor (1945) who, in their checklist of Mexican snakes, included the taxon as "species inquirendae", remembering that Mexico as the country of origin was also questioned by Dunn (1941).

**Table 2**. Meristic characters of *Anomalepis* species from the specimens examined in this study. PEF = Number of scales contacting posterior edge of frontal; SL = Supralabials; IL = Infralabials; ASR = number of anterior scale rows around body; MSR = number of scale rows around the midbody; PSR = number of posterior scale rows around body; DSR = number of dorsal scale rows; VSR = number of ventral scales rows; SC = number of subcaudal scales. N = number of specimens examined. [N] = specimens examined by James Peters (1957), and not in this study. [1]Number of scales presented as ranges with minimum, maximum and mode in parentheses.

| | | Counts[1] | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| **Species** | **N** | **PEF** | **SL** | **IL** | **ASR** | **MSR** | **PSR** | **DSR** | **VSR** | **SC** |
| ***A. aspinosus*** | 1 | 5 | 4 | 3 | 26 | 24 | 22 | 283 | 271 | 9 |
| ***A. colombia*** | 1 | 5 | 4 | 3 | 31 | 29 | 27 | 387 | 354 | 11 |
| ***A. flavapices*** [N] | 2 | 5-5 (5) | 4-4 (4) | 4-4 (4) | 26-26 (26) | 26-26 (26) | 24-24 (24) | 304-308 | - | 7-10 |
| ***A. mexicanus*** | 3 | 5-5 (5) | 4-4 (4) | 3-3 (3) | 25-26 (25) | 22-24 (22) | 21-23 (21) | 277-312 | 261-293 | 10-11 (10) |

***Helminthophis* Peters, 1860**

*Helminthophis* Peters, 1860, Monatsberichte der Preussischen Akademie Wissenschaften zu Berlin. 1860: 517-521 [518]; Type species: *Helminthophis frontalis* (Peters, 1860).

*Idiotyphlops* Jan in Jan and Sordelli, 1860, Iconographie Générale des Ophidiens I, livr. 1: [index to pl. 5 (fig. 10)]; Type species: *Idiotyphlops flavoterminatus*.

**Diagnosis.** *Helminthophis* is diagnosed from other Anomalepididae by the following synapomorphies: (1) frontals fused (character 16, state 1, Fig. 23A) (vs. frontals paired, Fig. 23B); (2) exoccipital overlaps and extends in front of the occipital condyle (character 48, state 0, Fig. 24A) (vs. exoccipital not overlapping and not extending in front of the occipital condyle, Fig. 24B); and (3) rostral frontal scales not in contact (character 64, state 1). It is further distinguished from *Typhlophis* by having differentiated scales of the head (vs. undifferentiated scales of the head). It is distinguished from *Liotyphlops* by having contralateral prefrontals contacting each other behind the rostral scale, preventing the later to contact the frontal (Fig. 25A) (vs. separate prefrontals, rostral in contact with frontal, Fig. 25B). It is distinguished from *Anomalepis* by having triangular, elongated prefrontals (Fig. 18B) (vs. pentagonal, short prefrontals, Fig. 18A).

**Species included.** Three species, *Helminthophis flavoterminatus* (Peters, 1858), *Helminthophis frontalis* (Peters, 1860), and *Helminthophis praeocularis* Amaral, 1924

**Distribution.** Lower Central America and northwestern South America: Costa Rica, Panama, Colombia, and Venezuela.

**Key to species of *Helminthophis*.**

**1**. Three scales contacting posterior edge of prefrontal; scales in rows around the body 22/ 21/ 21; dorsals 461-574 …………..…...…………..……..... *Helminthophis frontalis*

**1'**. Two scales contacting posterior edge of prefrontal ………………..….…………..…. **2**

**2**. Scales in rows around the body 25/ 24/ 24;
dorsals 597-643 …………………………...……………. *Helminthophis flavoterminatus*

**2'**. Scales in rows around the body 20/ 20/ 20;
dorsals 412-428 ……………………………………………. *Helminthophis praeocularis*

**Remarks.** Except for the contact between the prefrontal scales behind the rostral scale, preventing contact between the rostral and the frontal scales, the cephalic scales of *Helminthophis* resemble those of *Liotyphlops*. This resemblance is to such a degree that several species of *Helminthophis* have been described and later transferred to *Liotyphlops*, and most of those species were synonymized (for example see Peters 1857, Boulenger 1896, Amaral 1924).

***Helminthophis flavoterminatus* (Peters, 1858)**

*Typhlops flavoterminatus* Peters, 1857, Monatsberichte der Preussischen Akademie Wissenschaften zu Berlin. 1857: 402 [402]. Type-locality: Caracas, Venezuela.

*Idiotyphlops flavoterminatus*.−Jan and Sordelli, 1860, Iconographie Générale des Ophidiens I, livr. 1: [index to pl. 5 (fig. 10), pl. 6].

*Helminthophis flavoterminatus*.−Boulenger, 1893, Catalogue of the Snakes in the British Museum 1: 448 Pp. [5].

**Syntypes.** (6): ZMB 1426-1430, and ZMH, destroyed in July 1943 during World War II. Type-locality: “Carácas” [= Caracas, Distrito Federal State, NorthVenezuela].

**Diagnosis.** *Helminthophis flavoterminatus* is distinguished from its congeners by having 25/ 24/ 24 scales in rows around body, and 597-643 scales on dorsal middle row (vs. 22/ 21/ 21 scales in rows around body, and 461-574 scales on dorsal middle row in *H. frontalis*, and 20/ 20/ 20 scales in rows around body, 412-428 scales on dorsal middle row in *H. praeocularis*). It is further distinguished from *H. frontalis* by having two scales contacting the posterior edge of the prefrontal (vs. three scales contacting posterior edge of prefrontal), and from *Helminthophis praeocularis* by having 18 subcaudal scales (vs. 11-13 subcaudal scales).

**Redescription.** Meristic data in Table 3. Standard length 211.5-216.1 mm (mean 213.8 ± 3.3), head length 1.7-1.8% of standard length (1.8 mean ± 0.1), head width 1.2-1.3% of standard length (1.3 mean ± 0.1), head height 0.9% of standard length (0.9 mean ± 0.0), snout-vent length 97.9-98.1% of standard length (98.0 mean ± 0.2), tail length 1.9-2.1% of standard length (2.0 mean ± 0.2), head width 72.2-74.4% of head length (73.3 mean ± 1.5), and head height 51.3-55.6% of head length (53.4 mean ± 3.0). Body covered with cycloid scales. Snout rounded, rostral large, longer than wide, contacting nasals anterolaterally, and prefrontals posterolaterally. Pair of triangular prefrontals contacting each other behind rostral, separating latter from frontal, bordered anteriorly by rostral, laterally by large divided nasal, and posteriorly by single frontal. Two scales contacting posterior edge of prefrontal. Single frontal bordered anteriorly by prefrontals, and posteriorly by first scale on dorsal middle row. Divided nasal scale bordered anteriorly by rostral, dorsally by prefrontal, ventrally by first supralabial, and posteriorly by one scale that lies between prefrontal and second supralabial. Eye spot poorly visible. Mental triangular, not divided, wider than long, contacting the first infralabials. Supralabials 4, infralabials 3. Scales around body 25/ 24/ 24. Dorsal scales 597-643, 583-625 ventrals, and 18 subcaudal scales.

**Coloration in alcohol.** Dorsal and ventral surfaces of body dark brown. Head pale cream. Scales close to opening of cloaca pale cream. Small pale cream spots randomly distributed along ventral surface.

**Distribution.** Northwestern Venezuela (Amazonas, Aragua, Distrito Federal, Miranda, Zulia) and West Colombia (Chocó, north of Santander) (Fig. 26).

**Remarks.** According to Hahn (1980), *H. flavoterminatus* may have been introduced into Mauritius.

### ***Helminthophis frontalis*** **(Peters, 1860)**

*Typhlops* (*Helminthophis*) *frontalis* Peters, 1860, Monatsberichte der Preussischen Akademie Wissenschaften zu Berlin. 1860: 517-521 [517, figs. 1-1c]. Type-locality: Costa Rica.

*H*[*elminthophis*] *frontalis.*−Peters, 1881, Sitzungsberichte der Gesellschaft Naturforschender Freunde zu Berlin. 1881: 69-71 [69].

*Helminthophis frontalis.*−Boulenger, 1893, Catalogue of the Snakes in the British Museum 1: 448 Pp. [5].

**Lectotype**: ZMB 3925 (designated by Hahn 1980). Paralectotype: ZMB 3823.

**Diagnosis.** *Helminthophis frontalis* is distinguished from its congeners by having 22/ 21/ 21 scales in rows around body, and 461-574 scales on dorsal middle row (vs. 25/ 24/ 24 scales in rows around body, and 597-643 scales on dorsal middle row in *H. flavoterminatus*, and 20/ 20/ 20 scales in rows around body, 412-428 scales on dorsal middle row in *H. praeocularis*). It is further distinguished from *H. flavoterminatus* by having three scales contacting the posterior edge of the prefrontal (vs. two scales contacting posterior edge of prefrontal), and from *Helminthophis praeocularis* by having 20-22 subcaudal scales (vs. 11-13 subcaudal scales).

**Redescription.** Meristic data in Table 3. Standard length 134.7-263.5 mm (mean 199.1 ± 91.1), head length 1.6-2.4% of standard length (2.0 mean ± 0.6), head width 1.1-1.4% of standard length (1.3 mean ± 0.2), head height 0.8-1.0% of standard length (0.9 mean ± 0.1), snout-vent length 97.9-98.0% of standard length (98.0 mean ± 0.1), tail length 2.0-2.1% of standard length (2.0 mean ± 0.1), head width 57.6-69.0% of head length (63.3 mean ± 8.1), and head height 39.4-50.0% of head length (44.7 mean ± 7.5). Body covered with cycloid scales. Snout rounded, rostral large, longer than wide, contacting nasals anterolaterally, and prefrontals laterally-posteriorly. Pair of triangular prefrontals in contact behind rostral, separating latter from frontal, bordered anteriorly by rostral, laterally by large divided nasal, and posteriorly by single frontal. Three scales contacting posterior edge of prefrontal. Single frontal bordered anteriorly by prefrontals, and posteriorly by first scale on dorsal middle row. Divided nasal scale bordered anteriorly by rostral, dorsally by prefrontal, ventrally by first supralabial, and posteriorly by one scale that lies between prefrontal and second supralabial. Eye spot not visible or poorly visible. Mental triangular, not divided, wider than long, contacting the first infralabials. Supralabials 4, infralabials 3. Scales around body 22/ 21/ 21. Dorsal scales 461-574, 426-549 ventrals, and 20-22 subcaudal scales.

**Coloration in alcohol.** Dorsal and ventral body coloration dark brown, and pale cream head.

**Distribution.** Costa Rica (Alajuela, Heredia, San José) and West Panama (Chiriquí) (Fig. 27).

**Remarks.** *Helminthophis frontalis* is the only species of Anomalepididae with distribution restricted to Central America (Costa Rica and Panama).

***Helminthophis praeocularis* Amaral, 1924**

*Helminthophis praeocularis* Amaral, 1924, Proceedings of the New England Zöological Club 9: 25-30 [28]. Type-locality: Honda, Colombia.

**Holotype.** MCZ R 17960, total length 214 mm.

**Diagnosis.** *Helminthophis praeocularis* is clearly distinguished from its congeners by having 20/ 20/ 20 scales in rows around body, and 412-428 scales on dorsal middle row (vs. 25/ 24/ 24 scales in rows around body, and 597-643 scales on dorsal middle row in *H. flavoterminatus*, and 22/ 21/ 21 scales in rows around body, 461-574 scales on dorsal middle row in *H. frontalis*). It is further distinguished from *H. frontalis* by having two scales contacting the posterior edge of the prefrontal (vs. three scales contacting posterior edge of prefrontal), and from *Helminthophis flavoterminatus* by having 11-13 subcaudal scales (vs. 18 subcaudal scales).

**Redescription.** Meristic data in Table 3. Standard length 150.5-164.4 mm (157.4 mean ± 9.8), head length 2.3-2.4% of standard length (2.3 mean ± 0.1), head width 1.1-1.3% of standard length (1.2 mean ± 0.2), head height 0.7-0.9% of standard length (0.8 mean ± 0.1), snout-vent length 98.3-98.5% of standard length (98.4 mean ± 0.1), tail length 1.5-1.7% of standard length (1.6 mean ± 0.1), head width 46.2-58.8% of head length (52.5 mean ± 9.0), and head height 30.8-38.2% of head length (34.5 mean ± 5.3). Body covered with cycloid scales. Snout rounded, rostral large, longer than wide, contacting nasals anterolaterally, and prefrontals posterolaterally. Pair of triangular prefrontals contacting each other behind rostral, separating latter from frontal, bordered anteriorly by rostral, laterally by large divided nasal, and posteriorly by single frontal. Two scales contacting posterior edge of prefrontal. Single frontal bordered anteriorly by prefrontals, and posteriorly by first scale on dorsal middle row. Divided nasal scale bordered anteriorly by rostral, dorsally by prefrontal, ventrally by first supralabial, and posteriorly by one scale that lies between prefrontal and second supralabial. Eye spot not visible. Mental triangular, not divided, wider than long, contacting first infralabials. Supralabials 4, infralabials 3. Scales around body 20/ 20/ 20. Dorsal scales 412-428, 399-416 ventrals, and 11-13 subcaudal scales.

**Coloration in alcohol.** Dorsal and ventral surfaces of body dark brown; head pale cream.

**Distribution.** Inter-andean area of northern Colombia in Tolima, Santander, and North Santander provinces, from 200 to 1,200 m above sea level (Fig. 28).

**Remarks.** In the course of the present study it was observed that, for some reason, several specimens representatives of another family of blind snakes, the Leptotyphlopidae, were determined as *Helminthophis*. This was more common with *H. praeocularis* where some databases provide data in this species but, in the images that are available, specimens of Leptotyphlopidae, specifically the subfamily Epictinae, are shown.

**Table 3**. Meristic characters of *Helminthophis* species from the specimens examined in this study. PEP = number of scales contacting posterior edge of prefrontal; Scales PEN = number of scales contacting posterior edge of nasal between second supralabial and prefrontal; Supralabials = number of supralabial scales; Infralabials = number of infralabial scales; ASR = number of anterior scale rows around body; MSR = number of scale rows around the midbody; PSR = number of posterior scale rows around body; DSR = number of dorsal scale rows; VSR = number of ventral scales rows; SC = number of subcaudal scales. N = number of specimens examined in this study. [1]Number of scales presented as ranges with minimum, maximum and mode in parentheses.

| | Counts[1] | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| **Species** | **N** | **SPEP** | **SPEN** | **SL** | **IL** | **ASR** | **MSR** | **PSR** | **DSR** | **VSR** | **SC** |
| ***H. flavoterminatus*** | 2 | 2-2 (2) | 1-1 (1) | 4-4 (4) | 3-3 (3) | 25-25 (25) | 24-24 (24) | 24-24 (24) | 597-643 | 583-625 | 18-18 (18) |
| ***H. frontalis*** | 2 | 3-3 (3) | 1-1 (1) | 4-4 (4) | 3-3 (3) | 22-22 (22) | 21-21 (21) | 21-21 (21) | 461-574 | 426-549 | 20-22 |
| ***H. praeocularis*** | 2 | 2-2 (2) | 1-1 (1) | 4-4 (4) | 3-3 (3) | 20-20 (20) | 20-20 (20) | 20-20 (20) | 412-428 | 399-416 | 11-13 |

***Liotyphlops* Peters, 1881**

*Rhinotyphlos* Peters, 1857, Monatsberichte der Preussischen Akademie Wissenschaften zu Berlin. 1857: 402 [402]. [Preoccupied by *Rhinotyphlops* Fitzinger, 1843: Typhlopidae]. Type species: *Rhinotyphlos albirostris* Peters, 1857, by monotypy.

*Liotyphlops* Peters, 1881, Sitzungsberichte der Gesellschaft Naturforschender Freunde zu Berlin. 1881: 69-71 [69]. [Replacement name for *Rhinotyphlops* Peters, 1857].

**Diagnosis.** *Liotyphlops* is currently not diagnosed by synapomorphies. It can be distinguished from *Anomalepis* by having separate prefrontals behind the rostral (Fig. 17B) (vs. polygonal prefrontals in contact behind rostral, Fig. 17A) and by having the parietal paired (Fig. 29A) (vs. parietal fused, Fig. 29B). It is distinguished from *Helminthophis* by having separate prefrontals, rostral in contact with frontal (Fig. 25B) (vs. prefrontals in contact behind rostral, rostral not contacting frontal, Fig. 25A) and frontal paired (Fig. 23B) (vs. frontal fused, Fig. 23A). It is distinguished from *Typhlophis* by having differentiated scales of the head (vs. undifferentiated scales of the head), premaxilla with a lateral flange forming the dorsal margin of the external naris (Fig. 30A) (vs. premaxilla without lateral flange, Fig. 30B), and by having a posterior extension of the medial nasal septum not overlapping the anterior margins of the frontal subolfactory processes (Fig. 31A) (vs. posterior extension of the medial nasal septum overlapping the anterior margins of the frontal subolfactory processes, Fig. 31B).

**Species included.** Eleven species. *Liotyphlops albirostris* (Peters, 1858), *Liotyphlops anops* (Cope, 1899), *Liotyphlops argaleus* Dixon & Kofron, 1984, *Liotyphlops caissara* Centeno, Sawaya & Germano, 2010, *Liotyphlops haadi* Silva-Haad, Franco & Maldonado, 2008, *Liotyphlops schubarti* Vanzolini, 1948, *Liotyphlops ternetzii* (Boulenger, 1896), *Liotyphlops trefauti* Freire, Caramaschi & Argôlo, 2007, *Liotyphlops wilderi* (Garman, 1883) , *Liotyphlops ss* new species, *Liotyphlops tt* new species.

**Distribution.** Central and South America, from Costa Rica to Argentina.

**Key to species of *Liotyphlops*.**

**1**. Three scales contacting posterior edge of prefrontal ……………………………….. **2**

**1'**. Four scales contacting posterior edge of prefrontal …..…………………………… **3**

**2**. Supralabials 3, infralabials 3 ………………………..……… *Liotyphlops caissara*

**2'**. Supralabials 4, infralabials 2 ........................................… *Liotyphlops tt* new species

**2"**. Supralabials 4, infralabials 3 …………………………….……………..…………. **4**

**3**. Number of dorsals 562-597 …….……...………………….......... *Liotyphlos anops*

**3'**. Number of dorsals 497 ……...…..…………….……..……........ *Liotyphlos argaleus*

**3"**. Number of dorsals 520-543 ……..………........…..……….…..... *Liotyphlos trefauti*

**3'"**. Number of dorsals 439 ..……..………...……....…......... *Liotyphlos ss* new species

**4**. One scale contacting posterior edge of nasal between second supralabial and prefrontal …………………………….………………………………………………… **5**

**4'**. Two scales contacting posterior edge of nasal between second supralabial and prefrontal ………………………………………………...……….…………….. **6**

**5**. Number of dorsals 432-478 …..………………………….……….. *Liotyphlos albirostris*

**5'**. Number of dorsals 385-402 ……..………………………….…........ *Liotyphlos wilder*

**5".** Number of dorsals 333-384 ………...………………………….….. *Liotyphlops haadi*

**6**. Body coloration light brown ……….…………………….……....... *Liotyphlos schubarti*

**6'**. Body coloration pale cream, dark brown or black ……….......... *Liotyphlos ternetzii*

**Remarks.** Currently 10 valid species are known for the genus *Liotyphlops*. The taxonomic arrangement presented here proposes 11 valid species based on the description of two new species and the synonymization of *Liotyphlops beui* under *L. ternetzii*.

***Liotyphlops albirostris* (Peters, 1857)**

*Rhinotyphlops albirostris* Peters, 1857, Monatsberichte der Preussischen Akademie Wissenschaften zu Berlin 1857: 402 [402]. Type-locality: "Veragua" [Veraguas, Veraguas Province, Panama].

*Liotyphlops albirostris*.−Peters, 1881, Sitzungsberichte der Gesellschaft Naturforschender Freunde zu Berlin 1881: 69-71 [69].

*Typhlops* (*Idiotyphlops*) *emunctus* Garman, 1884 [dated 1883], Memoirs of the Museum of Comparative Zoology 8: 1-185 p. [3]. Holotype: MCZ R 3971. Type-locality: “Panama.” Placed in synonymy by Dunn (1932:175).

*Helminthophis emunctus*.−Cope, 1887, Bulletin of the United States National Museum 32: 98 Pp. [91].

*Helminthophis petersii* Boulenger, 1889, Annals and Magazine of Natural History (6) 4: 360-363 [360]. Holotype: BMNH 1946.1.11.26 (formerly BMNH 1860.6.16.218). Type-locality: “Guayaquil, Ecuador.” Placed in synonymy by Dixon and Kofron, 1984 [dated 1983], Amph. Rept. 4: 241-264 [246].

*Helminthophis petersii*.−Boulenger, 1893, Catalogue of the Snakes in the British Museum l: 448 Pp. [6, pl. l (figs. 1a-b)].

*Helminthophis albirostris*.−Boulenger, 1893, Catalogue of the Snakes in the British Museum 1: 448 Pp. [6].

*Helminthophis canellei* Mocquard, 1903, Bulletin du Muséum National d’Histoire Naturalle, Paris 9: 209-220 [211]. Holotype: MNHN 3189A. Type-locality: “I’isthme de Panama” [= Isthmus of Panama]. Placed in synonymy by Dunn (1932: 175).

*Helminthophis bondensis* Griffin, 1916 [dated 1915], Memoirs of the Carnegie Museum 7: 163-277 [165]. Holotype: CM 216. Type-locality: “Bonda, [Magdalena] Colombia.” Placed in synonymy by Dunn (1932:175).

*Liotyphlops albirostris*.−Dunn, 1932, Proceedings of the Biological Society of Washington 45: 173-176 [175].

*Liotyphlops petersii*.−Dunn, 1932, Proceedings of the Biological Society of Washington 45: 173-176 [175].

*Liotyphlops cucutae* Dunn, 1944, Caldasia 3: 47- 55 [49, figs. 5-6]. Holotype: MLS, an unnumbered specimen. Type-locality: “Cúcuta, Norte de Santander, [Colombia], 215 meters.” Placed in synonymy by Dixon and Kofron (1984:246).

*Liotyphlops caracasensis* Roze, 1952, Memorias de la Sociedad de Ciencias Naturales La Salle 12: 143-158 [150, figs. 1-2]. Holotype: SCN 4327. Type-locality: “Cuartel

Urdaneta, Caracas, D. F., Venezuela." Placed in synonymy by Dixon and Kofron (1984:246).

*Liotyphlops rowani* H. M. Smith and Grant, 1958, Herpetologica 14: 207-222 [207]. Holotype: UIMNH 41731. Type-locality: "Pacific shoreline, Ft. Clayton Reservation, Canal Zone" [Panama]. Placed in synonymy by Dixon and Kofron (1984:246).

**Syntypes.** (2): ZMB 9529 and ZMB 63438, a 190 mm and 158 mm specimen.

**Diagnosis.** *Liotyphlops albirostris* is distinguished from *L. anops*, *L. argaleus*, *L. ss* sp. nov., and *L. trefauti* by having three scales contacting posterior edge of prefrontal (vs. four scales contacting posterior edge of prefrontal). It is distinguished from *L. caissara* by having four supralabial scales (vs. three supralabial scales), and from *L. haadi* by having 24-26/ 22/ 22 scales in rows around the body (vs. 20/ 19-20/ 18-20 scales in rows around the body). It is distinguished from *L. schubarti*, *L. ternetzii*, and *L. tt* new species by having one scale contacting the posterior edge of the nasal between second supralabial and prefrontal (vs. two scales contacting posterior edge of nasal), and of *L. wilderi* by having five scales in the first vertical row of dorsals and 432-478 dorsals (vs. four scales in the first vertical row of dorsals and 385-402 dorsals).

**Redescription.** Meristic data in Table 4. Standard length 75.6-225.5 mm (171.7 mean ± 50.6), head length 1.7-3.3% of standard length (2.2 mean ± 0.6), head width 1.2-2.1% of standard length (1.4 mean ± 0.4), head height 0.8-1.6% of standard length (1.1 mean ± 0.3), snout-vent length 96.6-98.9% of standard length (98.2 mean ± 0.8), tail length 1.1-3.4% of standard length (1.8 mean ± 0.8), head width 58.5-71.4% of head length (65.6 mean ± 4.9), and head height 48.0-54.3% of head length (50.2 mean ± 2.4). Body covered with cycloid scales. Rostral large, longer than wide, contacting nasals anterolaterally, prefrontals laterally, and single frontal posteriorly. Pair of triangular prefrontals, bordered anterolaterally by rostral, ventrally by large divided nasal, and posterodorsally by frontal. Posterior edge of prefrontals passing posterior edge of rostral. Divided nasal scale bordered anteriorly by rostral, dorsally by prefrontal, ventrally by first and second supralabials, and posteriorly by one scale that lie between prefrontal and second supralabial. Eye spot poorly visible. Three scales contacting posterior edge of prefrontal. One scale contacting posterior edge of nasal between second supralabial and prefrontal. Five scales in first vertical row of dorsal scales. Mental triangular, not divided, wider than long, contacting first infralabials.

Supralabials 4, infralabials 3. Scales around body 24-26/ 22/ 22. Dorsal scales 432-478, 417-453 ventrals and 12-17 subcaudal scales.

**Coloration in alcohol.** Dorsal and ventral surface of body dark brown. Head pale cream. Scales close to opening of cloaca pale cream.

**Distribution.** Southern Central America and northern South America, including Costa Rica, Panama, Colombia, Ecuador, Venezuela, and Curaçao (Fig. 32).

**Remarks.** Dixon and Kofron (1984) transferred *Liotyphlops caracasensis* Roze, 1952 to the synonymy of *Liotyphlops albirostris*. The specimen designated as the holotype of *L. caracasensis* (MHNLS 514, formerly SCN 4327) was examined and strong overlap with *L. albirostris* was observed in morphological features, for example: three scales contacting posterior edge of prefrontal, one scale contacting posterior edge of nasal between second supralabial and prefrontal, five scales in first vertical row of dorsal scales, supralabials 4, infralabials 3, scales around body 26/ 22/ 22, dorsal scales 478, 453 ventrals and 12 subcaudal scales. The data obtained through the morphology of *L. albirostris* in this study reinforce the taxonomic arrangement of Dixon and Kofron (1984) relative to the synonymy of *L. caracasensis*.

***Liotyphlops anops* (Cope, 1899)**

*Helminthophis anops* Cope, 1899, Philadelphia Museum's Scientific Bulletin 1: 3-19 [10, pl. 4 (figs. la-f)]. Type locality: "New Grenada", Colombia. According to McDiarmid et al. (1999), Dunn (1944: 48) listed the type-locality as "near Bogotá". The latter was the specific locality mentioned on the first page of Cope's (1899: 3) posthumous publication and the source of much of the material.

*Liotyphlops anops*.−Dunn, 1944, Caldasia 3:47-55 [48].

*Liotyphlops metae* Dunn, 1944, Caldasia 3: 47-55 [49, figs. 3-4]. Holotype: MLS 8. Type-locality: "Villavicencio, Meta, [Colombia], 498 meters". Placed in synonymy by Dixon and Kofron, 1984, Amphibia-Reptilia 4: 241- 264 [259].

**Syntypes.** (2): PCM 14a-b, longest syntype 372 mm, lost fide Dunn (1944c: 48) according to Wallach et al. (2014).

**Diagnosis.** *Liotyphlops anops* is distinguished from all other *Liotyphlops*, except *L. argaleus*, *L. ss* new species, and *L. trefauti* by having four scales contacting posterior edge of prefrontal (vs. three scales contacting posterior edge of prefrontal). It is distinguished from *L. argaleus* and *L. trefauti* by having two scales contacting posterior edge of nasal (vs. one scale contacting posterior edge of nasal), and from *L. ss* new species by having 26/ 24/ 24 scales in rows around the body (vs. 24/ 22/ 20 scales in rows around the body).

**Redescription.** Meristic data in Table 4. Standard length 186.2-337.7 mm (274.2 mean ± 78.7), head length 1.3-1.7% of standard length (1.5 mean ± 0.2), head width 1.1-1.3% of standard length (1.2 mean ± 0.1), head height 0.8-1.0% of standard length (0.9 mean ± 0.1), snout-vent length 98.3-98.8% of standard length (98.6 mean ± 0.3), tail length 1.2-1.7% of standard length (1.4 mean ± 0.3), head width 78.1-85.7% of head length (82.6 mean ± 4.0), and head height 56.2-63.6% of head length (59.0 mean ± 4.0). Body covered with cycloid scales. Rostral large, longer than wide, contacting nasals anterolaterally, prefrontals laterally, and single frontal posteriorly. Pair of triangular prefrontals, bordered anterolaterally by rostral, ventrally by large divided nasal, and posterodorsally by frontal. Posterior edge of prefrontals passing posterior edge of rostral. Divided nasal scale bordered anteriorly by rostral, dorsally by prefrontal, ventrally by first and second supralabials, and posteriorly by two scales that lie between prefrontal and second supralabial. Eye spot poorly visible. Four scales contacting posterior edge of prefrontal. Two scales contacting posterior edge of nasal between second supralabial and prefrontal. 5-6 scales in first vertical row of dorsal scales. Mental triangular, not divided, wider than long, contacting first infralabials. Supralabials 4, infralabials 3. Scales around body 26/ 24/ 24. Dorsal scales 562-597, 531-572 ventrals and 12-14 subcaudal scales.

**Coloration in alcohol.** Dorsal and ventral surface of body brown. Head pale cream. Scales close to opening of cloaca pale cream.

**Distribution.** Central Colombia (Cundinamarca, Meta, Santander), 250–1,040 m (Fig. 33).

**Remarks.** According to McDiarmid et al. (1999), Dixon and Kofron (1984: 260-261) suggested that Dunn's records from Santander and Cudinamarca might be referable to *Liotyphlops argaleus* and that *Liotyphlops anops* might be known only from the vicinity of Villavicencio, Meta Province. Also, Vanzolini, in Peters et al. (1986), concurred with Dixon and Kofron (1984).

***Liotyphlops argaleus* Dixon & Kofron, 1984**

*Liotyphlops argaleus* Dixon & Kofron, 1984 Amphibia-Reptilia 4: 241- 264 [261]. Holotype. MCZ R 67933, total length 266 mm. Type-locality: "La Selva, Cundinamarca, Colombia".

**Paratypes.** MCZ R 66383, 67934, topotypes.

**Diagnosis.** *Liotyphlops argaleus* is distinguished from all other *Liotyphlops*, except *L. anops*, *L. ss* new species, and *L. trefauti* by having four scales contacting posterior edge of prefrontal (vs. three scales contacting posterior edge of prefrontal). It is distinguished from *L. anops*, and *L. ss* new species by having one scale contacting posterior edge of nasal (vs. two scales contacting posterior edge of nasal). It is distinguished from *L. trefauti* by having four scales in the first vertical row of dorsals and 16 subcaudal scales (vs. five scales in the first vertical row of dorsals and eight subcaudal scales).

**Redescription.** Meristic data in Table 4. Standard length 208.6 mm, head length 1.6% of standard length, head width 1.2% of standard length, head height 0.9% of standard length, snout-vent length 98.3% of standard length, tail length 1.7% of standard length, head width 76.5% of head length, and head height 55.9% of head length. Body covered with cycloid scales. Rostral large, longer than wide, contacting nasals anterolaterally, prefrontals laterally, and single frontal posteriorly. Pair of triangular prefrontals, bordered anterolaterally by rostral, ventrally by large divided nasal, and dorsoposteriorly by frontal. Posterior edge of prefrontals passing posterior edge of rostral. Divided nasal scale bordered anteriorly by rostral, dorsally by prefrontal, ventrally by first and second supralabials, and posteriorly by one scale that lie between prefrontal and second supralabial. Eye spot poorly visible. Four scales contacting posterior edge of prefrontal. One scale contacting posterior edge of nasal between second supralabial and prefrontal. Four scales in first vertical row of dorsal scales. Mental triangular, not divided, wider than long, contacting first infralabials. Supralabials 4, infralabials 3. Scales around body 25/ 23/ 22. Dorsal scales 497, 472 ventrals and 16 subcaudal scales.

**Coloration in alcohol.** Dorsal and ventral body coloration dark brown. Pale cream head. Scales close to opening of cloaca pale cream.

**Distribution.** Colombia (Cundinamarca) (Fig. 34).

**Remarks.** Of the three paratypes of *Liotyphlops argaleus*, two are topotypes, and the specimen on MCZ R 66383 was examined in this study.

***Liotyphlops caissara* Centeno, Sawaya & Germano, 2010**

*Liotyphlops caissara* Centeno, Sawaya & Germano 2010 Herpetologica 66 (1): 86-91. Holotype. IBSP 76774, total length 195 mm. Type-locality: Ilha de São Sebastião (23°50’45”S, 45°21’12”W), municipality of Ilhabela, São Paulo, Brazil.

**Holotype.** IBSP 76774, total length 195 mm. Type-locality: Ilha de São Sebastião (23°50’45”S, 45°21’12”W), municipality of Ilhabela, São Paulo, Brazil.

**Diagnosis.** *Liotyphlops caissara* is distinguished from *L. anops*, *L. argaleus*, *L. ss* sp. nov., and *L. trefauti* by having three scales contacting posterior edge of prefrontal (vs. four scales contacting posterior edge of prefrontal). It is distinguished from *L. albirostris*, *L. haadi*, *L. schubarti*, *Liotyphlops tt* sp. nov., and *L. wilderi* by having three supralabial scales (vs. four supralabial scales).

**Redescription.** Meristic data in Table 4. Standard length 195 mm, head length 2.3% of standard length, head width 1.4% of standard length, snout-vent length 97.9% of standard length, tail length 2.1% of standard length, and head width 62.2% of head length. Body covered with cycloid scales. Rostral large, longer than wide, contacting nasals anterolaterally, prefrontals laterally, and single frontal posteriorly. Pair of triangular prefrontals, bordered anterolaterally by rostral, ventrally by large divided nasal, and dorsoposteriorly by frontal. Posterior edge of prefrontals passing posterior edge of rostral. Divided nasal scale bordered anteriorly by rostral, dorsally by prefrontal, ventrally by first and second supralabials, and posteriorly by one scale that lie between prefrontal and second supralabial. Eye spot poorly visible. Three scales contacting posterior edge of prefrontal. One scale contacting posterior edge of nasal between second supralabial and prefrontal. Four scales in first vertical row of dorsal scales. Mental triangular, not divided, wider than long, contacting first infralabials.

Supralabials 3, infralabials 3. Scales around body 22/ 20/ 20. Dorsal scales 326, 308 ventrals and 10 subcaudal scales.

**Coloration in alcohol.** Dorsal color uniform dark brown, and continuous pale cream color throughout the venter. Specimens show similar color pattern in life (Centeno et al. 2010).

**Distribution.** Known only from the type locality in Ilha de São Sebastião, municipality of Ilhabela, São Paulo, Brazil (Fig. 35).

**Remarks.** The information on diagnosis and redescription presented here for *Liotyphlops caissara* were compiled from the original description and compared to the data obtained from specimens examined during this study. The holotype of *L. caissara* was destroyed in 15 May 2010 during the fire of the Instituto Butantan. The distribution of *L. caissara* is restricted to the type locality on the Island of São Sebastião. For this reason, in 2015 a campaign was conducted on this island to collect additional specimen of *L. caissara* but, despite the exhausting effort, no specimen was found.

### *Liotyphlops haadi* Silva-Haad, Franco & Maldonado, 2008

*Liotyphlops haadi* Silva-Haad, Franco & Maldonado 2008 Biota Colombiana 9 (2): 295-300. Holotype. IAvH 5434, total length 180 mm. Type-locality: southern Colombian Amazon, in the Amazonas Department, middle region of the Caquetá River, Vereda de los Engleses, La Pedrera district (01º19'42"S, 69º30'33"W).

**Holotype.** IAvH 5434, total length 180 mm. Type-locality: southern Colombian Amazon, in the Amazonas Department, middle region of the Caquetá River, Vereda de los Engleses, La Pedrera district (01º19'42"S, 69º30'33"W).

**Paratype.** IAvH 5435, total length 155 mm. Vereda de los Lagos, Leticia (04°12'55"S, 59°56'26"W), Colombia. Collected by a native in October 1990.

**Diagnosis.** *Liotyphlops haadi* is distinguished from *L. anops*, *L. argaleus*, *L. ss* sp. nov., and *L. trefauti* by having three scales contacting posterior edge of prefrontal (vs. four scales contacting posterior edge of prefrontal). It is distinguished from *L. albirostris* by having 20/ 19-20/ 18-20 scales in rows around the body (vs. 24-26/ 22/ 22 scales in rows around the body). It is distinguished from *L. caissara* by having four supralabial scales (vs. three supralabial scales). It is distinguished from *L. schubarti*, *L. ternetzii*, and *L. tt* new species by having one scale contacting posterior edge of nasal between second supralabial and prefrontal (vs. two scales contacting posterior edge of nasal), and of *L. wilderi* by having 20 scales in anterior scale rows, 19-20 scales in midbody scale rows, and 309-348 ventral scale rows (vs. 22-24 scales in anterior scale rows, 22 scales in midbody scale rows, and 371-383 ventral scale rows).

**Redescription.** Meristic data in Table 4. Standard length 155.0-180.0 mm (167.5 mean ± 17.7), head length 1.6-2.3% of standard length (2.0 mean ± 0.5), head width 1.6-1.7% of standard length (1.6 mean ± 0.1), head height 0.9-1.0% of standard length (1.0 mean ± 0.1), snout-vent length 97.3-97.7% of standard length (97.5 mean ± 0.2), tail length 2.3-2.7% of standard length (2.5 mean ± 0.2), head width 72.2-96.6% of head length (84.4 mean ± 17.2), and head height 44.4-58.6% of head length (51.5 mean ± 10.0). Body covered with cycloid scales. Rostral large, longer than wide, contacting nasals anterolaterally, prefrontals laterally, and single frontal posteriorly. Pair of triangular prefrontals, bordered anterolaterally by rostral, ventrally by large divided nasal, and dorsoposteriorly by frontal. Posterior edge of prefrontals passing posterior edge of rostral. Divided nasal scale bordered anteriorly by rostral, dorsally by prefrontal, ventrally by first and second supralabials, and posteriorly by one scale that lie between prefrontal and second supralabial. Eye spot not visible. Three scales contacting posterior edge of prefrontal. One scale contacting posterior edge of nasal between second supralabial and prefrontal. Four scales in first vertical row of dorsal scales. Mental triangular, not divided, wider than long, contacting first infralabials. Supralabials 4, infralabials 3. Scales around body 20/ 19-20/ 18-20. Dorsal scales 333-384, 309-348 ventrals and 11-12 subcaudal scales.

**Coloration in alcohol.** Dorsal and ventral body coloration light brown. Pale cream head, and continuous pale cream throughout venter. Scales close to opening of cloaca pale cream.

**Distribution.** Southeastern Colombia (Amazonas) (Fig. 36).

**Remarks.** In addition to the light brown coloration, *Liotyphlops haadi* still shows continuous pale cream throughout the venter, different from specimens of other species of *Liotyphlops* examined in this study where the coloration of the body shows no differences from dorsum to venter.

***Liotyphlops schubarti* Vanzolini, 1948**

*Liotyphlops schubarti* Vanzolini, 1948, Revista Brasileira de Biologia 8: 377-400 [379, figs. 1-2].

**Holotype.** MZUSP 425, total length 191 mm. Type-locality: Cachoeira de Emas, Municipality of Pirassununga, São Paulo state, Brazil.

**Diagnosis.** *Liotyphlops schubarti* is distinguished from *L. anops*, *L. argaleus*, *L. ss* sp. nov., and *L. trefauti* by having three scales contacting posterior edge of prefrontal (vs. four scales contacting posterior edge of prefrontal). It is distinguished from *L. albirostris*, *L. caissara*, *L. haadi*, and *L. wilderi* by having two scales contacting posterior edge of nasal (vs. one scale contacting posterior edge of nasal). It is distinguished from *L. caissara* by having four supralabials (vs. three supralabials). It is distinguished from *L. tt* new species by having three infralabials (vs. two infralabials), and of *L. ternetzii* by having dorsal-ventral coloration light brown (vs. dorsal-ventral coloration pale cream, dark brown or black).

**Redescription.** Meristic data in Table 4. Standard length 85.2-99.5 mm (93.9 mean ± 6.2), head length 3.2-3.4% of standard length (3.3 mean ± 0.1), head width 1.9-2.2% of standard length (2.1 mean ± 0.1), head height 1.6-2.0% of standard length (1.8 mean ± 0.1), snout-vent length 97.0-97.5% of standard length (97.3 mean ± 0.2), tail length 2.5-3.0% of standard length (2.7 mean ± 0.2), head width 57.6-67.9% of head length (62.8 mean ± 4.0), and head height 48.5-60.7% of head length (53.2 mean ± 4.9). Body covered with cycloid scales. Rostral large, longer than wide, contacting nasals anterolaterally, prefrontals laterally, and single frontal posteriorly. Pair of triangular prefrontals, bordered anterolaterally by rostral, ventrally by large divided nasal, and dorsoposteriorly by frontal. Posterior edge of prefrontals passing posterior edge of rostral. Divided nasal scale bordered anteriorly by rostral, dorsally by prefrontal, ventrally by first and second supralabials, and posteriorly by two scales that lie between prefrontal and second supralabial. Eye spot poorly visible. Three scales contacting posterior edge of prefrontal. Two scales contacting posterior edge of nasal between second supralabial and prefrontal. Five scales in first vertical row of dorsal scales. Mental triangular, not divided, wider than long, contacting first infralabials. Supralabials 4, infralabials 3. Scales around body 22-24/20-22/ 20. Dorsal scales 417-463, 398-451 ventrals and 11-14 subcaudal scales.

**Coloration in alcohol.** Dorsal and ventral body coloration light brown. Pale cream head. Scales close to opening of cloaca pale cream.

**Distribution.** Southeastern Brazil (Minas Gerais and São Paulo) (Fig. 37).

**Remarks.** Dixon and Kofron (1984) observed that *Liotyphlops schubarti* is very similar to *Liotyphlops beui* (removed from the synonymy of *Liotyphlops ternetzii* by them, and returned to the synonymy of *L. ternetzii* here; see redescription of *Liotyphlops ternetzii*) in total length, number of dorsal scales, number of scales around body, and in head scale arrangements. The same authors pointed a single difference, described as "perhaps vertically divided nasal?" to separate *L. beui* from *L. schubarti* and that consisted in an extra scale inserted between the second supralabial and the nasal in the later. No specimen of *L. schubarti* examined during this study showed this scale or any other structure that can differentiate *L. schubarti* of *L. ternetzii*. Despite this, the synonymy of *L. schubarti* with *L. ternetizii* is not proposed here, because of the need of examination of more numerous specimens, mainly in observance to the character noted for Dixon and Kofron (1984).

***Liotyphlops ss*** sp. nov.

**Figs. 38-40, Table 4**

**Holotype.** UFRGS 6274, total length 191.4 mm, Pequena Central Hidrelétrica Passos Maia (26°42'14"S, 51°55'05"W), Municipality of Passos Maia, Santa Catarina state, Brazil, January 2012, Simone Leonardi collected.

**Diagnosis.** *Liotyphlops ss* sp. nov. is distinguished from all other *Liotyphlops*, except *L. anops*, *L. argaleus*, and *L. trefauti* by having four scales contacting posterior edge of prefrontal (vs. three scales contacting posterior edge of prefrontal). It is distinguished from *L. anops* by having 24-22-20 scales around the body, and 439 dorsal scales (vs. 26-24-24 scales around the body, and 562-597 dorsal scales), and *L. argaleus* and *L.*

*trefauti* by having two scales contacting posterior edge of nasal between second supralabial and prefrontal (vs. one scale contacting posterior edge of nasal).

**Description.** Meristic data in Table 4. Standard length 191.4 mm, head length 2.2% of standard length, head width 1.5% of standard length, head height 1.0% of standard length, snout-vent length 97.2% of standard length, tail length 2.8% of standard length, head width 66.7% of head length, and head height 47.6% of head length. Body covered with cycloid scales. Rostral large, longer than wide, contacting nasals anterolaterally, prefrontals laterally, and single frontal posteriorly. Pair of triangular prefrontals, bordered anterolaterally by rostral, ventrally by large divided nasal, and dorsoposteriorly by frontal. Posterior edge of prefrontals passing posterior edge of rostral. Divided nasal scale bordered anteriorly by rostral, dorsally by prefrontal, ventrally by first and second supralabials, and posteriorly by two scales that lie between prefrontal and second supralabial. Eye spot poorly visible. Four scales contacting posterior edge of prefrontal. Two scales contacting posterior edge of nasal between second supralabial and prefrontal. Six scales in first vertical row of dorsal scales. Mental triangular, not divided, wider than long, contacting first infralabials. Supralabials 4, infralabials 3. Scales around body 24/ 22/ 20. Dorsal scales 439, 427 ventrals and 13 subcaudal scales.

**Coloration in alcohol.** Dorsal and ventral body coloration dark brown. Head pale cream. Scales close to opening of cloaca pale cream.

**Distribution.** Known only from the type locality in the Pequena Central Hidrelétrica Passos Maia, Municipality of Passos Maia, Santa Catarina, Brazil (Fig. 41).

**Etymology.** Epithet in honour of the Brazilian Army Colonel Fernando Machado de Sousa (January, 11 1822 - December 6, 1868), recognized as the greatest military hero of the State of Santa Catarina, Brazil.

**Remarks.** Dixon & Kofron (1984) organized *Liotyphlops* species into three groups based on the arrangement of scales on the head. One of these groups was formed by *L. anops* and *L. argaleus* (and *L. trefauti* years later), which share the character of having four scales contacting the posterior edge of the prefrontal. Now, *L. ss* sp. nov. is one more species that shares with the other three species of *Liotyphlops* four scales contacting the posterior edge of the prefrontal. *Liotyphlops ss* is the species of

Anomalepididae which was described further south of the American continent, collected during the filling of the reservoir in fauna rescue work.

***Liotyphlops tt*** sp. nov.

**Figs. 42-44, Table 4**

**Holotype.** MZUSP-S 14975, total length 239.4 mm, Estação Ecológica Serra das Araras (15°38’31”S, 57°11’23”W), Municipality of Porto Estrela, Mato Grosso state, Brazil, 22 October 2002, Cristiano Nogueira collected.

**Diagnosis.** *Liotyphlops tt* sp. nov. is distinguished from all other *Liotyphlops* by having two infralabials. It is further distinguished from congeners, except *L. albirostris*, *L. caissara*, *L. haadi*, *L. schubarti*, *L. ternetzii*, and *L. wilderi* by having three scales contacting posterior edge of prefrontal (vs. four scales contacting posterior edge of prefrontal).

**Description.** Meristic data in Table 4. Standard length 239.4 mm, head length 2.0% of standard length, head width 1.3% of standard length, head height 0.9% of standard length, snout-vent length 98.2% of standard length, tail length 1.8% of standard length, head width 65.3% of head length, and head height 44.9% of head length. Rostral large, longer than wide, contacting nasals anterolaterally, prefrontals laterally, and single frontal posteriorly. Pair of triangular prefrontals, bordered anterolaterally by rostral, ventrally by large divided nasal, and dorsoposteriorly by frontal. Posterior edge of prefrontals passing posterior edge of rostral. Divided nasal scale bordered anteriorly by rostral, dorsally by prefrontal, ventrally by first and second supralabials, and posteriorly by two scales that lie between prefrontal and second supralabial. Eye spot poorly visible. Three scales contacting posterior edge of prefrontal. Two scales contacting posterior edge of nasal between second supralabial and prefrontal. Five scales in first vertical row of dorsal scales. Mental triangular, not divided, wider than long, contacting the first infralabials. Supralabials 4, infralabials 2. Scales around body 22/ 20/ 20. Dorsal scales 455, 441 ventrals and 14 subcaudal scales.

**Coloration in alcohol.** Dorsal and ventral body coloration brown. Pale cream head. Scales close to opening of cloaca pale cream.

**Distribution.** Known only from the type locality in Estação Ecológica Serra das Araras in Porto Estrela, Mato Grosso, Brazil (Fig. 45).

**Etymology.** Epithet in honour of Dr. Edward Harrison Taylor (April 23, 1889 - June 16, 1978), American herpetologist who described the family Anomalepididae.

**Remarks.** The description of a new species based on only one specimen is generally discouraged due to the obvious limitations, for example in the amplitude of variation of characters. However, the collection of *Liotyphlops* is very difficult, and also *L. tt* sp. nov. possesses an important diagnostic character (two infralabials) that distinguishes it from all other known species of *Liotyphlops*.

### *Liotyphlops ternetzii* (Boulenger, 1896)

**Figs. 46-48, Tables 4-5**

*Helminthophis ternetzii* Boulenger, 1896, Catalogue of the Snakes in the British Museum 3: 727 pp. [584]. Type locality: Paraguay.

*Helminthophis incertus* Amaral, 1924, Proceedings of the New England Zoological Club. 9: 25-30 [29]. Holotype: MCZ R17846. Type-locality: “Surinam” [Suriname]. [Placed in synonymy by Dixon and Kofron, 1984 [dated 1983], Amph. Rept. 4: 241-264 [255-256], who also rejected the type-locality as Suriname].

*Helminthophis collenettei* Parker, 1928, Annals and Magazine of Natural History (10) 2: 96-99 [97]. Holotype: BMNH 1946.1.10.73 (formerly BMNH 1928.1.12.1). Type-locality: “Burity, 2250 ft., 30 miles northeast of Coyaba, Mato Grosso” [Brazil]. [Placed in synonymy by Amaral, 1954, Mem. Inst. Butantan 26: 191-195 [192]].

[*Liotyphlops*] *incertus*.−Vanzolini, 1948, Revista Brasileira de Biologia 8: 377-400 [380].

[*Liotyphlops*] *ternetzi*.−Smith and Grant, 1958, Herpetologica 14: 207-222 [207].

*Liotyphlops ternetzii*.−Peters and Orejas-Miranda, 1970, Bulletin of the United States National Museum 297 (1): 1-347 [183]. [In part; included *L. beui* in the synonymy].

*Liotyphlops ternetzii*.−McDiarmid, Campbell and Touré, 1999, The Herpetologists'League: 1-511 [51-52].

*Liotyphlops ternetzii*.−Wallach, Williams and Boundy, 2014, CRC Press Taylor & Francis Group: 3-1227 [397-398].

*Liotyphlops beui* (Amaral, 1924), Proceedings of the New England Zoological Club 9: 25-30. Holotype: IB 1806. Type-locality: Butantan, São Paulo, Brazil. (NEW SYNONYM).

**Holotype.** BMNH 1946.1.11.77, total length 325.1 mm.

**Diagnosis.** *Liotyphlops ternetzii* is distinguished from *L. anops*, *L. argaleus*, *L. ss* sp. nov., and *L. trefauti* by having three scales contacting posterior edge of prefrontal (vs. four scales contacting posterior edge of prefrontal). It is distinguished from *L. albirostris*, *L. caissara*, *L. haadi*, and *L. wilderi* by having two scales contacting posterior edge of nasal between second supralabial and prefrontal (vs. one scale contacting posterior edge of nasal), and of *L. schubarti* by dorsal-ventral coloration pale cream, dark brown or black (vs. dorsal-ventral coloration light brown).

**Redescription.** Meristic data in Table 4. Standard length 100.5-390.0 mm (234.0 mean ± 54.7), head length 1.3-3.2% of standard length (1.9 mean ± 0.4), head width 1.0-2.3% of standard length (1.4 mean ± 0.2), head height 0.7-1.6% of standard length (1.0 mean ± 0.2), snout-vent length 95.5-98.6% of standard length (97.4 mean ± 0.9), tail length 1.4-4.5% of standard length (2.6 mean ± 0.9), head width 55.6-86.3% of head length (71.8 mean ± 7.1), and head height 40.4-65.9% of head length (52.2 mean ± 6.1). Body covered with cycloid scales. Rostral large, longer than wide, contacting nasals anterolaterally, prefrontals laterally, and single frontal posteriorly. Pair of triangular prefrontals, bordered anterolaterally by rostral, ventrally by large divided nasal, and dorsoposteriorly by frontal. Posterior edge of prefrontals passing posterior edge of rostral. Divided nasal scale bordered anteriorly by rostral, dorsally by prefrontal, ventrally by first and second supralabials, and posteriorly by two scales that lie between prefrontal and second supralabial. Eye spot poorly visible. Three scales contacting posterior edge of prefrontal. Two scales contacting posterior edge of nasal between second supralabial and prefrontal. 5-6 scales in first vertical row of dorsal scales. Mental triangular, not divided, wider than long, contacting first infralabials.

Supralabials 4, infralabials 3. Scales around body 22-26/20-23/20-22. Dorsal scales 353-539, 341-514 ventrals and 11-22 subcaudal scales.

**Coloration in alcohol.** Dorsal-ventral coloration pale cream with head and scales near opening of cloaca lighter than rest of body. Coloration sometimes dark brown or black.

**Distribution.** Brazil (states of Mato Grosso, Goiás, Minas Gerais, São Paulo, Paraná, Santa Catarina, and Rio Grande do Sul), Paraguay (Amambay, Caazapá, Canendiyu, Itapúa, Presidente Hayes), Uruguay (Rio Negro, Salto), and Argentina (Corrientes, Entre Ríos, Formosa, Jujuy, Misiones, Salta) (Fig. 49).

**Remarks.** The specimens of *Liotyphlops beui* and *Liotyphlops ternetzii* examined in this study (Fig. 50) showed limited meristic and morphometric variation (Table 5) that does not warrant the rcognition of two species. Through the examination of head scales it is not possible to distinguish the two species because they do not exhibit any differences in the form and quantity (Figs. 46-47): (1) three scales contacting the posterior edge of prefrontal; (2) two scales contacting posterior edge of nasal between second supralabial and prefrontal; (3) five or six scales in the first vertical row of dorsals; (4) four supralabials, and (5) three infralabials. In Anomalepididae snakes, the supratemporal is very reduced or absent (*Anomalepis*), and based on high-resolution X-ray computed tomography (HRXCT), it was observed that the two paratypes of *Liotyphlops beui* (MCZ R-16702, Fig. 48 and MCZ R-17842) do not have the reduced supratemporal, but the reduced supratemporal is present in all other specimens of *L. beui* scanned and examined in this study. *Liotyphlops beui* was removed from the synonymy of *L. ternetzii* by Dixon & Kofron (1984) based on the following characters: (1) 20 scales rows posteriorly around the body (*L. ternetzii*, 22), and (2) its lower dorsal scale count of 384-455 (*L. ternetzii*, 463-510). These two characters proposed by Dixon & Kofron (1984) to remove *L. beui* from synonymy of *L. ternetzii*, however, resulted in overlapping characters and were not diagnostic for *L. beui* in the present study (Table 5). Both meristic and morphometric characters, the coloration pattern, and the osteology of the skull showed no significant variation that can be used as diagnostic characters for *L. beui*.

After a detailed morphological examination of specimens of *L. beui* and *L. ternetzii*, including type material, and osteology of the skull of both taxa, *Liotyphlops beui* is considered as a junior synonym of *Liotyphlops ternetzii* (Boulenger, 1896). The characters considered diagnotic of *L. beui* based on the posterior scale rows and dorsal scale rows proposed by Dixon & Kofron (1984) do not distinguish *L. beui* from *L. ternetzii*.

***Liotyphlops trefauti*** **Freire, Caramaschi & Argôlo, 2007**

*Liotyphlops trefauti* Freire, Caramaschi & Argôlo, 2007, 2007, Zootaxa 1393: 19-26. Holotype**.** MZUSP 12178, total length 362 mm. Type-locality: Fazenda Bananeira, Municipality of Murici (9°14'S, 35°48'W), State of Alagoas, Brazil.

**Holotype.** MZUSP 12178, total length 362 mm. Type-locality: Fazenda Bananeira, Municipality of Murici (9°14'S, 35°48'W), State of Alagoas, Brazil.

**Paratype.** MZUSP 12179, total length 385 mm. Collected at Regional Center of the CEPLAC (Comissão Executiva do Plano da Lavoura Cacaueira), Municipality of Ilhéus (14°46'S, 39°13'W), State of Bahia, Brazil, on 29 January 1992, by C. Jared, M. Antoniazzi, and L. Ferreira.

**Diagnosis.** *Liotyphlops trefauti* is distinguished from all other *Liotyphlops*, except *L. anops, L. argaleus*, and *L. ss* new species by having four scales contacting posterior edge of prefrontal (vs. three scales contacting posterior edge of prefrontal). It is distinguished from *L. anops* and *L. ss* new species by having one scale contacting posterior edge of nasal (vs. two scales contacting posterior edge of nasal). It is distinguished from *L. argaleus* by having four infralabials, 22 scales on anterior anterior scale rows around body, and 520-543 dorsals (vs. three infralabials, 25 scales on anterior anterior scale rows around body, and 497 dorsals).

**Redescription.** Meristic data in Table 4. Standard length 362-385 mm. Body covered with cycloid scales. Rostral large, longer than wide, contacting nasals anterolaterally, prefrontals laterally, and single frontal posteriorly. Pair of triangular prefrontals, bordered anterolaterally by rostral, ventrally by large divided nasal, and dorsoposteriorly by frontal. Posterior edge of prefrontals passing posterior edge of rostral. Divided nasal scale bordered anteriorly by rostral, dorsally by prefrontal, ventrally by first and second supralabials, and posteriorly by one scale that lie between prefrontal and second supralabial. Eye spot absent. Four scales contacting posterior edge of prefrontal. One scale contacting posterior edge of nasal between second supralabial and prefrontal. Five scales in first vertical row of dorsal scales. Mental triangular, not divided, wider than long, contacting first infralabials. Supralabials 4, infralabials 4. Scales around body 22/ 22/ 22. Dorsal scales 520-543, 499-531 ventrals and eight subcaudal scales.

**Coloration in alcohol.** Body coloration uniform yellowish brown. In life, dorsal and ventral color uniform bright yellowish brown.

**Distribution.** Northeastern Brazil (Alagoas, Bahia, Pernambuco) (Fig. 51).

**Remarks.** Because of the impossibility to examine specimens of *Liotyphlops trefauti* during this study, the diagnosis and redescription presented here is based on original description of *L. trefauti* by Freire et al. 2007, as well as on our interpretation of data in the taxonomic literature on *Liotyphlops*. Because the authors of the original description had not reported on measurement data, in addition to the total length and tail length (362 mm and 4 mm, respectively) for the holotype of *L. trefauti* (MZUSP 12178), and the total length (385 mm) for the paratype (MZUSP 12179), morphometric information for this species is not available.

### *Liotyphlops wilderi* (Garman, 1883)

*Typhlops wilderi* Garman, 1883, Scientific Observations 4:47-48 [48]. Syntypes**:** (3) MCZ R 5126, MCZ R 19585, formerly Museum of Vertebrates, Cornell University (CU), and FMNH 73387, formerly Cornell University (CU) & MCZ R l8138. The latter two specimens were formerly in the CU collection but deposited in the MCZ in May, 1924. Type locality: “São Cyriaco, Brazil” [= Cipriano, Minas Gerais State, SE Brazil, 19º45’S, 43º57’W, elevation 850 m].

*Helminthophis guentheri* Boulenger, 1889, Annals and Magazine of Natural History (6) 4: 360-363 [361]. Holotype: BMNH 1946.1.11.3 (formerly BMNH 1887.12.29.8). Type-locality: “Porto Real, Province Rio de Janeiro” [Brazil]. Placed in synonymy by Dixon and Kofron, 1984, Amphibia-Reptilia 4: 241-264 [251].

*Typhlops wilderi*.−Boulenger, 1893, Catalogue of the Snakes in the British Museum 1: 448 pp. [7, footnote].

*Helminthophis guentheri*.−Boulenger, 1893, Catalogue of the Snakes in the British Museum 1: 448 Pp. [6, pl. 1 (figs. 2a- b)].

*Helminthophis wilderi*.−Hammar, 1908, Annals and Magazine of Natural History (8) 1: 334-335 [334].

*Liotyphlops wilderi*.−Vanzolini, 1948, Revista Brasileira de Biologia 8: 377-400 [380].

*Liotyphlops guentheri*.−Peters and Orejas-Miranda, 1970, Bulletin of the United States National Museum 297 (1): 1-347 [182].

*Liotyphlops wilderi*.−Dixon and Kofron, 1984, Amphibia-Reptilia 4: 241-264 [251].

**Diagnosis.** *Liotyphlops wilderi* is distinguished from *L. anops*, *L. argaleus*, *L. ss* sp. nov., and *L. trefauti* by having three scales contacting posterior edge of prefrontal (vs. four scales contacting posterior edge of prefrontal). It is distinguished from *L. schubarti*, *L. tt* new species, and *L. ternetzii* by having one scale contacting posterior edge of nasal between second supralabial and prefrontal (vs. two scales contacting posterior edge of nasal). It is distinguished from *L. albirostris* by having four scales in the first vertical row of dorsals, and 385-402 dorsals (vs. five scales in the first vertical row of dorsals, and 432-478 dorsals). It is distinguished from *L. caissara* by having four supralabials (vs. three supralabials), and *L. haadi* by having 22-24 scales in anterior scale rows, 22 scales in midbody scale rows, and 371-383 ventral scale rows (vs. 20 scales in anterior scale rows, 19-20 scales in midbody scale rows, and 309-348 ventral scale rows).

**Redescription.** Meristic data in Table 4. Standard length 95.5-231.2 mm (172.9 mean ± 69.9), head length 1.8-3.5% of standard length (2.4 mean ± 0.9), head width 1.1-2.1% of standard length (1.5 mean ± 0.5), head height 0.7-1.5% of standard length (1.1 mean ± 0.4), snout-vent length 96.5-97.4% of standard length (97.1 mean ± 0.5), tail length 2.6-3.5% of standard length (2.9 mean ± 0.5), head width 58.3-73.8% of head length (64.2 mean ± 8.4), and head height 38.9-57.1% of head length (46.2 mean ± 9.7). Body covered with cycloid scales. Rostral large, longer than wide, contacting nasals anterolaterally, prefrontals laterally, and single frontal posteriorly. Pair of triangular prefrontals, bordered anterolaterally by rostral, ventrally by large divided nasal, and dorsoposteriorly by frontal. Posterior edge of prefrontals passing posterior edge of rostral. Divided nasal scale bordered anteriorly by rostral, dorsally by prefrontal, ventrally by first and second supralabials, and posteriorly by one scale that lie between prefrontal and second supralabial. Eye spot poorly visible. Three scales contacting posterior edge of prefrontal. One scale contacting posterior edge of nasal between second supralabial and prefrontal. Four scales in first vertical row of dorsal scales. Mental triangular, not divided, wider than long, contacting first infralabials. Supralabials 4, infralabials 3. Scales around body 22-24/ 22/ 20-21. Dorsal scales 385-402, 371-383 ventrals and 12-19 subcaudal scales.

**Coloration in alcohol.** Dorsal and ventral body coloration dark brown. Head pale cream. Scales close to opening of cloaca pale cream.

**Distribution.** Southeastern Brazil (states of Minas Gerais and Rio de Janeiro) and Paraguay (Fig. 52).

**Remarks.** According to Van Wallach et al. (2014), MCZ 5126 was recorded as the holotype in 1883 by S.W. Garman following MCZ catalogue and specimen data label. Two Cornell University (CU) specimens were exchanged with MCZ in May 1924 (MCZ 18138, 19585). The former specimen was subsequently exchanged with FMNH in 1954 (FMNH 73387). Hammar (1908: 335) mentioned two CU specimens as the types and that three specimens were from Cyriaco, near Serra Providencia, Minas Gerais, Brazil. Hahn (1980a: 5) suggested the two CU syntypes were lost, and Dixon & Kofron (1984: 253) mentioned one being lost.

**Table 4**. Meristic characters of *Liotyphlops* species from the specimens examined in this study. PEP = number of scales contacting posterior edge of prefrontal; Scales PEN = number of scales contacting posterior edge of nasal between second supralabial and prefrontal; Scales FVRD = number of scales in the first vertical row of dorsals; Supralabials = number of supralabial scales; Infralabials = number of infralabial scales; ASR = number of anterior scale rows around body; MSR = number of scale rows around the midbody; PSR = number of posterior scale rows around body; DSR = number of dorsal scale rows; VSR = number of ventral scales rows; SC = number of subcaudal scales. N = number of specimens examined in this study. [N1] = specimen examined by Centeno et al. (2010). [N2] = specimens examined by Freire et al. (2007). [1]Number of scales presented as ranges with minimum, maximum and mode in parentheses.

| | | Counts[1] | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Species** | **N** | **SPEP** | **SPEN** | **SFVRD** | **SL** | **IL** | **ASR** | **MSR** | **PSR** | **DSR** | **VSR** | **SC** |
| ***L. albirostris*** | 6 | 3-3 (3) | 1-1 (1) | 5-5 (5) | 4-4 (4) | 3-3 (3) | 24-26 (26) | 22-22 (22) | 22-22 (22) | 432-478 | 417-453 | 12-17 (12) |
| ***L. anops*** | 3 | 4-4 (4) | 2-2 (2) | 5-6 (5) | 4-4 (4) | 3-3 (3) | 26-26 (26) | 24-24 (24) | 24-24 (24) | 562-597 | 531-572 | 12-14 |
| ***L. argaleus*** | 1 | 4 | 1 | 4 | 4 | 3 | 25 | 23 | 22 | 497 | 472 | 16 |
| ***L. caissara*** [N1] | 1 | 3 | 1 | 4 | 3 | 3 | 22 | 20 | 20 | 326 | 308 | 10 |
| ***L. haadi*** | 2 | 3-3 (3) | 1-1 (1) | 4-4 (4) | 4-4 (4) | 3-3 (3) | 20-20 (20) | 19-20 | 18-20 | 333-384 | 309-348 | 11-12 |
| ***L. schubarti*** | 5 | 3-3 (3) | 2-2 (2) | 5-5 (5) | 4-4 (4) | 3-3 (3) | 22-24 (22) | 20-22 (20) | 20-20 (20) | 417-463 | 398-451 | 11-14 (13) |
| ***L. ss* sp. nov.** | 1 | 4 | 2 | 6 | 4 | 3 | 24 | 22 | 20 | 439 | 427 | 13 |
| ***L. tt* sp. nov.** | 1 | 3 | 2 | 5 | 4 | 2 | 22 | 20 | 20 | 455 | 441 | 14 |
| ***L. ternetzii*** | 103 | 3-3 (3) | 2-2 (2) | 5-6 (5) | 4-4 (4) | 3-3 (3) | 22-26 (22) | 20-23 (20) | 20-22 (20) | 353-539 (373) | 341-514 (381) | 11-22 (14) |
| ***L. trefauti*** [N2] | 2 | 4-4 (4) | 1-1 (1) | 5-5 (5) | 4-4 (4) | 4-4 (4) | 22-22 (22) | 22-22 (22) | 22-22 (22) | 520-543 | 499-531 | 8 (8) |
| ***L. wilderi*** | 3 | 3-3 (3) | 1-1 (1) | 4-4 (4) | 4-4 (4) | 3-3 (3) | 22-24 (22) | 22-22 (22) | 20-21 (20) | 385-402 | 371-383 | 12-19 (12) |

**Table 5**. Meristic characters of *Liotyphlops* species from the specimens examined in this study. PEP = number of scales contacting posterior edge of prefrontal; Scales PEN = number of scales contacting posterior edge of nasal between second supralabial and prefrontal; Scales FVRD = number of scales in the first vertical row of dorsals; Supralabials = number of supralabial scales; Infralabials = number of infralabial scales; ASR = number of anterior scale rows around body; MSR = number of scale rows around the midbody; PSR = number of posterior scale rows around body; DSR = number of dorsal scale rows; VSR = number of ventral scales rows; SC = number of subcaudal scales. N = number of specimens examined in this study. [1]Number of scales presented as ranges with minimum, maximum and mode in parentheses.

| | | **Counts[1]** | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Species** | **N** | **SPEP** | **SPEN** | **SFVRD** | **SL** | **IL** | **ASR** | **MSR** | **PSR** | **DSR** | **VSR** | **SC** |
| ***L. beui* paratypes** | 2 | 3-3 (3) | 2-2 (2) | 5-5 (5) | 4-4 (4) | 3-3 (3) | 22-22 (22) | 20-20 (20) | 20-20 (20) | 462-477 | 439-452 | 19-20 |
| ***L. beui*** | 50 | 3-3 (3) | 2-2 (2) | 5-6 (5) | 4-4 (4) | 3-3 (3) | 22-26 (22) | 20-22 (22) | 20-22 (20) | 366-532 (453) | 348-511 (364) | 11-22 (12) |
| ***L. ternetzii* holotype** | 1 | 3 | 2 | 5 | 4 | 3 | 24 | 22 | 21 | 475 | 452 | 20 |
| ***L. ternetzii*** | 50 | 3-3 (3) | 2-2 (2) | 5-6 (5) | 4-4 (4) | 3-3 (3) | 22-26 (22) | 20-23 (20) | 20-22 (20) | 353-539 (417) | 341-514 (381) | 11-22 (15) |

***Typhlophis* Fitzinger, 1843**

*Typhlophis* Fitzinger, 1843, Systema Reptilium.106 Pp. [24]. Type species: *Typhlophis squamosus* (Schlegel, 1839), by monotypy.

*Cephalolepis* Duméril and Bibron, 1844, Erpetologie Générale ou histoire naturelle complète des reptiles 6: 609 Pp. [314]. Type-species: *Cephalolepis leucocephalus* Duméril and Bibron, 1844 [= *Typhlophis squamosus* (Schlegel, 1839), by monotypy].

**Diagnosis.** *Typhlophis* is diagnosed among the Anomalepididae by the following exclusive autapomorphies: (1) the posterior extension of the medial nasal septum overlapping the anterior margin of the frontal subolfactory process (character 19, state 1), (2) tiny point contact palatine-vomer (character 33, state 1), (3) coronoid contacting angular (character 52, state 1), (4) frontal scale absent (character 66, state 1), and (5) scales of the head undifferentiated (character 67, state 1). It is further distinguished from all remaining Anomalepididae by lacking the premaxilla lateral flange (Fig. 30B) (vs. premaxilla with with lateral flange forming dorsal margin of external naris, Fig. 30A).

**Species included.** One species, *Typhlophis squamosus* (Schlegel, 1839).

**Distribution.** Trinidad and the Atlantic coast of South America from the Guianas to Pará in northern Brazil.

**Remarks.** The cephalic scales of *Typhlophis squamosus* possess a unique configuration among the Anomalepididae, being completely undifferentiated, with only a small rostral, nasals and supra- and infralabials. However, the osteology of the skull shows synapomorphies shared with other Anomalepididae, for example, the absence of the lateral maxillary foramina, the possession of one discrete ossification (postorbitofrontal), and the possession of an ectopterygoid, which unequivocally place it within the family.

***Typhlophis squamosus* (Schlegel, 1839)**

*Typhlops squamosus* Schlegel, 1839 [1837-1844] Abbildungen neuer oder unvollständig bekannter amphibien, nach der Natur oder dem leben entworfen, herausgegeben und mit einem erläuternden texte begleitet. 141 Pp. [36, pl. 32 (figs. 9-12)]. RMNH 3685, total length 145 mm. Type-locality: "Cayenne" [= Cayenne, North Cayenne Department, French Guiana).

*Cephalolepis leucocephalus* Duméril and Bibron, 1844, Erpetologie Générale ou histoire naturelle complète des reptiles. 6: 609 Pp. [315]. Holotype: MNHN, lost according to Hahn, 1980, Das Tierreich 101: 1-93 [5]. Type-Jocality: "Guyane française" [French Guiana]. Listed in synonymy by Boulenger (1893:57).

*Typhlops squammosus*.−Duméril and Bibron, 1844, Erpetologie Générale ou histoire naturelle complète des reptiles. 6: 609 Pp. [315]. [Incorrect subsequent spelling, typographical error in the synonymy of *Cephalolepis leucocephalus*].

*Anilios* (?) *squamosus*.−Gray, 1845, Catalogue of the specimens of lizards in the collection of the British Museum. 289 Pp. [136].

*Cephalolepis squamosus*.−Jan and Sordelli, 1860, Iconographie génerale des ophidiens. 1, livr. l: [index to pl. 5 (fig. 11), pl. 6 (fig. 11)].

*Typhlophis squamosus*.−Boulenger, 1893, Catalogue of the Snakes in the British Museum. 1: 448 Pp. [57]; 1896, Catalogue of the Snakes in the British Museum. 3: 727 Pp. [590].

**Holotype.** RMNH 3685, total length 145 mm. Type-locality: "Cayenne" [= Cayenne, North Cayenne Department, French Guiana).

**Diagnosis.** Same as for genus.

**Redescription.** Meristic data in Table 6. Standard length 118.5-188.0 mm (147.9 mean ± 30.7), head length 2.1-3.1% of standard length (2.5 mean ± 0.4), head width 1.5-1.9% of standard length (1.7 mean ± 0.1), head height 1.1-1.6% of standard length (1.4 mean ± 0.2), snout-vent length 97.0-98.3% of standard length (97.7 mean ± 0.4), tail length 1.7-3.0% of standard length (2.3 mean ± 0.4), head width 55.0-79.5% of head length (69.0 mean ± 8.2), and head height 40.0-68.3% of head length (54.7 mean ± 9.9). Body covered with cycloid scales. Head with only undifferentiated scales. Rostral small, wider than long, visible only frontally and ventrally, contacting first supralabial laterally. Divided nasal separated from rostral by one scale, and bordered posteriorly by rows of undifferentiated scales from remaining of body. Eye spot poorly visible. Mental triangular, not divided, wider than long, contacting first infralabials. Supralabials 4, infralabials 3. Scales around body 22-24/ 20-24/ 20-22. Dorsal scales 301-427, 289-399 ventrals and 10-11 subcaudal scales.

**Coloration in alcohol.** Body coloration usually dark brown dorsally and pale cream ventrally. Sometimes dark brown to completely black both dorsally and ventrally. Head pale cream. Scales close to opening of cloaca pale cream.

**Distribution.** Trinidad, Eastern Venezuela (Bolívar), Guyana (Cuyuni-Mazaruni), Surinam (Nickerie), French Guiana (Cayenne, Saint-Laurent-du-Maroni) and North Brazil (Amazonas, Pará) (Fig. 53).

**Remarks.** Hanh (1980: 5) stated the holotype of *Typhlophis squamosus* as "M.N.H.P.; now lost.", but Van Wallach et al. (2014) indicated that this information was incorrect, and that the holotype (RMNH 3685) was not lost.

**Table 6**. Meristic characters of *Typhlophis* species from the specimens examined in this study. PEF = Number of scales contacting posterior edge of frontal; SL = Supralabials; IL = Infralabials; ASR = number of anterior scale rows around body; MSR = number of scale rows around the midbody; PSR = number of posterior scale rows around body; DSR = number of dorsal scale rows; VSR = number of ventral scales rows; SC = number of subcaudal scales. N = number of specimens examined in this study. [1]Number of scales presented as ranges with minimum, maximum and mode in parentheses.

| | | Counts[1] | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| **Species** | **N** | **SL** | **IL** | **ASR** | **MSR** | **PSR** | **DSR** | **VSR** | **SC** |
| ***T. squamosus*** | 7 | 4-4 (4) | 3-3 (3) | 22-24 (24) | 20-24 (24) | 20-22 (22) | 301-427 | 289-399 | 10-11 (10) |

**Phylogenetic relationships**

**Character description**

Neurocranium

Character 1. Ascending process of premaxilla. State 0, without lateral flange. State 1, with lateral flange forming dorsal margin of external naris. Lee & Scanlon (2002).

Character 2. Premaxillary palatal foramina. State 0, paired. State 1, single. State 2, multiple. Lee & Scanlon (2002) (Fig. 54).

Character 3. Main body of premaxilla. State 0, on anterior end of the snout. State 1, on ventral surface of snout. Lee & Scanlon (2002).

Character 4. Maxilla-premaxilla contact. State 0, close, suture or strong abutting contact. State 1, close but not abutting, connected by short ligament. State 2, loose, widely separated. Lee & Scanlon (2002).

Character 5. Lateral maxillary foramina. State 0, present. State 1, absent. Lee & Scanlon (2002).

Character 6. Maxilla. State 0, alveolar (tooth) row oriented longitudinally. State 1, alveolar (tooth) row oriented transversely. Lee & Scanlon (2002) (Fig. 55).

Character 7. Nasal. State 0, paired. State 1, fused. Gauthier et al. (2012).

Character 8. Nasal-frontal boundary. State 0, concave posteriorly in dorsal view. State 1, approximately straight and transverse. State 2, convex posteriorly in a shallow W-shaped suture. Lee & Scanlon (2002).

Character 9. Prefrontal-nasal contact. State 0, prefrontal separated from nasal by external naris. State 1, prefrontal contacts nasal. State 2, prefrontal separated from nasal by ragged fissure that is not part of external naris. State 3, prefrontal separated from nasal by frontal-maxillary contact. Lee & Scanlon (2002).

Character 10. Prefrontal-maxilla contact. State 0, anterior process and ventrolateral margin of prefrontal contact maxilla. State 1, anterior process of prefrontal does not contact maxilla and projects freely, only ventrolateral margin of prefrontal contacting maxilla. State 2, anterior process and ventrolateral margin of prefrontal do not contact maxilla. Lee & Scanlon (2002).

Character 11. Prefrontal-frontal contact. State 0, prefrontal sutured to or tightly buttressed against frontal. State 1, prefrontal moveably articulated to frontal. Lee & Scanlon (2002).

Character 12. Postorbitofrontal ossification(s). State 0, one discrete ossification, conventionally termed the postorbitofrontal. State 1, two discrete ossifications, conventionally termed the postfrontal and postorbital. State 2, no discrete ossifications. Lee & Scanlon (2002).

Character 13. Lateral process of parietal. State 0, lateral process distinct. State 1, lateral process absent. Lee & Scanlon (2002). (Fig. 56).

Character 14. Posterior orbital margin. State 0, complete, closed by postorbital contacting jugal. State 1, complete, closed by postorbital contacting ectopterygoid-maxilla unit. State 2, incomplete. Lee & Scanlon (2002).

Character 15. Frontal shape. State 0, frontals gradually tapering anteriorly. State 1, frontals rectangular, at most slightly constricted in middle. State 2, Frontals gradually tapering posteriorly. State 3, Frontals greatly constricted in middle. Lee & Scanlon (2002).

Character 16. Frontal. State 0, paired. State 1, fused. Gauthier et al. (2012).

Character 17. Frontal-parietal contact (dorsal aspect). State 0, mostly straight and transverse, slight median notch in frontals at most. State 1, anteriorly concave, i.e. frontals extending posteriorly into broad median embayment in parietals. State 2, complex W or M shape. Lee & Scanlon (2002).

Character 18. Subolfactory (lateral descending) processes of frontal. State 0, not contacting one another ventromedially. State 1, meeting ventromedially, below medial descending processes of frontal if present. Lee & Scanlon (2002). (Fig. 57).

Character 19. Posterior extension of the medial nasal septum[N]. State 0, do not overlap the anterior margins of the frontal subolfactory processes. State 1, overlap the anterior margins of the frontal subolfactory processes.

Character 20. Medial descending processes of frontal. State 0, absent. State 1, present. Lee & Scanlon (2002).

Character 21. Optic foramen. State 0, posteriorly located, posterior border forming a deep notch in parietal. State 1, intermediate position, posterior border formed by straight margin of parietal. State 2, anteriorly located, posterior border within frontal. Lee & Scanlon (2002).

Character 22. Parietal. State 0, paired. State 1, fused. Gauthier et al. (2012).

Character 23. Posterior border of parietal. State 0, without median projection over supraoccipital. State 1, with median projection over supraoccipital. Lee & Scanlon (2002). (Fig. 58).

Character 24. Supratemporal. State 0, present. State 1, absent. Gauthier et al. (2012).

Character 25. Supratemporal-supraoccipital contact. State 0, supratemporal and supraoccipital separated by dorsal exposures of parietal and exoccipital. State 1, supratemporal and supraoccipital separated by dorsal exposures of prootic, parietal and exoccipital. State 2, supratemporal and supraoccipital in contact. Lee & Scanlon (2002). Inapplicable for species without supratemporal or supraoccipital.

Character 26. Quadrate. State 0, without small ossification ('stylohyal') on medial surface, contacting stapes. State 1, with such ossification. Lee & Scanlon (2002). (Fig. 59).

Character 27. Cephalic condyle of quadrate. State 0, situated dorsally, approximately level with dorsal margin of prootic. State 1, situated ventrally, well below level of dorsal margin of prootic. Lee & Scanlon (2002).

Character 28. Quadrate shaft. State 0, inclined slightly anteroventrally. State 1, inclined greatly anteroventrally. State 2, vertical. State 3, inclined posteroventrally. Lee & Scanlon (2002).

Character 29. Septomaxilla-frontal contact. State 0, posteromedial flange of septomaxilla short, not contacting frontal. State 1, posteromedial flange of septomaxilla long, contacting frontal adjacent to midline on lower part of interolfactory pillar. Lee & Scanlon (2002). (Fig. 60).

Character 30. Septomaxilla. State 0, maxilla, but not septomaxilla, contributes to posterior border of the external naris. State 1, septomaxilla with lateral flange contributing to the posterior border of the external naris. Lee & Scanlon (2002). (Fig. 61).

Character 31. Septomaxilla lateral flange. State 0, absent. State 1, present. State 2, reaches well above roof of vomeronasal organ. Gauthier et al. (2012). (Fig. 62).

Character 32. Fenestra for duct of Jacobson's organ. State 0, faces ventrally. State 1, faces posteroventrally. Lee & Scanlon (2002).

Character 33. Palatine-vomer contact. State 0, medial (choanal) process of palatine with extensive contact with vomer. State 1, tiny point contact. State 2, no contact. Lee & Scanlon (2002).

Character 34. Palatine-maxilla contact. State 0, palatine sutured to maxilla. State 1, palatine meets maxilla in a loose joint. State 2, palatine does not contact maxilla. Lee & Scanlon (2002). (Fig. 63).

Character 35. Medial (choanal or vomerine) process of palatine. State 0, anteroposteriorly broad plate of bone. State 1, narrow finger-like process. Lee & Scanlon (2002). (Fig. 64).

Character 36. Palatine pterygoid contact[N]. State 0, palatine contacts pterygoid. State 1, palatine does not contact pterygoid. (Fig. 65).

Character 37. Ectopterygoid. State 0, present. State 1, absent. Gauthier et al. (2012).

Character 38. Basioccipital-parabasisphenoid suture. State 0, positioned midway between fenestra ovalis and trigeminal foramen. State 1, posteriorly positioned, closer to fenestra ovalis than to trigeminal foramen. State 2, anteriorly positioned, closer to trigeminal foramen than to fenestra ovalis. Lee & Scanlon (2002).

Character 39. Posterior opening of vidian canal. State 0, within basisphenoid, not bordered by prootic. State 1, partly bordered by prootic (i.e. on basisphenoid-prootic suture) or entirely within prootic. Lee & Scanlon (2002).

Character 40. Vidian canal. State 0, does not open intracranially. State 1, opens intracranially, emerging on internal surface of sphenoid (primary opening) then emerging externally on sphenoid-parietal suture (secondary opening). Lee & Scanlon (2002).

Character 41. Vidian canals. State 0, symmetrical. State 1, asymmetrical, left larger than right or vice versa. Lee & Scanlon (2002) (Fig. 66).

Character 42. Supraoccipital[N]. State 0, present. State 1, absent. (Fig. 67).

Character 43. Supraoccipital. State 0, single. State 1, double. Gauthier et al. (2012) (Fig. 68). Inapplicable for species without supraoccipital.

Character 44. Supraoccipital contribution to internal sidewall of neurocranium. State 0, participates in sidewall. State 1, absent, only dorsal plate remains. State 2, dorsal plate absent. Gauthier et al. (2012). Inapplicable for species without supraoccipital.

Character 45. Supraoccipital. State 0, external (dorsoposterior) surface with no, or very weak transverse ridge. State 1, external surface with moderate transverse ridge. State 2, external surface with very high transverse ridge. Lee & Scanlon (2002). Inapplicable for species without supraoccipital.

Character 46. Supraoccipital-prootic contact. State 0, narrow, less than half supraoccipital-parietal contact. State 1, broad, subequal to or as long as supraoccipital-parietal contact. Lee & Scanlon (2002). Inapplicable for species without supraoccipital.

Character 47. Exoccipital separation dorsal to foramen magnum. State 0, exoccipitals widely separated above foramen magnum. State 1, exoccipitals narrowly separated above foramen magnum[N]. State 2, exoccipitals with point contact above foramen magnum. 3, exoccipitals in extensive median contact above foramen magnum. Lee & Scanlon (2002) (Fig. 69).

Character 48. Exoccipital occipital condyle contact[N]. State 0, exoccipital overlaps and extends in front of the occipital condyle. State 1, exoccipital does not overlaps and does not extend in front of the occipital condyle (Fig. 24).

Mandible

Character 49. Posterolateral margin of dentary. State 0, notch absent, posterolateral margin of dentary straight or slightly concave, dorsoposterior and ventroposterior processes indistinct. State 1, with shallow notch, processes short. State 2, with deep notch, processes long. Lee & Scanlon (2002) (Fig. 70).

Character 50. Meckel's canal (groove). State 0, lacks floor anteriorly, open ventrally anterior to level of anterior inferior alveolar foramen. State 1, floored by a horizontal ventral lamina for its full length. State 2, enclosed anteriorly, with ventral and medial lamina. Lee & Scanlon (2002).

Character 51. Splenial. State 0, splenial present as discrete element. State 1, splenial not present as discrete element. Lee & Scanlon (2002) (Fig. 71).

Character 52. Coronoid-angular contact. State 0, coronoid and angular separated by prearticular, or prearticular portion of compound bone. State 1, coronoid contacts angular. Lee & Scanlon (2002). (Fig. 72).

Character 53. Anterior surangular foramen. State 0, situated posteriorly, below apex of coronoid process or more posterior. State 1, situated anteriorly, between apex and anterior limit of coronoid process. State 2, situated far anteriorly, in front of anterior limit of coronoid process. Lee & Scanlon (2002) (Fig. 73).

Character 54. Retroarticular process length. State 0, long, longer than articular facet. State 1, short, not longer than articular facet. Lee & Scanlon (2002) (Fig. 74).

Dentition

Character 55. Premaxillary teeth. State 0, present. State 1, absent. Lee & Scanlon (2002) (Fig. 75).

Character 56. Maxillary teeth. State 0, ausent. State 1, present. Modified. Lee & Scanlon (2002) (Fig. 76).

Character 57. Dentary teeth. State 0, present. State 1, absent. Modified. Lee & Scanlon (2002) (Fig. 77).

Character 58. Palatine teeth. State 0, absent. State 1, present. Lee & Scanlon (2002) (Fig. 78).

Character 59. Pterygoid teeth. State 0, present. State 1, absent. Lee & Scanlon (2002) (Fig. 79).

External morphology

Character 60. Eyes. State 0, exposed, moveable eyelids present. State 1, covered by separate scale, a transparent spectacle (brille). State 2, covered by a normal cranial scale with transparent 'window'. State 3, covered by a normal cranial scale without transparent 'window'. Lee & Scanlon (2002).

Character 61. Midventral scales. State 0, undifferentiated. State 1, slightly expanded transversely, remaining much narrower than body width. State 2, greatly expanded transversely, approaching body width. Lee & Scanlon (2002) (Fig. 80).

Character 62. Subcaudals. State 0, undifferentiated. State 1, single row. State 2, paired row. Lee & Scanlon (2002) (Fig. 81).

Character 63. Anal shields. State 0, two or more. State 1, single. Lee & Scanlon (2002).

Character 64. Rostral frontal scales contact[N]. State 0, in contact. State 1, not in contact.

Character 65. Rostral scale. State 0, not wide. State 1, wide[N] (Fig. 13).

Character 66. Frontal scale. State 0, present. State 1, absent[N] (Fig 12).

Character 67. Scales of the head. State 0, differentiated. State 1, undifferentiated[N] (Fig. 12).

Character 68. Pentagonal frontal. State 0, absent. State 1, present$^{N}$ (Fig 13).

**Phylogenetic analysis**

The heuristic search resulted in nine maximally parsimonious trees with a length of 134 steps, consistency index (Ci) = 0.64, and retention index (Ri) = 0.78. The strict consensus tree is shown in Fig. 82. Anomalepididae includes *Anomalepis*, *Helminthophis*, *Liotyphlops*, and *Typhlophis* and was recovered as a monophyletic taxon, and sister to the Typhlopidae. Anomalepididae presented two exclusive synapomorphies: (1) the nasal bone fused (character 7, state 1), and (2) cephalic scales covering the "eye spot" making it invisible or poorly visible (character 60, state 3). Within Anomalepididae, *Anomalepis* was represented by the node 7 ((*Anomalepis aspinosus* + *Anomalepis mexicanus*) (*Anomalepis colombia* + *Anomalepis flavapices*)), and was recovered as sister to all other Anomalepididae, having as exclusive synapomorphy a pentagonal frontal (character 68, state 1). The node 10, formed by (*Typhlophis* (*Liotyphlops* + *Helminthophis*) have as diagnostic characters the exclusive synapomorphies nasal-frontal boundary convex posteriorly in a shallow W-shaped suture (character 8, state 2), and parietal divided, paired (character 22, state 0). *Typhlophis squamosus* has as exclusive autapomorphies the posterior extension of the medial nasal septum overlapping the anterior margin of the frontal subolfactory process (character 19, state 1), tiny point contact palatine-vomer (character 33, state 1), coronoid contacting angular (character 52, state 1), frontal scale absent (character 66, state 1), and scales of the head undifferentiated (character 67, state 1).

The node 11, formed by *Liotyphlops* + *Helminthophis* have as diagnostic characters the synapomorphies frontal-parietal contact (dorsal aspect) anteriorly concave, i.e. frontals extending posteriorly into broad median embayment in parietals (character 17, state 1), subolfactory (lateral descending) processes of contralateral frontals not contacting one another ventromedially (character 18, state), and rostral scale wide (character 65, state 1).

Inside the above clade, *Helminthophis* was recoved as monophyletic, supported by the following synapomorphies: (1) frontals fused (character 16, state 1); (2) exoccipital overlaps and extends in front of the occipital condyle (character 48, state 0);

and (3) rostral and frontal scales not in contact (character 64, state 1). On the other hand, the species of *Liotyphlops* were recovered completely unresolved in a polytomy with *Helminthophis*. Based on this result, *Liotyphlops* can not be recognized as monophyletic and its sister-group relationship with *Helminthophis* is not demonstrated unambiguously at this time. Additional data, especially of molecular nature, will be necessary to test the monophyly and resolve the intra-relationships of *Liotyphlops*, and infer its relationships with *Helminthophis*.

Appendix I shows the list of synapomorphies for each node according to the numbering of nodes displayed in the strict consensus tree recovered by the parsimony search.

## Discussion

**Phylogenetic relationship of the Anomalepididae within of the Scolecophidia**. Scolecophidia was recovered as monophyletic with strong support (Bremer support = 7), and corroborated by the following exclusive synapomorphies: ascending process of premaxilla with lateral flange forming dorsal margin of external naris (character 1, state 1), multiple premaxillary palatal foramina (character 2, state 2), main body of premaxilla on ventral surface of snout (character 3, state 1), supratemporal vestigial or absent (character 24, state 1), cephalic condyle of quadrate situated ventrally, well below level of dorsal margin of prootic (character 27, state 1), fenestra for duct of Jacobson's organ posteroventrally (character 32, state 1), and pterygoid teeth absent (character 59, state 1). Scolecophidia as a monophyletic taxon coincides with the results of Lee & Scanlon (2002), among other authors, who recovered Scolecophidia as monophyletic based on morphological data (Tchernov et al. 2000, Lee et al. 2007). Lee et al. (2007) recovered Scolecophidia as monophyletic combining morphological and molecular data. However, the present hypothesis for the phylogenetic relationship of Anomalepididae within Scolecophidia does not corroborates recent works of snake phylogeny based on molecular data (Pyron et al. 2013, Figueroa et al. 2016, Zheng & Wiens 2016), where the phylogenetic relationship of Scolecophidia remains unresolved. However, a note regarding sampling of taxa of Anomalepididae in the construction of molecular datasets analyzed by different authors, must be made, because in these molecular dataset only two species of Anomalepididae were included: *Liotyphlops* *albirostris* (Peters, 1857) and *Typhlophis squamosus* (Schlegel, 1839), while our morphological dataset was constructed from 16 out of the 19 valid species.

**Phylogenetic relationship within of Anomalepididae**. In this study we recovered the four know genera of Anomalepididae (*Anomalepis*, *Helminthophis*, *Liotyphlops*, and *Typhlophis*). Except for *Liotyphlops*, they are well delimited by morphological characters (see Appendix I). However, despite the characters obtained from skull osteology are useful on delimiting the genera, in the case of the species, we found little variation in bone characters examined. Some bony structures were important in delimitation of species, especially the presence of a supraoccipital (character 42) in *Liotyphlops* species with geographical distribution by Colombia (*L. albirostris, L. anops,* and *L. argaleus*). The supraoccipital is also present in *Anomalepis* species, and in *Helmintophis frontalis* and *H. praeocularis*, none of these with distribution in Brazil, so that none of the species examined of Anomalepididae with distribution in Brazil has supraoccipital. The ectopterygoid (character 37) is present in all the Anomalepididae examined as well as the supratemporal (character 24), except in *Anomalepis* and in the two paratypes of *Liotyphlops beui* (MCZ R-16702 and MCZ R-17842).

Interesting to note the absence of the splenial (character 51) in Anomalepididae, which is sometimes confused with the angular. In Scolecophidia, it is present in Leptotyphlopidae and Typhlopidae. It is possible that the invariant condition of some characters have influenced in the polytomy with *Liotyphlops* observed in the strict consensus tree (Fig. 82). However, despite the polytomy, and the low values of support, the species have morphological characters diagnosable within each genus, and Anomalepididae is a monophyletic clade. There is need to add new characters, especially DNA sequences, for the effort to solve the polytomy in *Liotyphlops* and *Helminthophis*.

**Acknowledgements**

We are grateful to all curators, collection managers, and their respective institutions for the loan of specimens, and for permission to examining specimens in their care: Adriana Dias, Paulo Roberto Manzani and Karina Rebelo (Museu de Zoologia da UNICAMP, Campinas); Alan Resetar (Field Museum of Natural History, Chicago); Carol L. Spencer and Jimmy A. McGuire (Museum of Vertebrate Zoology, Berkeley); David Kizirian (American Museum of Natural History, New York); Fernanda P. Werneck and Ariane Silva (Instituto Nacional de Pesquisas da Amazônia, Manaus); Fernando Rojas-Runjaic (Museo de Historia Natural La Salle, Caracas); Glaucia Maria Funk Pontes (Museu de Ciências e Tecnologia da Pontificia Universidade Católica do Rio Grande do Sul, Porto Alegre); Hélder Lúcio Rodrigues Silva and Bruno Barros Bittar (Centro de Estudos e Pesquisas Biológicas da Pontifícia Universidade Católica de Goiás, Goiânia); Hussam Zaher and Alberto Carvalho (Museu de Zoologia da Universidade de São Paulo, São Paulo); José Padial (Carnegie Museum of Natural History, Pittsburgh); José Rosado (Museum of Comparative Zoology, Cambridge); Márcio Borges Martins, Diego Janisch Alvares and Valentina Zaffaroni Caorsi (Universidade Federal do Rio Grande do Sul, Porto Alegre); Patrick Campbell (Natural History Museum, London); Paulo Gustavo Homem Passos (Museu Nacional da Universidade Federal do Rio de Janeiro, Rio de Janeiro); Sonia Zanini Cechin and Luiza Loebens (Coleção de Répteis da Universidade Federal de Santa Maria, Santa Maria). We thank the Dr. Christopher J Bell, Dr. Jessica Anderson Maisano and Patrick Stafford of The University of Texas at Austin for the support in the acquisition of specimens and CT scanning. We thank Adolpho Herbert Augustin of the Pontifícia Universidade Católica do Rio Grande do Sul for CT scanning specimens. To Programa de Pós-Graduação em Zoologia da PUCRS (PPG Zoo-PUCRS), and Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) for the fellowship during his graduate studies.

**Literature Cited.**

Amaral, A. do (1924) *Helminthophis*. Proceedings of the New England Zoological Club 9: 25-30.

Amaral, A. do (1929) Contribuição ao conhecimento dos ophidios do Brasil IV-Lista remissiva dos ophidios do Brasil. Memorias do Instituto Butantan (4): 3-57.

Amaral, A. do (1954) Contribuição ao conhecimento dos ofídios do Brasil: Observações a propósito de "cobas-cegas" (fam. Typhlopidae e fam. Leptotyphlopidae). Memorias do Instituto Butantan (26): 197-202.

Boulenger, G.A. (1896) Catalogue of the snakes in the British Museum (Natural History). Volume III, containing the Colubridae (Opisthoglyphae and Proteroglyphae), Amblycephalidae, and Viperidae. British Museum (Natural History), London: 727 p.

Bremer, K. (1994) Branch support and tree stability. Cladistics 10: 295-304.

Centeno, F.C., Sawaya, R.J., Germano, V.J. (2010) A New Species of *Liotyphlops* (Serpentes: Anomalepididae) from the Atlantic Coastal Forest in Southeastern Brazil. Herpetologica 66 (1): 86-91.

Conrad, J. L. (2008) Phylogeny and systematics of Squamata (Reptilia) based on morphology. New York, Bulletin of the American Museum of Natural History. 182 p.

Cope, E. D. (1864) On the Characters of the higher groups of Reptilia Squamata, and especially of the Diploglossa. Proceedings of the Academy of Natural Sciences of Philadelphia 16: 224-231.

Cope, E. D. (1899) Contributions to the Herpetology of New Granada and Argentina-with descriptions of new forms. The Philadelphia Museums Scientific Bulletin No. 1: 3-26.

Costa, H. C., Santos, F. J. M., Loebmann, D. (2015) New records of *Liotyphlops beui* (Amaral, 1924) (Serpentes: Anomalepididae) and an updated distribution map. Boletim do Museu de Biologia Mello Leitão 37(3): 241-253.

CTVox: Volume Rendering (2016). In: Bruker microCT. Available online at: http://bruker-microct.com/products/downloads.htm [Accessed: 09/05/2016].

Dixon, J.R., Kofron, C.P. (1984) The Central and South American anomalepid snakes of the genus *Liotyphlops*. Amphibia-Reptilia 4: 241-264.

Figueroa A., McKelvy, A. D., Grismer, L. L., Bell, C. D., Lailvaux, S. P. (2016) A Species-Level Phylogeny of Extant Snakes with Description of a New Colubrid Subfamily and Genus. PLoS ONE 11(9): 1-31.

Fitzinger, L. (1843) Systema Reptilium, fasciculus primus, Amblyglossae. Braumüller et Seidel, Wien: 1-106.

Freire, E. M. X., Caramaschi, U., Argôlo, A. J. S. (2007) A new species of *Liotyphlops* (Serpentes: Anomalepididae) from the Atlantic Rain Forest of Northeastern Brazil. Zootaxa 1393: 19-26.

Garman, S. (1883) North American Reptiles. Memoires of the Museum of Comparative Zoology at Harvard College VIII (3): 2-4.

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. Bulletin of the Peabody Museum of Natural History 53 (1): 3-308.

Goloboff, P. (1999) NONA ver. 2. Published by the author, Tucuman, Argentina.

Goloboff, P., Catalano, S. (2016) TNT ver. 1.5, with a full implementation of phylogenetic morphometrics. Cladistics DOI 10.1111/cla.12160.

Haad, J. J. S., Franco, F. L., Maldonado, J. (2008) Una nueva especie de *Liotyphlops* Peters, 1881 (Serpentes, Scolecophidia, Anomalepidae) del sur de la Amazonia Colombiana. Biota Colombiana 9 (2): 295-300.

Haas, G. (1968) Anatomical Observations on the Head of *Anomalepis aspinosus* (Typhlopidae. Ophidia). Acta Zoologica Bd XLIX 63-139.

Hahn, D. E. (1980) Liste der rezenten Amphibien und Reptilien Anomalepididae, Leptotyphlopidae, Typhlopidae. Das Tierreich 101: 1-93 [1-5].

Hammer, O., Harper, D. A. T., Ryan. P. D. 2001. PAST: Paleontological Statistics software package for education and data analysis. Palaeontologia Electronica, 4: 1-9.

Hornstedt, C. F. (1787) Beschryving van een nieuwe slang van Java. Kungliga Svenska vetenskapsakademiens handlingar 4: 307 p.

Hsiang, A. Y., Field, D. J., Webster, T. H., Behlke, A. D. B., Davis, M. B., Racicot, R. A., Gauthier, J. A. (2015) The origin of snakes: revealing the ecology, behavior, and evolutionary history of early snakes using genomics, phenomics, and the fossil record. BMC Evolutionary Biology 15 (87): 1-22.

Jan, G. (1860) Iconographie générale des ophidiens. Première livraison.

Kofron, C. P. (1988) The central and south american blindsnakes of the genus *Anomalepis*. Amphibia-Reptilia 9: 7-14.

Leach, W. E. (1819) Reptilia. Mission from Cape Coast Castle to Ashantee: 493-494.

Lee, M. S. Y., Scanlon J. D. (2002) Snake phylogeny based on osteology, soft anatomy and ecology. Biological Reviews 77 (3): 333-401.

Lee, M. S.Y., Hugall, A. F., Lawson, R., Scanlon, J. D. (2007) Phylogeny of snakes (Serpentes): combining morphological and molecular data in likelihood, Bayesian and parsimony analyses. Systematics and Biodiversity 5 (4): 371-389.

Linnaeus, C. (1758) Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Tomus I. Editio decima, reformata. Laurentii Salvii, Holmiæ. 10th Edition: 824 p.

Maddison, W. P., Maddison, D. R. 2015. Mesquite: a modular system for evolutionary analysis. Version 3.04. Available online at: http://mesquiteproject.org.

Marx, H. (1953) A new worm snake from Colombia, genus *Anomalepis*. Fieldiana: Zoology 34 (17): 197-198.

Mcdiarmid, R. W., Foster, M. S., Guyer, C., Gibbons, J. W., Chernoff, N. (2012) Reptile Biodiversity Standard Methods for Inventory and Monitoring. California, University of California Press. XII + 412 p.

McDiarmid, R.W., Campbell, J.A., Touré, T. (1999) Snake species of the world. A taxonomic and geographic reference. Washington, D.C., The Herpetologist's League. XI + 511 p.

Merrem, B. (1820) Versuch eines Systems der Amphibien I Tentamen Systematis Amphibiorum. J. C. Krieger, Marburg. XV + 191 p.

Nixon, K. C. (1999-2002) WinClada ver. 1.00.08. Published by the author, Ithaca, New York, USA.

Nopcsa, F. B. (1923) Die Familien der Reptilien. Berlin, Fortschritte der Geologie und Paläontologie 2: 210 p.

Oppel, M. (1811) Die ordnung, familien und gattungen der reptilien als prodrom einer naturgeschichte derselben. Lindauer, München. XII + 87 p.

Peters, J. A. (1957) Taxonomic Notes on Ecuadorian Snakes in the American Museum of Natural History. American Museum Novitates (1851): 1-13.

Peters, J. A., Donoso-Barros, R., Orejas-Miranda, B. (1986) Catalogue of the Neotropical Squamata-revised edition. Part I. Snakes. Washington, D.C., Smithsonian Institution Press. VIII + 293 p.

Peters, W. (1860) Drei neue Schlangen des k. zoologischen Museums aus America und Bemerkungen über die generelle Unterscheidung von anderen bereits bekannten Arten. Monatsberichte der Königlichen Preussischen Akademie der Wissenschaften zu Berlin: 517-521.

Peters, W. C. H. (1881) Einige herpetologische Mittheilungen, 1. Uebersicht der zu den Familien der Typhlopes und Stenostomi gehorigen Gattungen oder Untergattungen. Sitzungsberichte der Gesellschaft Naturforschender Freunde zu Berlin. (4): 69-71.

Peters, W. C. H. 1854. Diagnosen neuer Batrachier, welche zusammen mit der früher (24. Juli und 17. August) gegebenen Übersicht der Schlangen und Eidechsen mitgetheilt werden. Bericht über die zur Bekanntmachung geeigneten Verhandlungen der Königlich preussischen Akademie der Wissenschaften zu Berlin: 614-628.

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 (93): 1-53.

Queiroz, K. (2007) Species Concepts and Species Delimitation. Systematic Biology 56 (6): 879-86.

Reeder, T. W., Townsend, T. M., Mulcahy, D. G., Noonan, B. P., Wood, P. L., Sites Jr, J. W., Wiens, J. J. (2015) Integrated Analyses Resolve Conflicts over Squamate Reptile Phylogeny and Reveal Unexpected Placements for Fossil Taxa. PLoS ONE 10 (3): 1-22.

Reis, R. E. (2017) Unexpectedly high diversity in a small basin: A taxonomic revision of *Eurycheilichthys* (Siluriformes: Loricariidae), with descriptions of seven new species. Neotropical Ichthyology 15 (1): e160068 [1-28].

Reis, R. E., Fontoura, N. F. (1991). DATAX - Biometric Data Management System - version 4.1.

Rieppel, O., Kley, N. J., Maisano, J. A. (2009) Morphology of the Skull of the White-Nosed Blindsnake, *Liotyphlops albirostris* (Scolecophidia: Anomalepididae). Journal of Morphology 270 (5): 536-557.

Robb, J., Smith, H., M. (1966) The Systematic Position of the Group of Snakes Genera Allied to *Anomalepis*. Natural History Miscellanea, The Chicago Academy of Sciences 184: 1-8.

Schlegel, H. (1839) Abbildungen neuer oder unvollständig bekannter Amphibien, nach der Natur oder dem Leben entworfen und mit einem erläuternden Texte begleitet. Düsseldorf, Arne and Co.: 141 p.

Steindachner, F. (1878) Über zwei Eidechsen-Arten aus Süd-Amerika und Borneo. Denkschriften der Kaiserlichen Akademie der Wissenschaften 38: 93-96.

Stejneger, L. H. (1892) [dated 1891] Notes on some North American snakes. Proceedings of the United States National Museum 14: 501-505.

Taylor, E. H (1939) Two new species of the genus *Anomalepis* Jan, with a proposal of a new family of snakes. Proceedings of the New England Zoölogical Club 17: 87-96.

Tchernov, E., Rieppel, O., Zaher, H., Polcyn, M. J., Jacobs, L. L. (2000) A Fossil Snake with Limbs. Science 287: 2010-2012.

Townsend, T. M., Larson, A., Louis, E., Macey, J. R. (2004) Molecular Phylogenetics of Squamata: The Position of Snakes, Amphisbaenians, and Dibamids, and the Root of the Squamate Tree. Systematic Biology 53 (5):735-757.

Uetz, P., Freed, P., Hošek, J. (eds.) (2017) The Reptile Database. Available online at: http://www.reptile-database.org [Accessed: 28/01/2017].

Vidal, N., Hedges, S. B. (2002) Higher-level relationships of snakes inferred from four nuclear and mitochondrial genes. C. R. Biologies 325: 977-985.

Vidal, N., Marin, J., Morini M., Donnellan, S., Branch, W. R., Thomas, R., Vences, M., Wynn, A., Cruaud, C., Hedges, S. B. (2010) Blindsnake evolutionary tree reveals long history on Gondwana. Biology Letters 6: 558-561.

Vitt, L. J., Caldwell, J. P. (2014) Herpetology: An Introductory Biology of Amphibians and Reptiles. San Diego, Elsevier, 4th edition. XIV + 757 p.

Wallach, V.; Williams, K.L. & Boundy, J. (2014) Snakes of the World: A Catalogue of Living and Extinct Species. New York, CRC Press Taylor and Francis Group, XXVII + 1209 p.

Wiens, J. J., Hutter, Carl R., Mulcahy, D. G., Noonan, B. P., Townsend, T. M., Sites Jr, J. W., Reeder, T. W. (2012) Resolving the phylogeny of lizards and snakes (Squamata) with extensive sampling of genes and species. Biology Letters 8: 1043-1046.

Wiens, J. J., Kuczynski, C. A., Townsend, T., Reeder, T. W., Mulcahy, D. G., Sites Jr, J. W. (2010) Combining Phylogenomics and Fossils in Higher-Level Squamate Reptile Phylogeny: Molecular Data Change the Placement of Fossil Taxa. Systematic Biology 59 (6):674-688.

Zheng, Y., Wiens, J. J. (2016) Combining phylogenomic and supermatrix approaches, and a time-calibrated phylogeny for squamate reptiles (lizards and snakes) based on 52 genes and 4162 species. Molecular Phylogenetics and Evolution 94: 537-547.

**Table 1**. Taxon and character matrix used in analysis of Anomalepididae phylogeny. Symbols: - = inapplicable. ? = unknown. Polymorphism is shown as A = 0 and 1.

| **Outgroup** | 1 2 3 4 5 6 7 8 9 10 | 20 | 30 | 40 | 50 | 60 | 68 |
|---|---|---|---|---|---|---|---|
| *Lanthanotus borneensis* | 0 0 0 0 0 0 ? 0 0 0 | 0 0 0 0 0 ? 0 0 ? 0 | - ? 0 0 0 0 0 0 0 0 | 2 0 0 0 0 ? 0 0 1 0 | 0 0 0 0 0 - 0 ? 0 0 | 0 0 1 1 0 1 0 0 0 0 | ? 0 0 ? ? ? ? ? |
| *Anilius scytale* | 0 0 0 1 0 0 ? 1 1 0 | 1 2 1 2 2 ? 1 1 ? 1 | 1 ? 0 0 1 1 0 2 0 0 | 2 0 0 1 0 ? 0 1 A 1 | 0 0 0 0 0 0 3 ? 1 1 | 1 - 0 1 0 1 0 1 0 2 | 1 1 1 1 0 0 0 0 |
| *Acrochordus* | 0 0 0 1 1 0 ? 1 2 - | 1 0 0 2 2 ? 0 1 ? 1 | 0 1 0 0 2 1 0 3 1 0 | 2 0 2 1 0 ? 0 2 A 1 | A 0 0 0 1 1 2 ? 2 0 | 0 - 2 1 1 1 0 1 0 1 | 0 0 0 ? ? ? ? ? |
| *Epictia munoai* | 1 2 1 1 0 0 0 1 1 0 | 0 2 1 2 1 0 0 1 0 0 | 2 1 1 1 - 0 1 1 0 1 | 2 1 0 2 0 0 1 2 1 0 | 0 0 1 0 0 0 1 0 0 1 | 0 0 1 1 1 0 0 0 1 2 | 0 1 1 0 0 0 0 0 |
| *Trilepida fuliginosa* | 1 2 1 1 0 0 0 1 1 0 | 0 2 1 2 1 0 0 1 0 0 | 2 1 1 1 - 0 1 1 0 1 | 2 1 0 1 0 0 1 2 1 0 | 0 0 0 0 0 0 1 1 0 1 | 0 0 1 1 1 0 0 0 1 2 | 0 1 1 0 0 0 0 0 |
| *Trilepida koppesi* | 1 2 1 1 0 0 0 1 1 0 | 0 2 1 2 1 0 0 1 0 0 | 2 1 1 1 - 0 1 1 0 1 | 2 1 0 1 0 0 1 2 1 0 | 0 0 0 0 0 0 1 1 0 1 | 0 0 1 1 1 0 0 0 1 2 | 0 1 1 0 0 0 0 0 |
| *Amerotyphlops brongersmianus* | 1 2 1 2 0 1 0 0 1 2 | 0 2 0 2 3 0 0 1 0 0 | 2 1 0 1 - 0 1 1 0 1 | 0 1 2 1 1 1 1 1 1 0 | 0 0 1 0 0 0 1 1 0 1 | 0 0 0 0 1 1 1 0 1 2 | 0 1 0 0 0 0 0 0 |
| *Amerotyphlops reticulatus* | 1 2 1 2 0 1 0 0 1 2 | 0 2 0 2 3 0 0 1 0 0 | 2 1 0 1 - 0 1 1 0 1 | 0 1 2 1 1 1 1 1 1 0 | 0 0 1 0 0 0 1 1 0 1 | 0 0 0 0 1 1 1 0 1 2 | 0 1 0 0 0 0 0 0 |
| **Ingroup** | | | | | | | |
| *Anomalepis aspinosus* | 1 2 1 2 1 1 1 1 2 1 | 1 0 0 2 0 0 0 1 0 0 | 2 1 0 1 - 0 1 1 0 1 | 2 1 2 2 1 1 0 1 1 0 | 0 0 0 0 0 0 1 1 0 1 | 1 0 0 0 1 1 0 0 1 3 | 0 0 0 1 0 0 0 1 |
| *Anomalepis colombia* | 1 2 1 2 1 1 1 1 2 2 | 1 0 0 2 0 0 0 ? ? 0 | 2 1 1 1 - 0 1 1 0 1 | ? 1 2 2 1 1 0 1 1 0 | ? 0 1 0 0 0 ? 1 0 1 | 1 0 1 0 1 1 0 0 1 3 | 0 0 0 1 0 0 0 1 |
| *Anomalepis flavapices* | 1 2 1 2 1 1 1 1 2 2 | 1 0 0 2 0 0 0 1 0 0 | 2 1 0 1 - 0 1 1 0 1 | 2 1 2 2 1 1 0 1 1 1 | 0 0 0 0 0 0 1 1 0 1 | 1 0 1 0 1 1 0 0 1 3 | 0 0 0 1 0 0 0 1 |
| *Anomalepis mexicanus* | 1 2 1 2 1 1 1 1 2 1 | 1 0 0 2 0 0 0 1 0 0 | 2 1 1 1 - 0 1 1 0 1 | 2 1 2 2 1 1 0 1 1 0 | 0 0 0 0 0 0 1 1 0 1 | 1 0 0 0 1 1 0 0 1 3 | 0 0 0 1 0 0 0 1 |

Continues.

| **Ingroup** | 1 2 3 4 5 6 7 8 9 10 | 20 | 30 | 40 | 50 | 60 | 68 |
|---|---|---|---|---|---|---|---|
| *Helminthophis flavoterminatus* | 1 2 1 2 1 1 1 2 2 1 | 1 0 0 2 0 1 1 1 0 0 | 2 0 - 0 - 0 1 1 0 1 | 2 1 2 2 1 1 0 1 1 0 | 0 1 - 2 - - 3 0 0 1 | 1 0 0 0 1 1 0 0 1 3 | 0 0 0 1 1 0 0 0 |
| *Helminthophis frontalis* | 1 2 1 2 1 1 1 2 2 2 | 1 0 0 2 0 1 1 A 0 0 | 2 0 0 0 1 0 1 1 0 1 | 2 1 2 2 1 1 0 1 1 0 | 0 0 0 1 0 0 1 0 0 1 | 1 0 - 0 1 1 0 0 1 3 | 0 0 0 1 1 0 0 0 |
| *Helminthophis praeocularis* | 1 2 1 2 1 1 1 2 2 1 | 1 0 0 2 0 1 1 0 0 0 | 2 0 0 0 1 0 1 1 0 1 | 2 1 2 2 1 1 0 1 1 0 | 0 0 0 1 0 0 1 0 0 1 | 1 0 0 0 1 1 0 0 1 3 | 0 0 0 1 1 0 0 0 |
| *Liotyphlops albirostris* | 1 2 1 2 1 1 1 2 2 1 | 1 0 0 2 0 0 1 0 0 0 | 2 0 0 0 1 0 1 1 0 1 | 2 1 2 2 1 1 0 1 1 0 | 0 0 0 1 0 0 1 1 0 1 | 1 0 0 0 1 1 0 0 1 3 | 0 0 0 0 1 0 0 0 |
| *Liotyphlops anops* | 1 2 1 2 1 1 1 2 2 2 | 1 0 0 2 0 0 1 0 0 0 | 2 0 0 0 1 0 1 1 0 1 | 2 1 2 2 1 1 0 1 1 0 | 0 0 0 1 0 0 1 1 0 1 | 1 0 0 0 1 1 0 0 1 3 | 0 0 0 0 1 0 0 0 |
| *Liotyphlops argaleus* | 1 0 1 2 1 1 1 2 2 2 | 1 0 0 2 0 0 1 0 0 0 | 2 0 0 0 1 0 1 1 0 1 | 2 1 2 2 1 1 0 1 1 0 | 0 0 0 1 0 0 1 1 0 1 | 1 0 0 0 1 1 0 0 1 3 | 0 0 0 0 1 0 0 0 |
| *Liotyphlops schubarti* | 1 2 1 2 1 1 1 2 2 2 | 1 0 0 2 0 0 A 0 0 0 | 2 0 - 0 - 0 1 1 0 1 | 2 1 2 2 1 1 0 1 1 0 | 0 1 - 2 - - 1 1 0 1 | 1 0 0 0 1 1 0 0 1 3 | 0 0 0 0 1 0 0 0 |
| *Liotyphlops ss* | 1 2 1 2 1 1 1 2 2 2 | 1 0 0 2 0 0 1 0 0 0 | 2 0 - 0 - 0 1 1 0 1 | 2 1 2 2 1 1 0 1 1 0 | 0 1 - 2 - - 1 1 0 1 | 1 0 0 0 1 1 0 0 1 3 | 0 0 0 0 1 0 0 0 |
| *Liotyphlops tt* | 1 2 1 2 1 1 1 2 2 1 | 1 0 0 2 0 0 1 0 0 0 | 2 0 - 0 - 0 1 1 0 1 | 2 1 2 2 1 1 0 1 1 0 | 0 1 - 2 - - 1 1 0 1 | 1 0 0 0 1 1 0 0 1 3 | 0 0 0 0 1 0 0 0 |
| *Liotyphlops ternetzii* | 1 2 1 2 1 1 1 2 2 2 | 1 0 0 2 0 0 1 0 0 0 | 2 0 - 0 - 0 1 1 0 1 | 2 1 2 2 1 1 0 1 1 0 | 0 1 - 2 - - 1 1 0 1 | 1 0 0 0 1 1 0 0 1 3 | 0 0 0 0 1 0 0 0 |
| *Liotyphlops wilderi* | 1 2 1 2 1 1 1 2 2 2 | 1 0 0 2 0 0 A A 0 0 | 2 0 - 0 - 0 1 1 0 1 | 2 1 2 2 1 1 0 1 1 0 | 0 1 - 2 - - 1 1 0 1 | 1 0 0 0 1 1 0 0 1 3 | 0 0 0 0 1 0 0 0 |
| *Typhlophis squamosus* | 0 2 1 2 1 1 1 2 2 2 | 1 0 0 2 0 0 0 1 1 0 | 2 0 - 0 - 0 1 1 0 1 | 2 1 1 2 1 1 0 1 1 0 | 0 1 - 2 - - 1 1 0 0 | 1 1 0 0 1 1 0 0 1 3 | 0 0 0 - 0 1 1 - |

**Appendix I. List of synapomorphies for each node recovered by the parsimony analysis. In bold, exclusive synapomorphies.**

Node 1. Alethinophidia
(*Anilius scytale* + *Acrochordus*)
11 0 > 1
**15 0 > 2**
**20 0 > 1**
**26 0 > 1**
40 0 > 1
**58 0 > 1**

*Anilius scytale*
13 0 > 1
17 0 > 1
51 0 > 1
**61 0 > 1**
63 0 > 1

*Acrochordus*
5 0 > 1
9 1 > 2
**25 1 > 2**
**29 0 > 1**
33 0 > 2
**45 0 > 1**
**46 0 > 1**
**60 2 > 1**

Node 2. Scolecophidia
**1 0 > 1**
**2 0 > 2**
**3 0 > 1**
**24 0 > 1**
**27 0 > 1**
**30 0 > 1**
**32 0 > 1**
**59 0 > 1**

Node 3. Leptotyphlopidae
13 0 > 1
**15 0 > 1**
23 0 > 1
**56 1 > 0**
63 0 > 1

*Epictia munoai*
34 1 > 2
43 0 > 1
48 1 > 0

Node 4. Typhlopidae + Anomalepididae
**4 1 > 2**
**6 0 > 1**
10 0 > 2
33 0 > 2
**35 0 > 1**
**54 1 > 0**

Node 5. Typhlopidae
8 1 > 0
**15 0 > 3**
**31 2 > 0**
43 0 > 1
**57 0 > 1**

Node 6. Anomalepididae
5 0 > 1
**7 0 > 1**
9 1 > 2
11 0 > 1
34 1 > 2
51 0 > 1
**60 2 > 3**

Node 7. *Anomalepis*
64 0 > 1
**68 0 > 1**

Node 8. *Anomalepis aspinosus* + *Anomalepis mexicanus*
10 2 > 1

*Anomalepis mexicanus*
23 0 > 1

Node 9. *Anomalepis colombia* + *Anomalepis flavapices*
53 0 > 1

*Anomalepis colombia*
23 0 > 1
43 0 > 1

*Anomalepis flavapices*
40 0 > 1

Node 10. *Typhlophis* + *Liotyphlops* + *Helminthophis*
**8 1 > 2**
**22 1 > 0**
24 1 > 0
42 0 > 1
44 0 > 2

*Typhlophis squamosus*
1 1 > 0
**19 0 > 1**
**33 2 > 1**
50 1 > 0
**52 0 > 1**
**66 0 > 1**
**67 0 > 1**

Node 11. *Liotyphlops* + *Helminthophis*
17 0 > 1
18 1 > 0
**65 0 > 1**

*Liotyphlops albirostris*
10 2 > 1
42 1 > 0
44 2 > 1

*Liotyphlops anops*
42 1 > 0
44 2 > 1

*Liotyphlops argaleus*
2 2 > 0
42 1 > 0
44 2 > 1

*Liotyphlops tt*
10 2 > 1

Node 12. *Helminthophis*
**16 0 > 1**
48 1 > 0
64 0 > 1

*Helminthophis flavoterminatus*
18 0 > 1
47 1 > 3

**Appendix II. Specimens examined**.

**Ingroup**

***Anomalepis aspinosus***. Peru. Cajamarca, 28 km N of Santa Cruz: CM 90254.

***Anomalepis colombia***. Colombia. Caldas, Pueblo Rico, La Selva: FMNH 54986 holotype.

***Anomalepis flavapices***. Peru. Amazonas, vicinity of Huampami (Aguaruna village) Rio Cenepa: MVZ 163245.

***Anomalepis mexicanus***. Panama. Bocas del Toro, Río Changuinolar nr Quebrada El Guapo: AMNH R 119069. Panama, nr northeast edge La Chorrera: AMNH R 103749. Peru. Cajamarca, 28 km N of Santa Cruz: MZUSP-S 7201.

***Helminthophis flavoterminatus***. Venezuela. Distrito Capital: AMNH R 59407, CM 90255.

***Helminthophis frontalis***. Costa Rica. San José: MCZ R-34879; MCZ R-55117.

***Helminthophis praeocularis***. Colombia. Tolima, Honda: AMNH R 38125, AMNH R 62942.

***Liotyphlops albirostris***. **Colombia**. Bolívar, Arjona: CM 39565. **Panama**. Herrera, Santa Maria: CM 44652. **Venezuela**. Distrito Capital, road below Guaira, km 5, East of Caracas: CM 90256. **Venezuela**. Distrito Capital, Libertador: MHNLS 514. Miranda, Urbanización Altamira: MHNLS 11824. Urbanización Macaracuay: MHNLS 15550.

***Liotyphlops anops***. **Colombia**. Meta, Villavicencio: MCZ R-67936, MCZ R-67937, MZUSP-S-5998.

***Liotyphlops argaleus***. **Colombia**. Meta, La Selva: MCZ R-66383 paratype.

***Liotyphlops beui***. **Brazil**. Goiás, Goiânia: CEPB 1398, CEPB 1422, CEPB 2491, CEPB 3610. Luziânia: CEPB 6601, CEPB 6602, CEPB 6603, CEPB 6604, CEPB 6900, CEPB 6901, CEPB 6902, CEPB 6903, CEPB 6904, CEPB 6905, CEPB

6642, CEPB 6643, CEPB 6646, CEPB 6651, CEPB 6659, CEPB 6672, CEPB 8849. Minaçu: CEPB 8409. São Paulo, Botucatu: MNRJ 23247. Campinas: MNRJ 8143. Carapicuíba: MCP 16361, MNRJ 10578. Itu: MNRJ 8144. Pirapozinho: MNRJ 22022. São Caetano do Sul: MCP 16365. São Paulo: MCP 16366, MCP 16368, MNRJ 10577, ZUFSM 1569. Instituto Butantan, paratypes MCZ R-16702, MCZ R-17842. Paraná, Boa Vista da Aparecida: MCP 10853, MCP 10855, MCP 10854, MCP 10879. Cruzeiro do Iguaçu: MCP 10880. Curitiba: MCP 16362, MCP 16363. Três Barras do Paraná: MCP 10857, MCP 10858, MCP 10859, MCP 10862, MCP 10864. União da Vitótia: MCP 16360. Santa Catarina, Passos Maia: UFRGS 6275. Rio Grande do Sul, Erechim: UFRGS 6494. Frederico Westphalen: MCP 9494. Bom Progresso: MCP 19086.

***Liotyphlops haadi***. **Colombia**. Amazonas Department, middle region of the Caquetá River, La Pedrera district: IAvH 5434 holotype. Leticia, Vereda de los Lagos: IAvH 5435 paratype.

***Liotyphlops schubarti***. **Brazil**. São Paulo, Campinas: ZUEC REP 2278, ZUEC REP 2279, ZUEC REP 2280, ZUEC REP 2281. Sapucaí: MZUSP-S 4099.

***Liotyphlops ss* sp. nov**. **Brazil**. Santa Catarina, Passos Maia, Pequena Central Hidrelétrica Passos Maia: UFRGS 6274 holotype.

***Liotyphlops ternetzii***. **Brazil**. Mato Grosso, Itiquira: UFRGS 6458. Dsitrito Federal, Brasília: MCP 18381. Minas Gerais, Cabeceira Grande: MCP 19228. Indianópolis: MNRJ 8147. João Pinheiro: MNRJ 11329, MNRJ 14957. Patos de Minas: MNRJ 17300. São Paulo, Itu: MCP 10699. São Paulo: MCP 3680, MCP 6986. Taboão da Serra: MCP 7349. Paraná, Boa Vista da Aparecida: MCP 10849, MCP 10869, MCP 10870, MCP 10878, MCP 10850, MCP 10851, MCP 10852. Curitiba: MCP 1943. Cruzeiro do Iguaçu: MCP 10847, MCP 10872, MCP 10873, MCP 10874, 10875, MCP 10876, MCP 10877, MCP 10881, MCP 10882, MCP 10883, MCP 10885, MCP 10886. Diamante D'Oeste: MCP 16364. Pinhão: MCP 7186, MCP 7195, MCP 7196, MCP 7197, MCP 7198, MCP 7199, MCP 7361. Três Barras do Paraná: MCP 10856, MCP 10860, MCP 10861, MCP 10863, MCP 10865, MCP 10866, MCP 10867, MCP 10884. Rio Grande do Sul, Porto Vera Cruz: MCP 11676. Porto Xavier: MCP 11706. Santo Cristo: MCP 11661. **Paraguay**. BMNH 1946.1.11.77 holotype.

***Liotyphlops tt* sp. nov**. **Brazil**. Estação Ecológica Serra das Araras (15°38'31"S, 57°11'23"W), Municipality of Porto Estrela, Mato Grosso state, Brazil: MZUSP-S 14975 holotype.

***Liotyphlops wilderi***. **Brazil**. Bahia, Itapebi: MNRJ 15657. Minas Gerais, Caeté: MNRJ 20633, MZUSP-S 3842.

***Typhlophis squamosus***. **Brazil**. Amazonas, Rio Negro, Tapuracuara: CM 39897. Manaus: INPA-H 32097. Pará, Belém: AMNH R131787. Santarém: INPA-H 10684. Flona do Trairão: INPA-H 26052, INPA-H 27721. **Venezuela**. Bolívar, Serrania de Los Pijiguaos: MHNLS 12865.

**Outgroup**

***Epictia munoai***. Brazil. Rio Grande do Sul, Dom Pedrito: MCP 18596, MCP 18696.

***Trilepida fuliginosa***. Brazil. Goiás, Caldas Novas: MCP 8609, MCP 8610. Mato Grosso do Sul, Campo Grande: MCP 4042

***Trilepida koppesi***. Brazil. Goiás, Cristalina: MCP 19227.

***Typhlops brongersmianus***. Brazil. Rio Grande do Sul, Bom Progresso: MCP 19087, MCP 19088.

***Typhlops reticulatus***. Brazil. Rondônia, Porto Velho: MCP 18939.

***Anilius scytale***. Brazil. Mato Grosso, Vale de São Domingos: MCP 14069, MCP 14070. Pará, Bragança: MCP 19066. Itaituba: MCP 4454.

**Appendix III.** Scanning basic parameters for specimens examined in the ingroup and outgroup. Specimens examined for the synonymy of *Liotyphlops beui* to *Liotyphlops ternetzii* are also listed here.

**Pontifícia Universidade Católica do Rio Grande do Sul**

*Anomalepis aspinosus*
CM 90254
Source Voltage (kV) = 46
Source Current (µA) = 55
Voxels (µm) = 7.16

*Anomalepis mexicanus*
AMNH R103749
Source Voltage (kV) = 46
Source Current (µA) = 55
Voxels (µm) = 7.16

*Anomalepis mexicanus*
AMNH R119069
Source Voltage (kV) = 46
Source Current (µA) = 55
Voxels (µm) = 7.16

*Helminthophis flavoterminatus*
AMNH R59407
Source Voltage (kV) = 46
Source Current (µA) = 55
Voxels (µm) = 7.16

*Helminthophis flavoterminatus*
CM 90255
Source Voltage (kV) = 46
Source Current (µA) = 55
Voxels (µm) = 7.16

*Helminthophis praeocularis*
AMNH R38125
Source Voltage (kV) = 46
Source Current (µA) = 55
Voxels (µm) = 7.16

*Helminthophis praeocularis*
AMNH R62942
Source Voltage (kV) = 46
Source Current (µA) = 55
Voxels (µm) = 7.16

*Liotyphlops albirostris*
CM 39565
Source Voltage (kV) = 46
Source Current (µA) = 55
Voxels (µm) = 7.16

*Liotyphlops albirostris*
CM 90256
Source Voltage (kV) = 46
Source Current (µA) = 55
Voxels (µm) = 7.16

*Liotyphlops anops*
MZUSP-S 5998
Source Voltage (kV) = 46
Source Current (µA) = 55
Voxels (µm) = 7.16

*Liotyphlops beui*
MCP 10853
Source Voltage (kV) = 46
Source Current (µA) = 55
Voxels (µm) = 7.16

*Liotyphlops beui*
MCP 16362
Source Voltage (kV) = 46
Source Current (µA) = 55
Voxels (µm) = 7.16

*Liotyphlops schubarti*
ZUEC REP 2278
Source Voltage (kV) = 46
Source Current (µA) = 55
Voxels (µm) = 7.16

*Liotyphlops schubarti*
ZUEC REP 2280
Source Voltage (kV) = 46
Source Current (µA) = 55
Voxels (µm) = 7.16

*Liotyphlops ss* sp. nov.
UFRGS 6274-Holotype
Source Voltage (kV) = 46
Source Current (µA) = 55
Voxels (µm) = 7.16

*Liotyphlops ternetzii*
MCP 10878
Source Voltage (kV) = 46
Source Current (µA) = 55
Voxels (µm) = 7.16

*Liotyphlops ternetzii*
MCP 10881
Source Voltage (kV) = 46
Source Current (µA) = 55
Voxels (µm) = 7.16

*Liotyphlops ternetzii*
MCP 19228
Source Voltage (kV) = 46
Source Current (µA) = 55
Voxels (µm) = 7.16

*Liotyphlops tt* sp. nov.
MZUSP-S 14975 Holotype
Source Voltage (kV) = 46
Source Current (µA) = 55
Voxels (µm) = 7.16

*Liotyphlops wilderi*
MNRJ 15657
Source Voltage (kV) = 46
Source Current (µA) = 55
Voxels (µm) = 7.16

*Liotyphlops wilderi*
MNRJ 20633
Source Voltage (kV) = 46
Source Current (µA) = 55
Voxels (µm) = 7.16

*Typhlophis squamosus*
AMNH 131787
Source Voltage (kV) = 46
Source Current (µA) = 55
Voxels (µm) = 7.16

*Typhlophis squamosus*
CM 39897
Source Voltage (kV) = 46
Source Current (µA) = 55
Voxels (µm) = 7.16

*Epictia munoai*
MCP 18596
Source Voltage (kV) = 46
Source Current (µA) = 55
Voxels (µm) = 7.16

*Epictia munoai*
MCP 18696
Source Voltage (kV) = 46
Source Current (µA) = 55
Voxels (µm) = 7.16

*Trilepida fuliginosa*
MCP 4042
Source Voltage (kV) = 46
Source Current (µA) = 55
Voxels (µm) = 10.02

*Trilepida fuliginosa*
MCP 8609
Source Voltage (kV) = 46
Source Current (µA) = 55
Voxels (µm) = 7.16

*Trilepida fuliginosa*
MCP 8610
Source Voltage (kV) = 46
Source Current (µA) = 55
Voxels (µm) = 7.16

*Trilepida koppesi*
MCP 19227
Source Voltage (kV) = 46
Source Current (µA) = 55
Voxels (µm) = 7.16

*Typhlops reticulatus*
MCP 18939
Source Voltage (kV) = 46
Source Current (µA) = 55
Voxels (µm) = 7.16

*Typhlops brongersmianus*
MCP 19087
Source Voltage (kV) = 46
Source Current (µA) = 55
Voxels (µm) = 7.16

*Typhlops brongersmianus*
MCP 19088
Source Voltage (kV) = 46
Source Current (µA) = 55
Voxels (µm) = 7.16

**The University of Texas at Austin**

*Anomalepis flavapices*
MVZ 163245
Source Voltage (kV) = 70
Source Current (W) = 10
Voxels (µm) = 4.79

*Anomalepis colombia*
FMNH 54986 Holotype
Source Voltage (kV) = 80
Source Current (W) = 10
Voxels (µm) = 5.08

*Helminthophis frontalis*
MCZ R 34879
Source Voltage (kV) = 80
Source Current (W) = 10
Voxels (µm) = 4.98

*Helminthophis frontalis*
MCZ R 55117
Source Voltage (kV) = 80
Source Current (W) = 10
Voxels (µm) = 3.58

*Liotyphlops argaleus*
MCZ R 66383 Paratype
Source Voltage (kV) = 80
Source Current (W) = 10
Voxels (µm) = 3.32

*Liotyphlops beui*
MCZ R 16702 Paratype
Source Voltage (kV) =80
Source Current (W) = 10
Voxels (µm) = 4.02

*Liotyphlops beui*
MCZ R 17842 Paratype
Source Voltage (kV) = 80
Source Current (W) = 10
Voxels (µm) = 4.02

*Liotyphlops ternetzi*
BMNH 1946.1.11.77 Holotype
Source Voltage (kV) = 80
Source Current (W) = 10
Voxels (µm) = 4.79

**FIGURES**

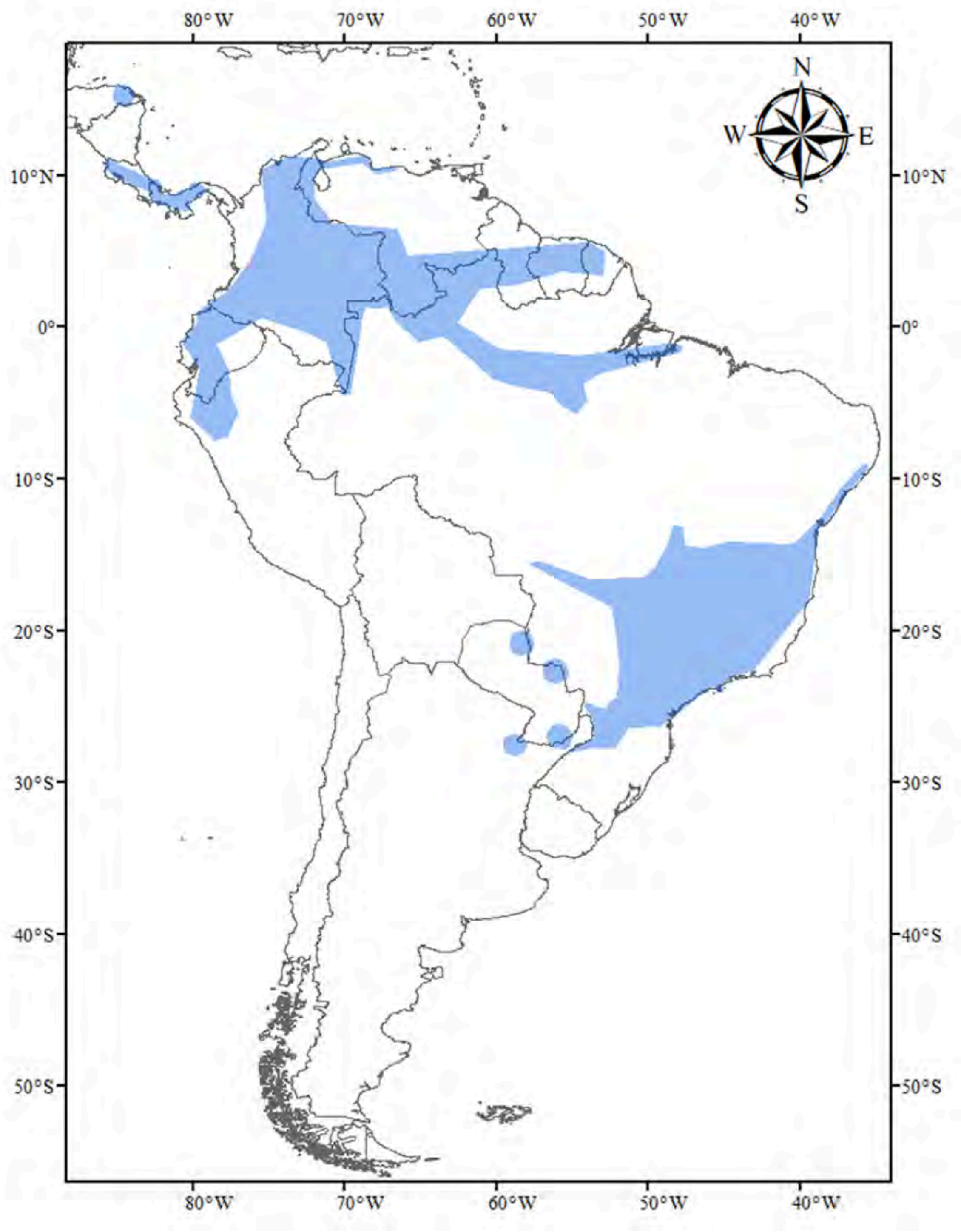


**Figure 1**. Geographic distribution of the extant Anomalepididae.

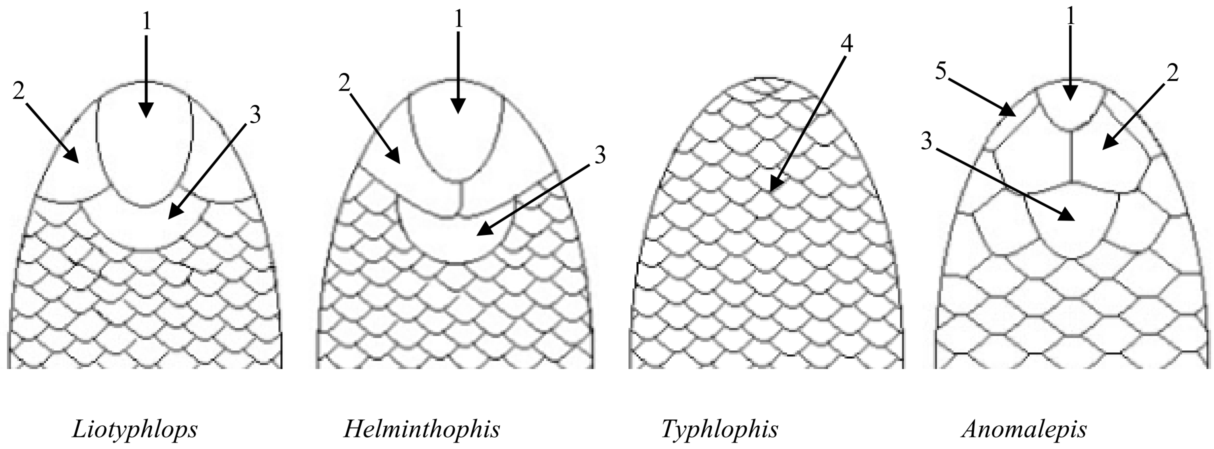


**Figure 2**. Head scales in Anomalepididae snakes; dorsal view. 1 = rostral scale, 2 = prefrontal scale, 3 = frontal scale, 4 = undifferenctiated scales, and 5 = nasal scale.

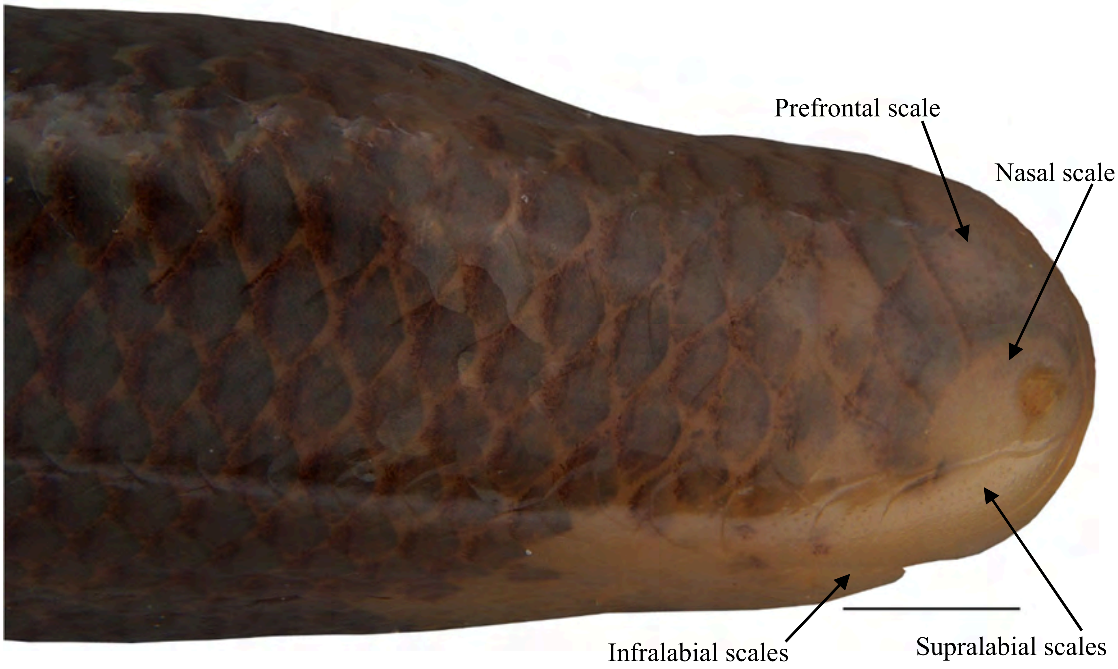


**Figure 3**. Cephalic scales covering "eye spot" making it invisible in *Liotyphlops ternetzii* (MCP 10878). Scale bar = 1 mm.

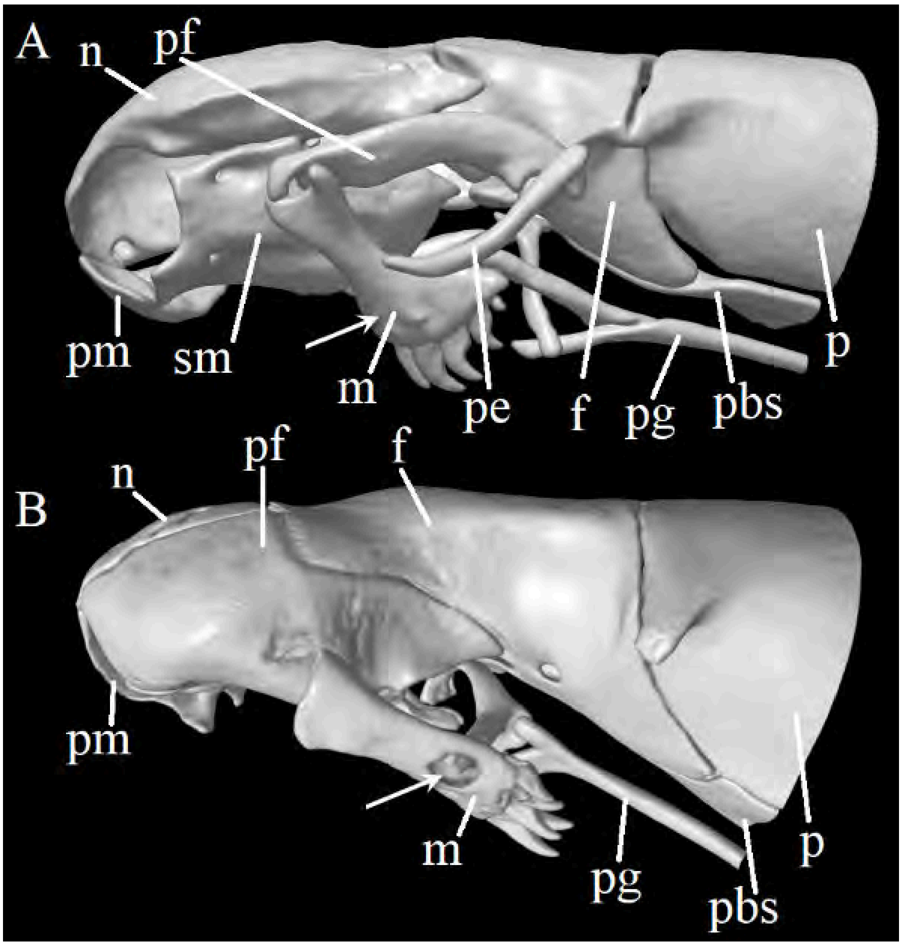


**Figure 4**. Lateral maxillary foramina. A: absent in *Liotyphlops albirostris* (CM 39565, lateral view), and B: present in *Amerotyphlops brongersmianus* (MCP 19088, lateral view). Anatomical abbreviations: f, frontal; m, maxilla; n, nasal; p, parietal; pbs, parabasisphenoid; pe, postorbital element; pf, prefrontal; pg, pterygoid; pm, premaxilla; sm, septomaxilla.

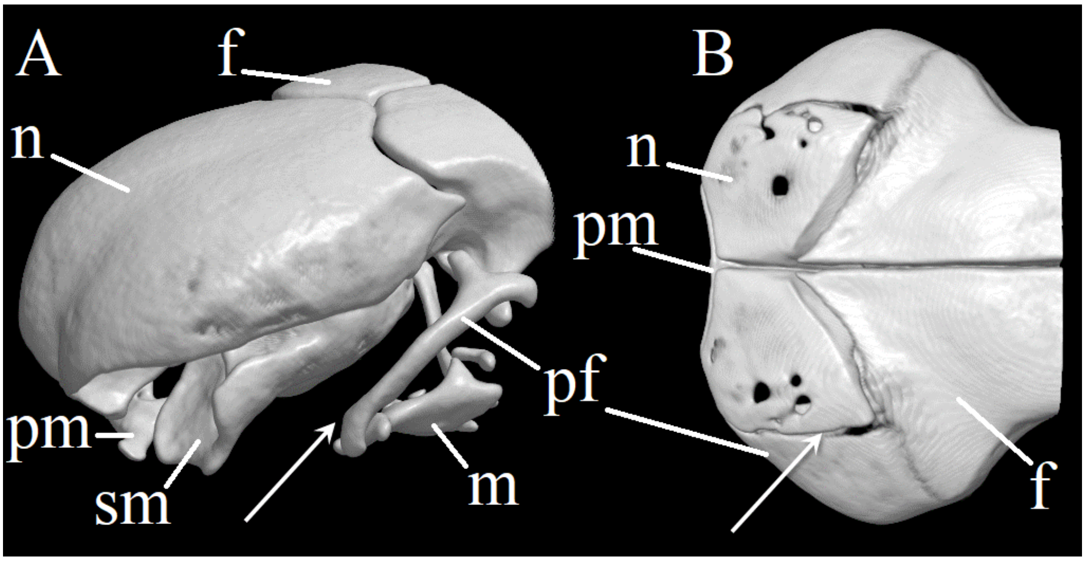


**Figure 5**. Prefrontal-nasal contact. A: prefrontal separated from nasal by ragged fissure that is not part of external naris (*Typhlophis squamosus* AMNH R 131787, dorsolateral view). B: prefrontal contacts nasal (*Amerotyphlops brongersmianus* MCP 19088, dorsal view). Anatomical abbreviations: f, frontal; m, maxilla; n, nasal; p, parietal; pbs, parabasisphenoid; pe, postorbital element; pf, prefrontal; pg, pterygoid; pm, premaxilla; sm, septomaxilla.

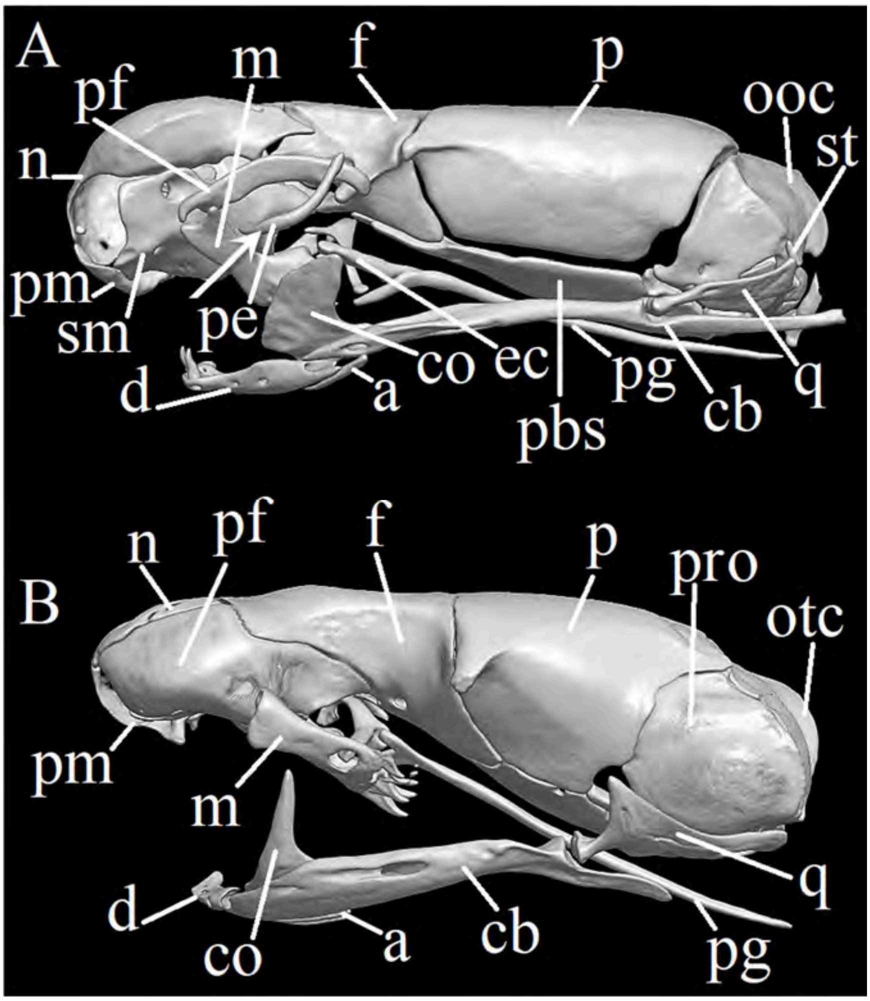


**Figure 6**. Postorbitofrontal ossification(s). A: one discrete ossification, conventionally termed the postorbitofrontal (*Liotyphlops ternetzii* MCP 10881, lateral view). B: no discrete ossifications (*Amerotyphlops brongersmianus* MCP 19088, lateral view). Anatomical abbreviations: a, angular; cb, compound bone; co, coronoid; d, dentary; ec, ectopterygoid; f, frontal; m, maxilla; n, nasal; ooc, otico-occipital (fused prootic + opisthotic + exoccipital); otc, otooccipital (fused exoccipital + opisthotic); p, parietal; pbs, parabasisphenoid; pe, postorbital element; pf, prefrontal; pg, pterygoid; pm, premaxilla; pro, prootic; q, quadrate; sm, septomaxilla; st, supratemporal.

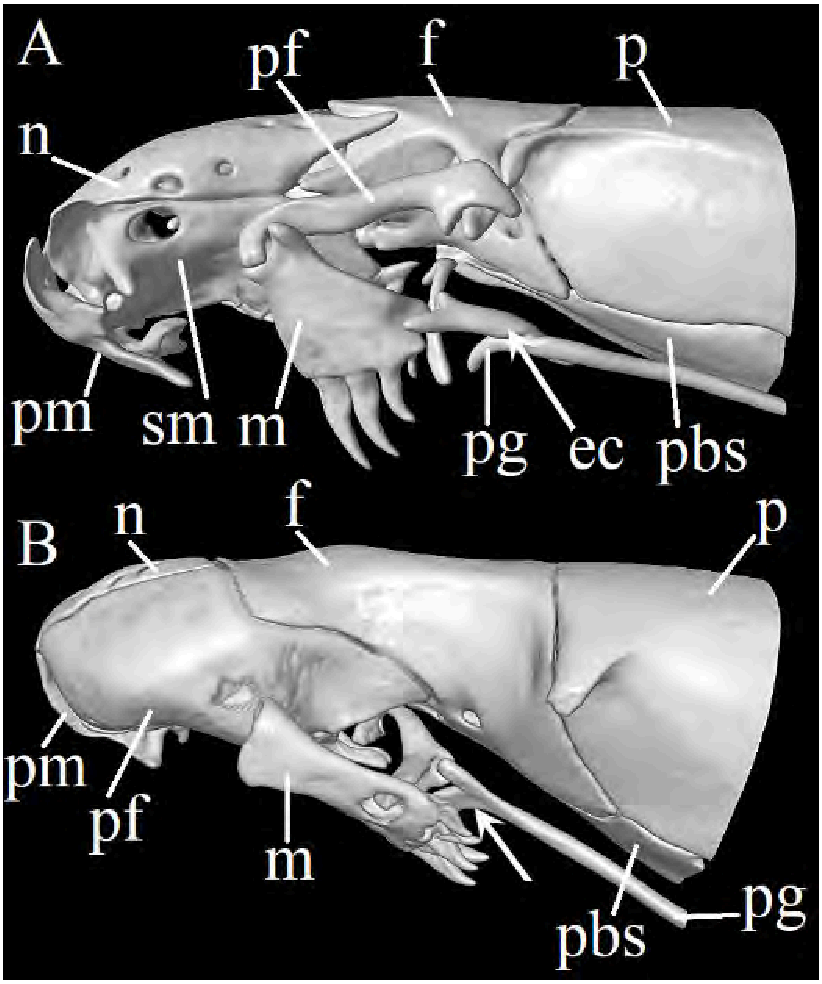


**Figure 7**. Ectopterygoid. A: present (*Anomalepis aspinosus* CM 90254, lateral view). B: absent (*Amerotyphlops brongersmianus* MCP 19088, lateral view). Anatomical abbreviations: ec, ectopterygoid; f, frontal; m, maxilla; n, nasal; p, parietal; pbs, parabasisphenoid; pf, prefrontal; pg, pterygoid; pm, premaxilla; sm, septomaxilla.

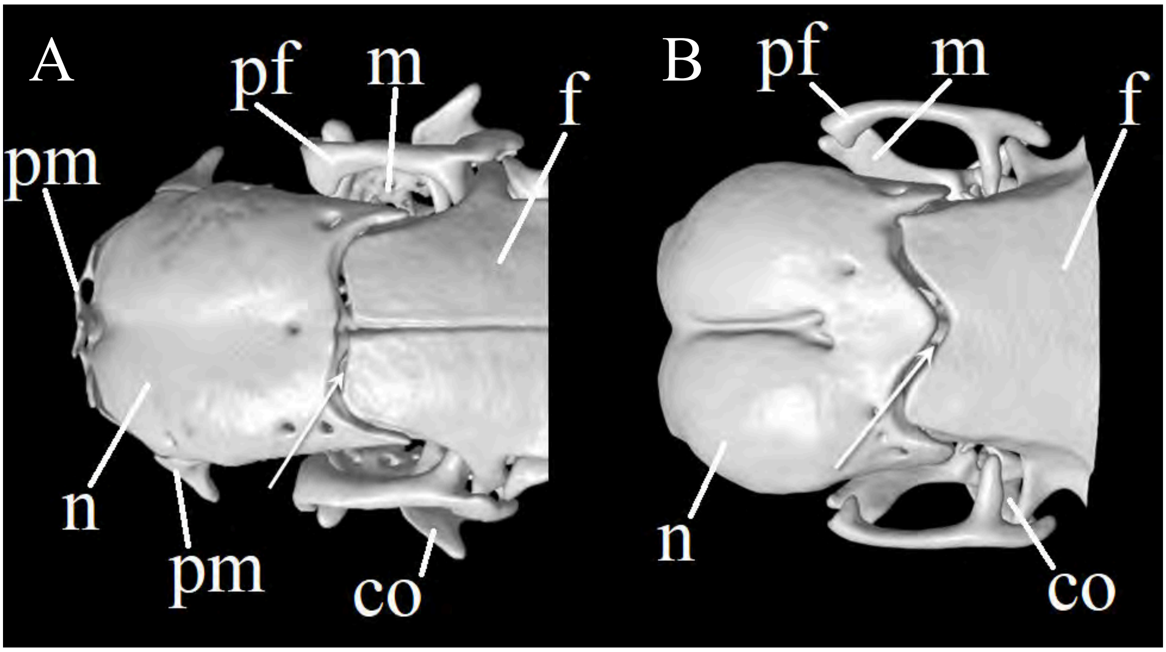


**Figure 12**. Nasal-frontal boundary. A: nasal-frontal boundary approximately straight and transverse (*Anomalepis aspinosus* CM 90254, dorsal view). B: convex posteriorly in a shallow W-shaped suture (*Helminthophis flavoterminatus* AMNH R 59407, dorsal view). Anatomical abbreviations: co, coronoid; f, frontal; m, maxilla; n, nasal; pf, prefrontal; pm, premaxilla.

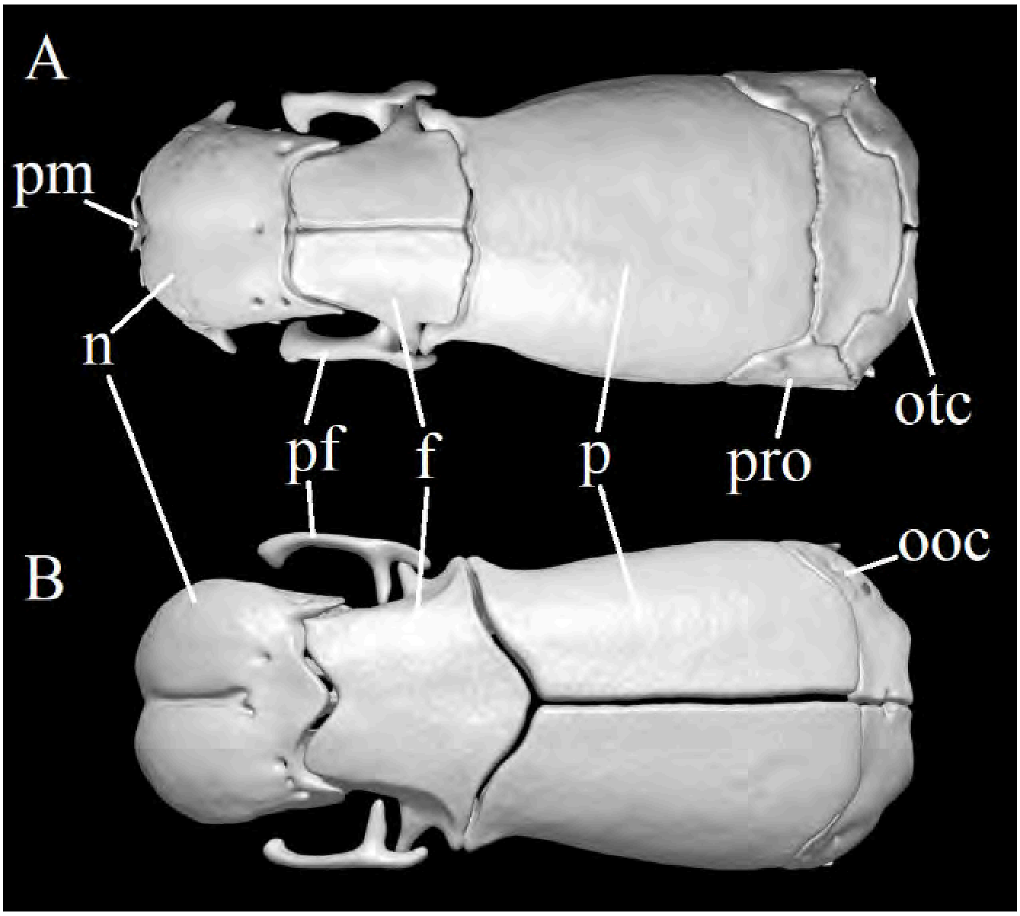


**Figure 13**. Parietal. A: fused, single parietal (*Anomalepis aspinosus* CM 90254, dorsal view). B: paired parietal (*Helminthophis flavoterminatus* AMNH R 59407, dorsal view). Anatomical abbreviations: f, frontal; n, nasal; ooc, otico-occipital (fused prootic + opisthotic + exoccipital); otc, otooccipital (fused exoccipital + opisthotic); p, parietal; pf, prefrontal; pm, premaxilla; pro, prootic.

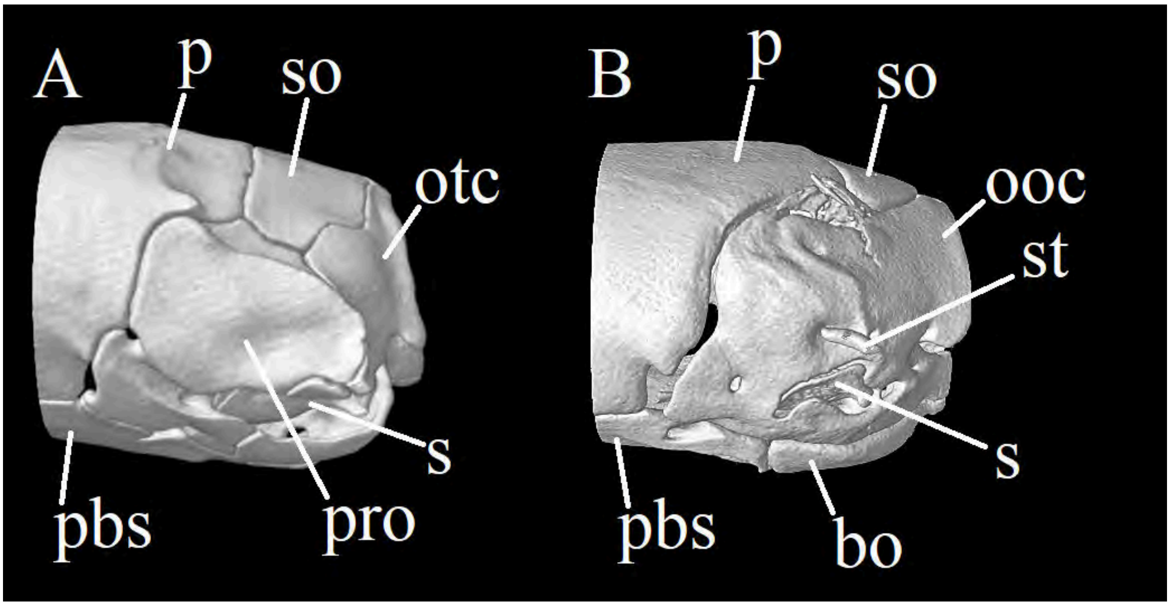


**Figure 14**. Supratemporal. A: lacking supratemporal (*Anomalepis flavapices* MVZ 163245, lateral view). B: supratemporal present (*Liotyphlops argaleus* MCZ R-66383; paratype, lateral view). Anatomical abbreviations: bo, basioccipital; ooc, otico-occipital (fused prootic + opisthotic + exoccipital); otc, otooccipital (fused exoccipital + opisthotic); p, parietal; pbs, parabasisphenoid; pro, prootic; so, supraoccipital; s, stapes; st, supratemporal.

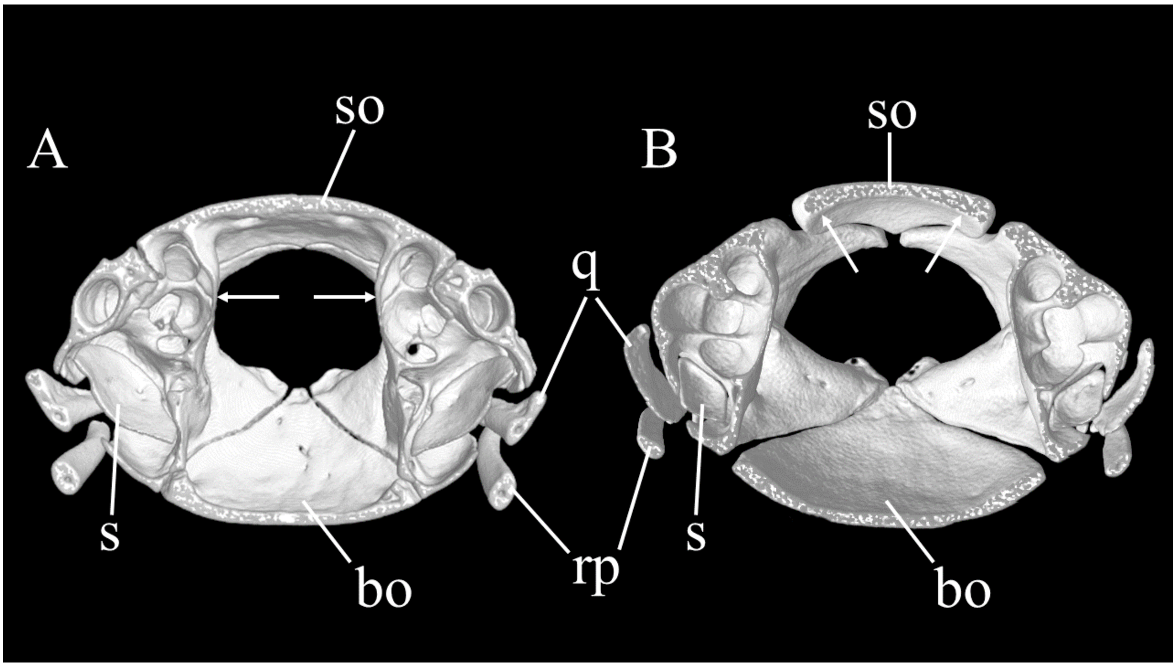


**Figure 15**. Supraoccipital contribution to internal sidewall of neurocranium. A: supraoccipital participating in internal sidewall of neurocranium (*Anomalepis flavapices* MVZ 163245, transverse view). B: absent, only dorsal plate remains and not participating in internal sidewall of neurocranium (*Helminthophis frontalis* MCZ R 55117, transverse view). Anatomical abbreviations: bo, basioccipital; q, quadrate; rp, retroarticular process; s, stapes; so, supraoccipital.

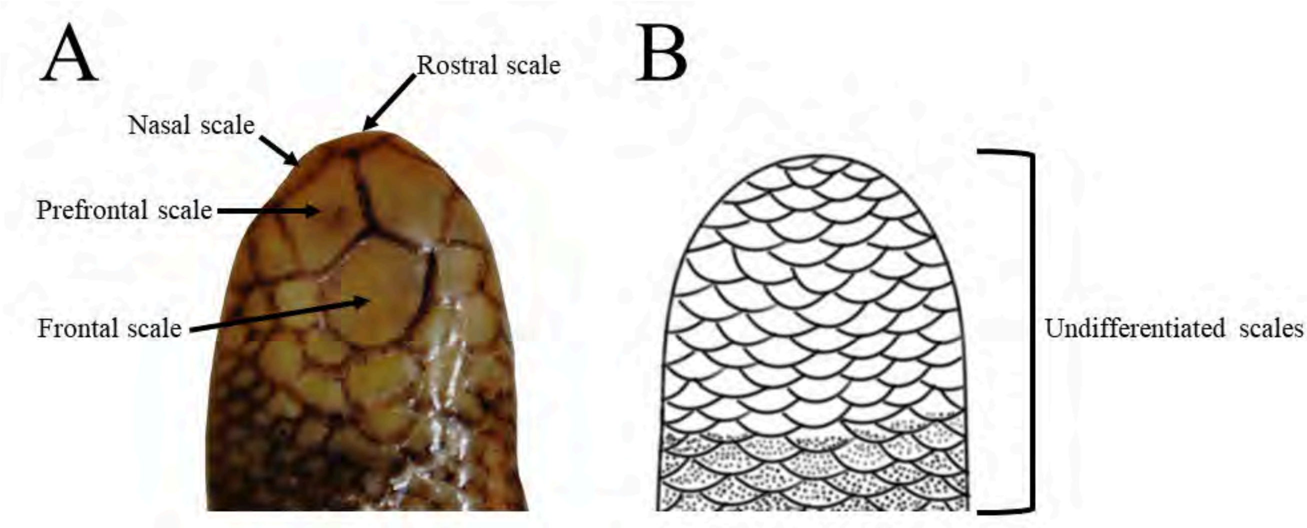


**Figure 16**. Scales of the head. A: differentiated scales of the head (*Anomalepis colombia* FMNH 54986 - holotype). B: undifferentiated scales of the head (*Typhlophis squamosus* INPA - H 27721).

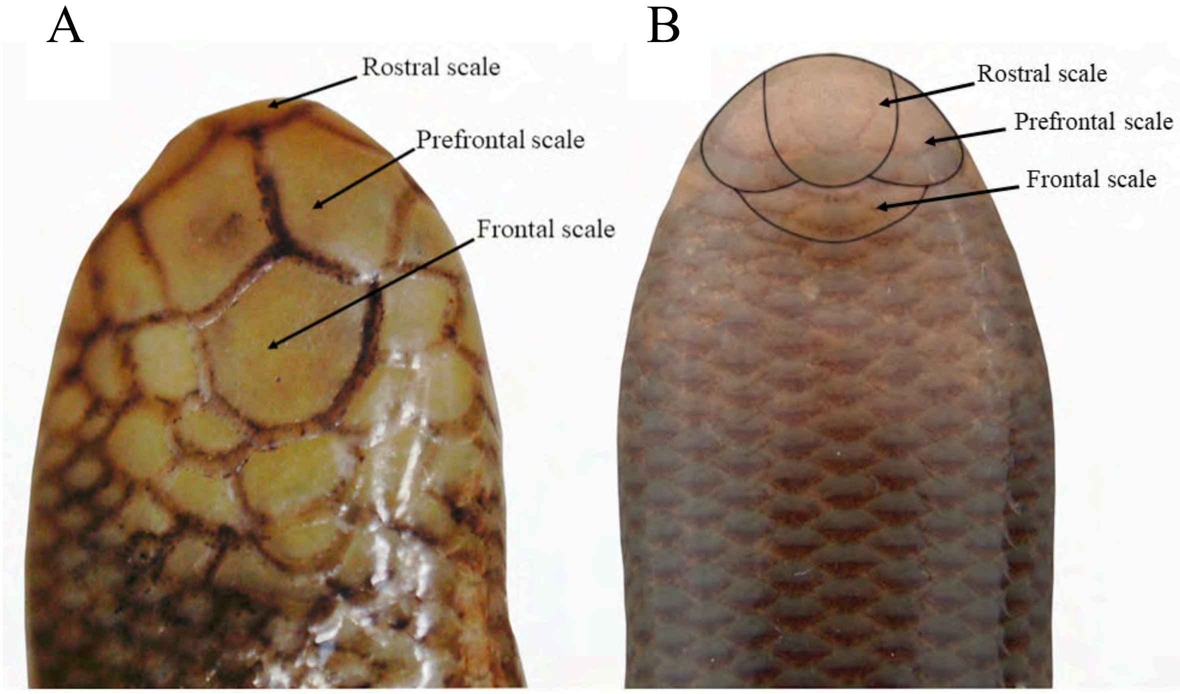


**Figure 17**. Prefrontals: A: polygonal prefrontals in contact behind the rostral (*Anomalepis colombia* FMNH 54986 - holotype). B: prefrontals separated behind the rostral (*Liotyphlops ternetzii* MCP 10878).

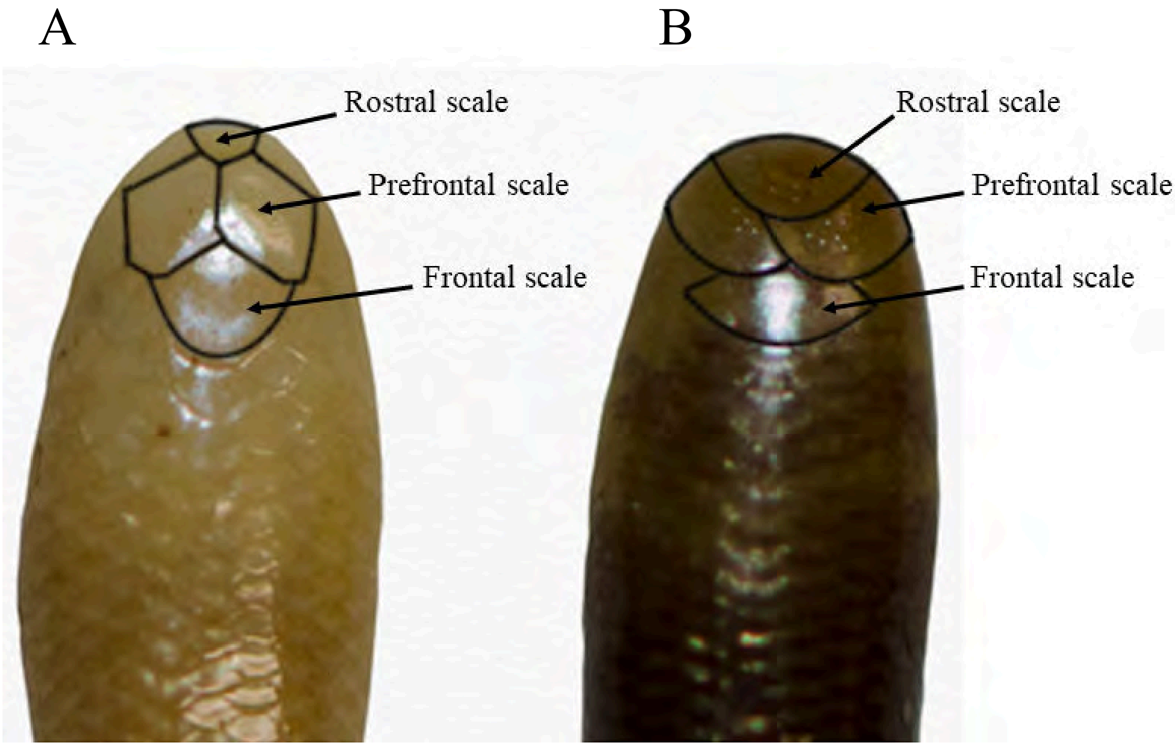


**Figure 18**. Prefrontal scale shape. A: short, pentagonal prefrontals (*Anomalepis mexicanus* AMNH R 119069). B: elongate, triangular prefrontals (*Helminthophis praeocularis* AMNH R 38125).


**Figure 19.** Location of the *Anomalepis aspinosus* (dot) examined in this study.

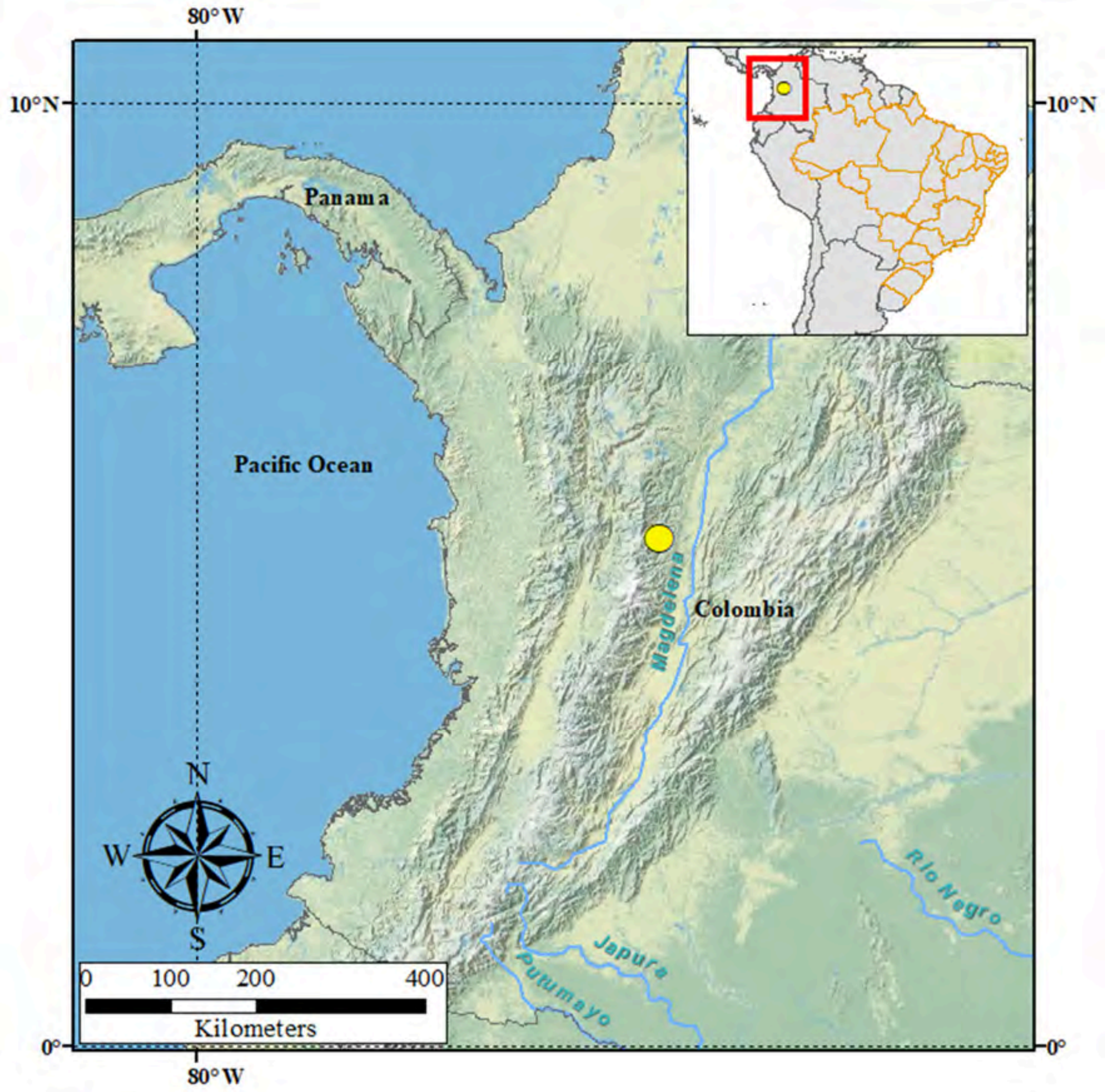


**Figure 20.** Location of the *Anomalepis colombia* (dot) examined in this study.


**Figure 21.** Location of the *Anomalepis flavapices* (dot) examined in this study.


**Figure 22**. Location of the *Anomalepis mexicanus* (dots) examined in this study.

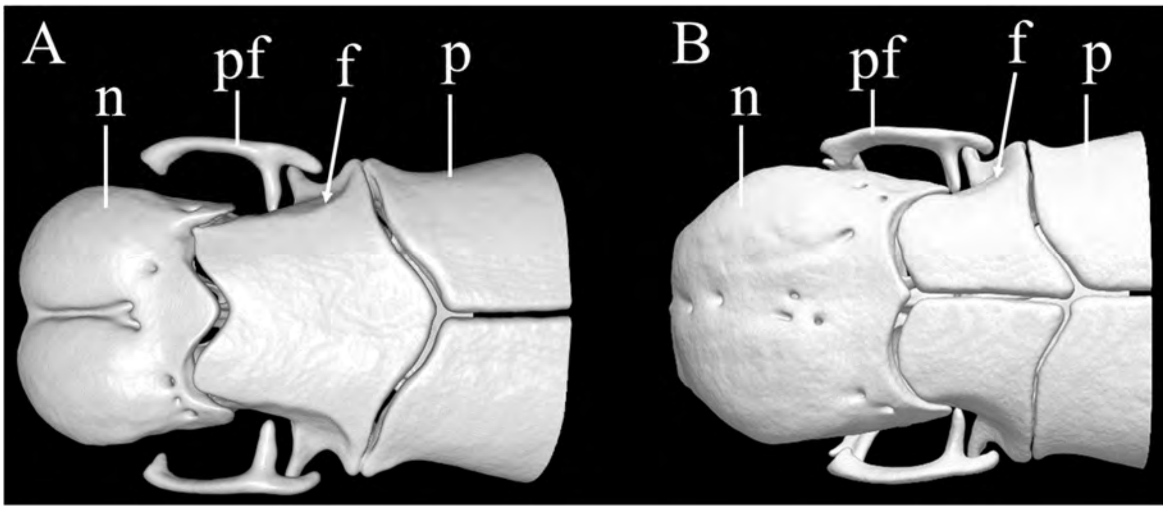


**Figure 23**. Frontal. A: frontal fused (*Helminthophis flavoterminatus* AMNH R 59407, dorsal view). B: frontal paired (*Liotyphlops wilder* MZUSPS 3842, dorsal view). Anatomical abbreviations: f, frontal; n, nasal; p, parietal; pf, prefrontal.

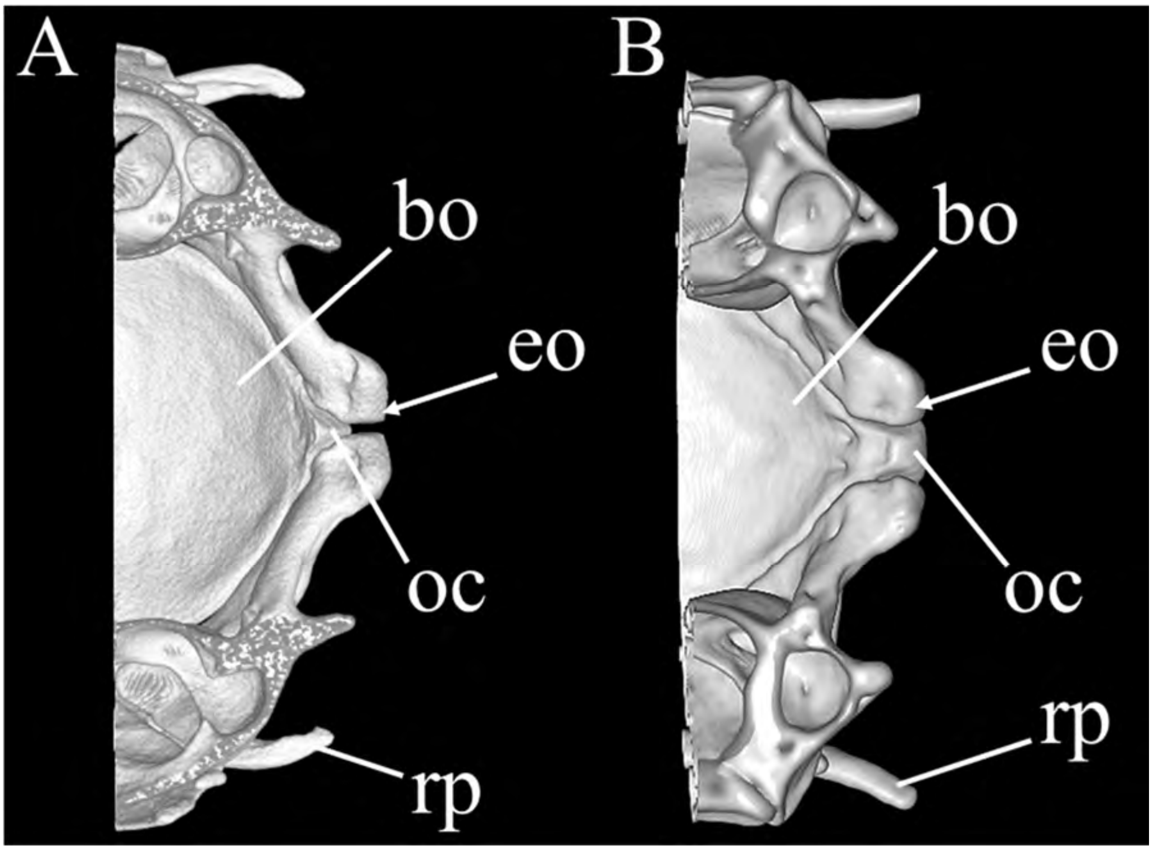


**Figure 24**. Exoccipital occipital condyle contact[N]. A: exoccipital overlaps and extends in front of the occipital condyle (*Helminthophis frontalis* MCZ R 55117, frontal axis view). B: exoccipital does not overlaps and does not extend in front of the occipital condyle (*Anomalepis aspinosus* CM 90254, frontal axis view). Anatomical abbreviations: bo, basioccipital; eo, exoccipital; oc, occipital condyle; rp, retroarticular process.

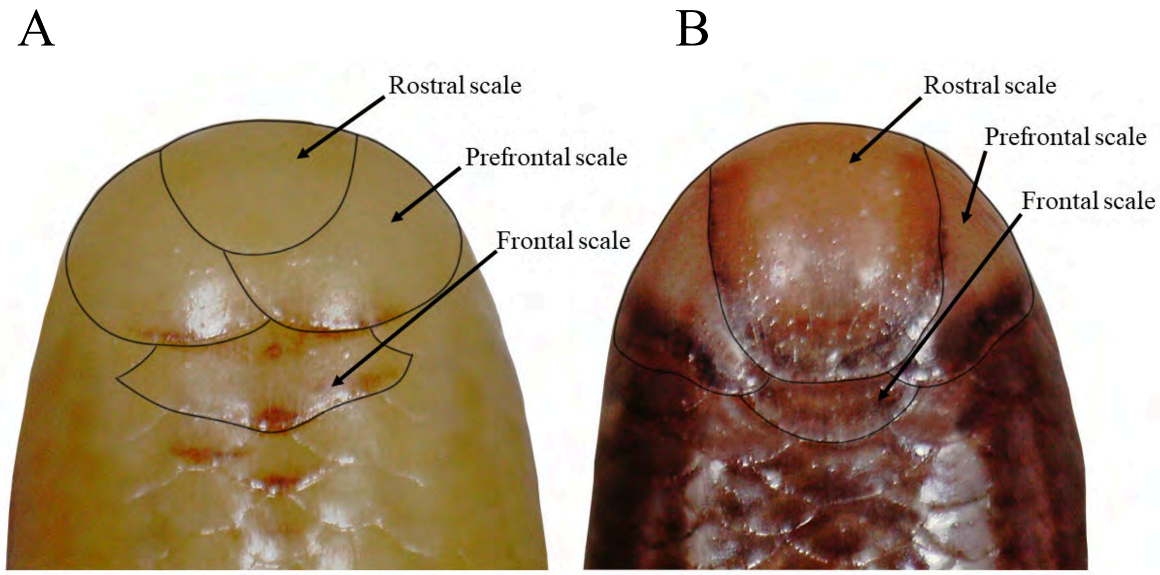


**Figure 25**. Rostral-prefrontal scales contact. A: contralateral prefrontals contacting each other behind the rostral scale, preventing the later to contact the frontal (*Helminthophis frontalis* MCZ R 55117). B: separate prefrontals, rostral in contact with frontal (*Liotyphlops argaleus* MCZ R-66383, paratype).

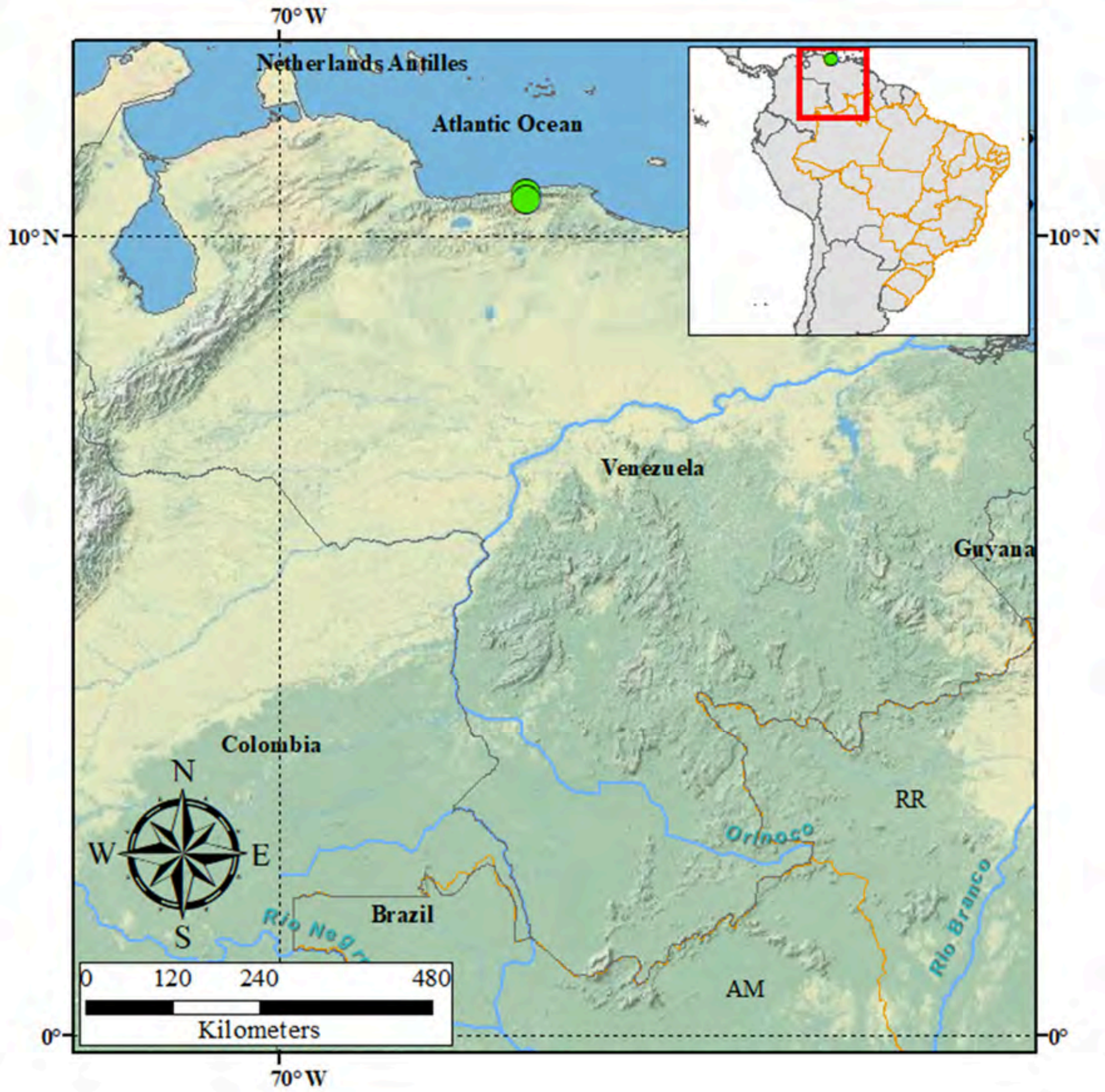


**Figure 26**. Location of the *Helminthophis flavoterminatus* (dots) examined in this study.


**Figure 27**. Location of the *Helminthophis frontalis* (dot) examined in this study.

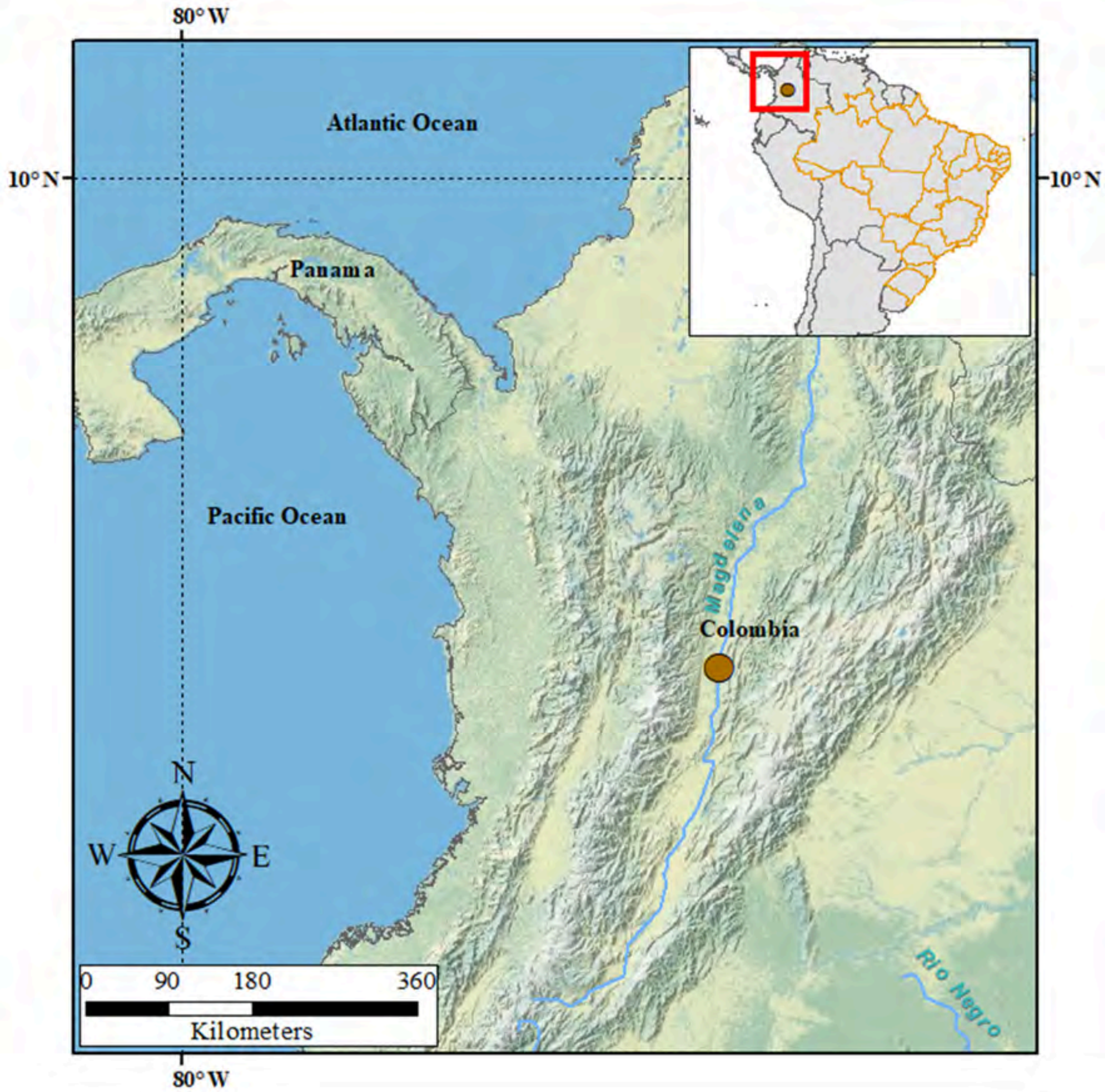


**Figure 28**. Location of the *Helminthophis praeocularis* (dot) examined in this study.

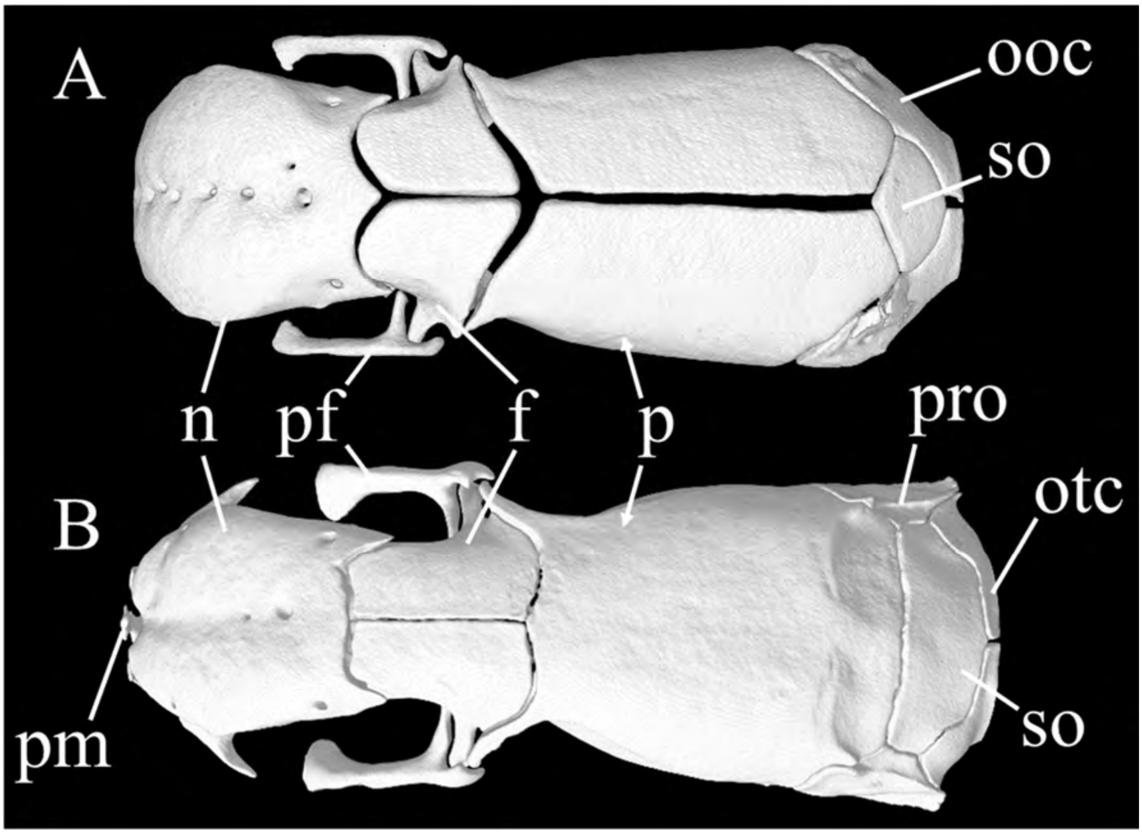


**Figure 29**. Parietals. A: parietal paired (*Liotyphlops argaleus* MCZ R-66383; paratype, dorsal view). B: parietal fused (*Anomalepis flavapices* MVZ 163245, dorsal view). Anatomical abbreviations: f, frontal; n, nasal; ooc, otico-occipital (fused prootic + opisthotic + exoccipital); otc, otooccipital (fused exoccipital + opisthotic); p, parietal; pf, prefrontal; pm, premaxilla.

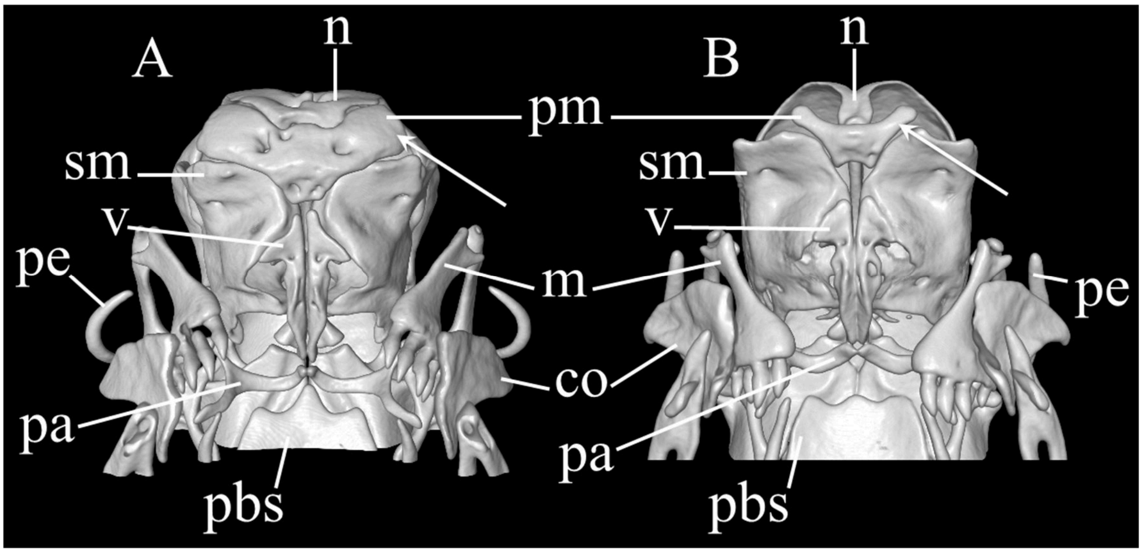


**Figure 30**. Ascending process of premaxilla. A: with lateral flange forming dorsal margin of external naris (*Liotyphlops ternetzii* MCP 10881, ventral view). B: without lateral flange (*Typhlophis squamosus* AMNH R 131787, ventral view). Anatomical abbreviations: co, coronoid; m, maxilla; n, nasal; pa, palatine; pbs, parabasisphenoid; pe, postorbital element; pm, premaxilla; sm, septomaxilla; v, vomer.

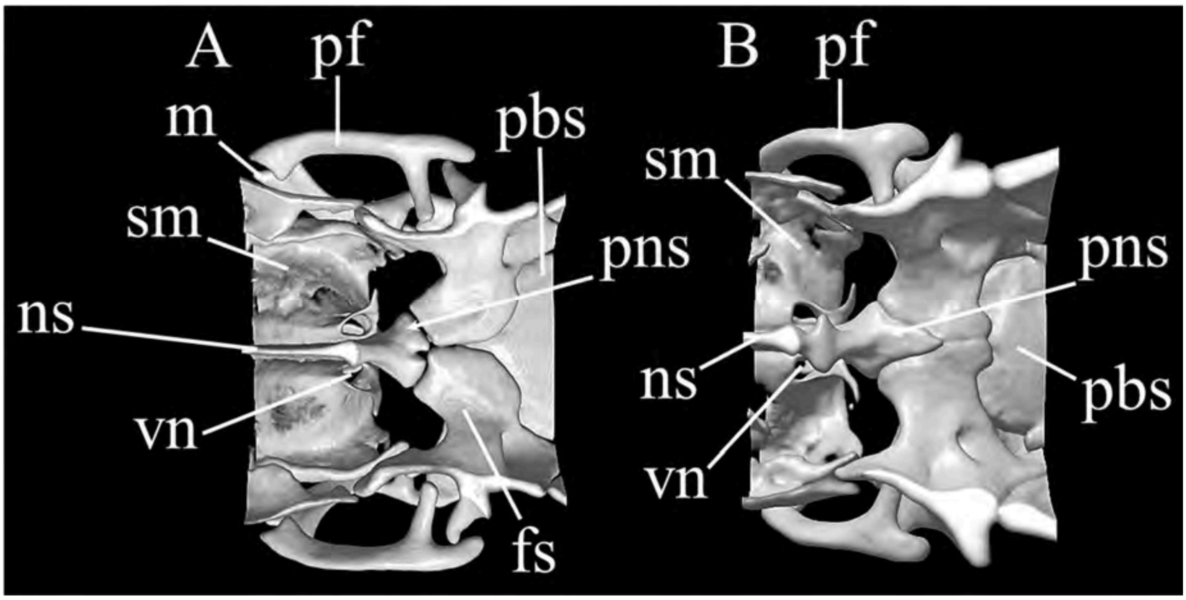


**Figure 31**. Posterior extension of the medial nasal septum[N]. A: do not overlap the anterior margins of the frontal subolfactory processes (*Liotyphlops ternetzii* MCP 10878, frontal axis view). B: overlap the anterior margins of the frontal subolfactory processes (*Typhlophis squamosus* AMNH R 131787, frontal axis view). Anatomical abbreviations: fs, frontal subolfactory process; m, maxilla; ns, medial nasal septum; pbs, parabasisphenoid; pf, prefrontal; pns, posterior extension of the medial nasal septum; sm, septomaxilla; vn, vomeronasal nerve passage.

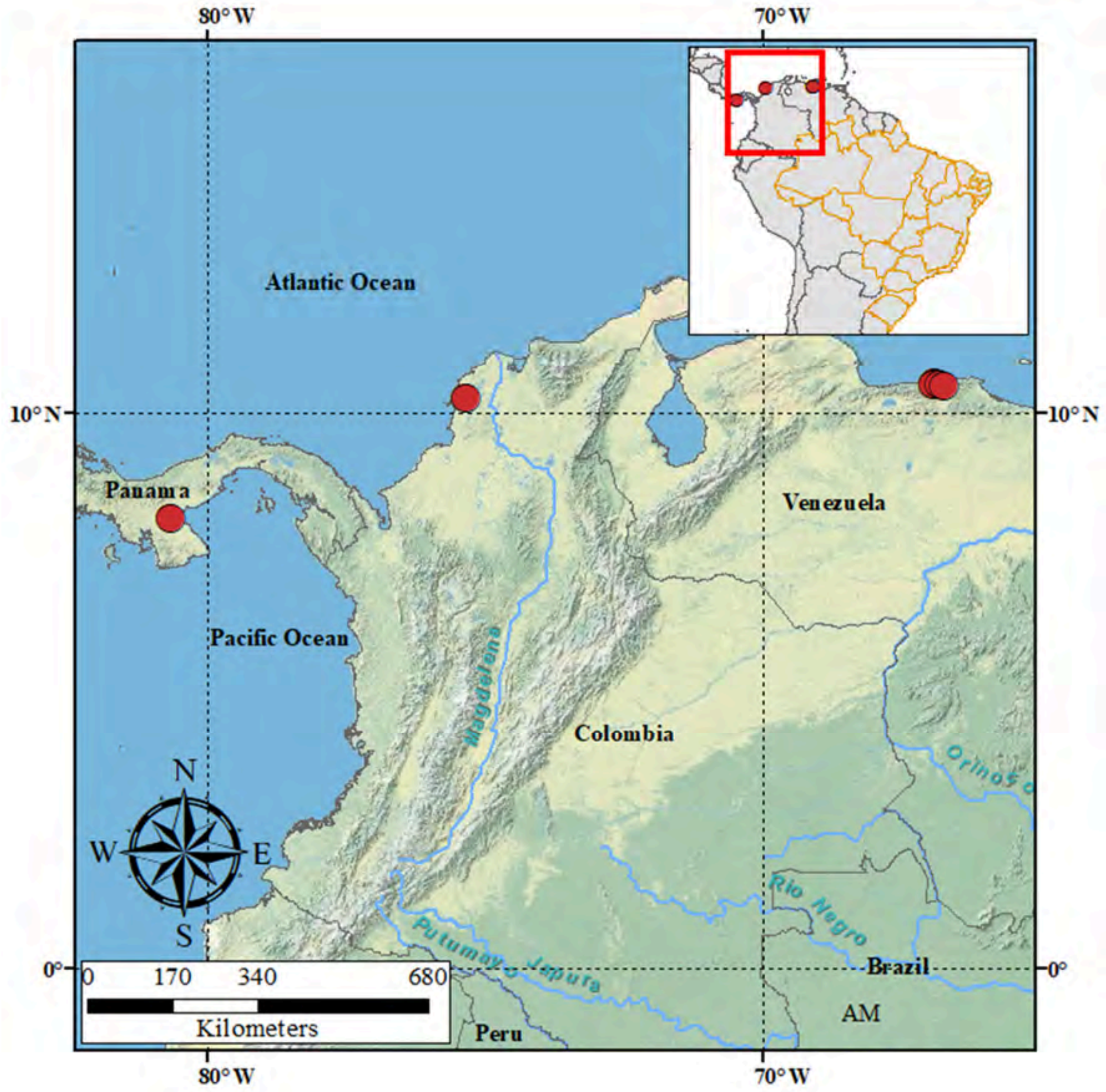


**Figure 32**. Location of the *Liotyphlops albirostris* (dots) examined in this study.

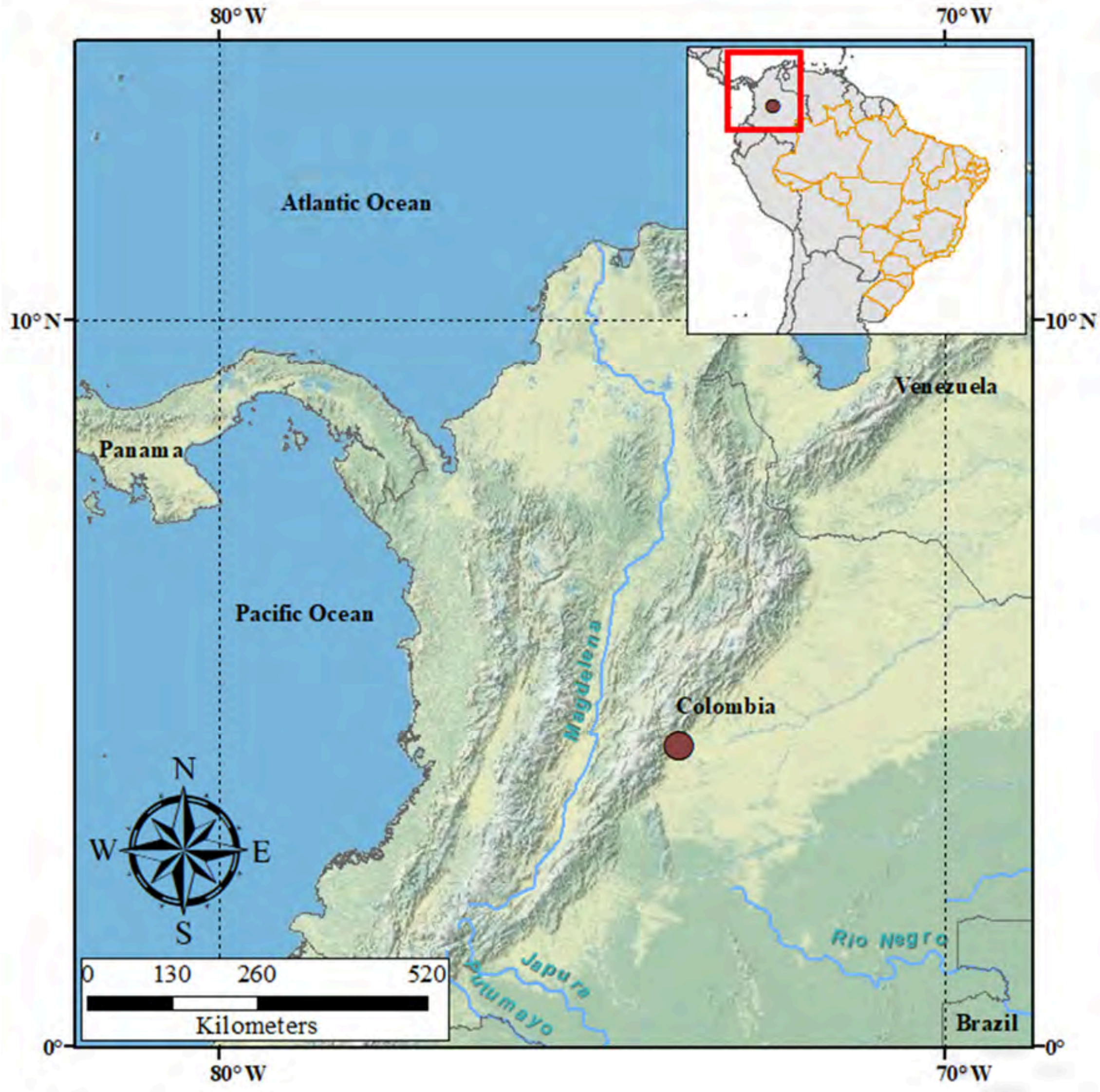


**Figure 33**. Location of the *Liotyphlops anops* (dot) examined in this study.

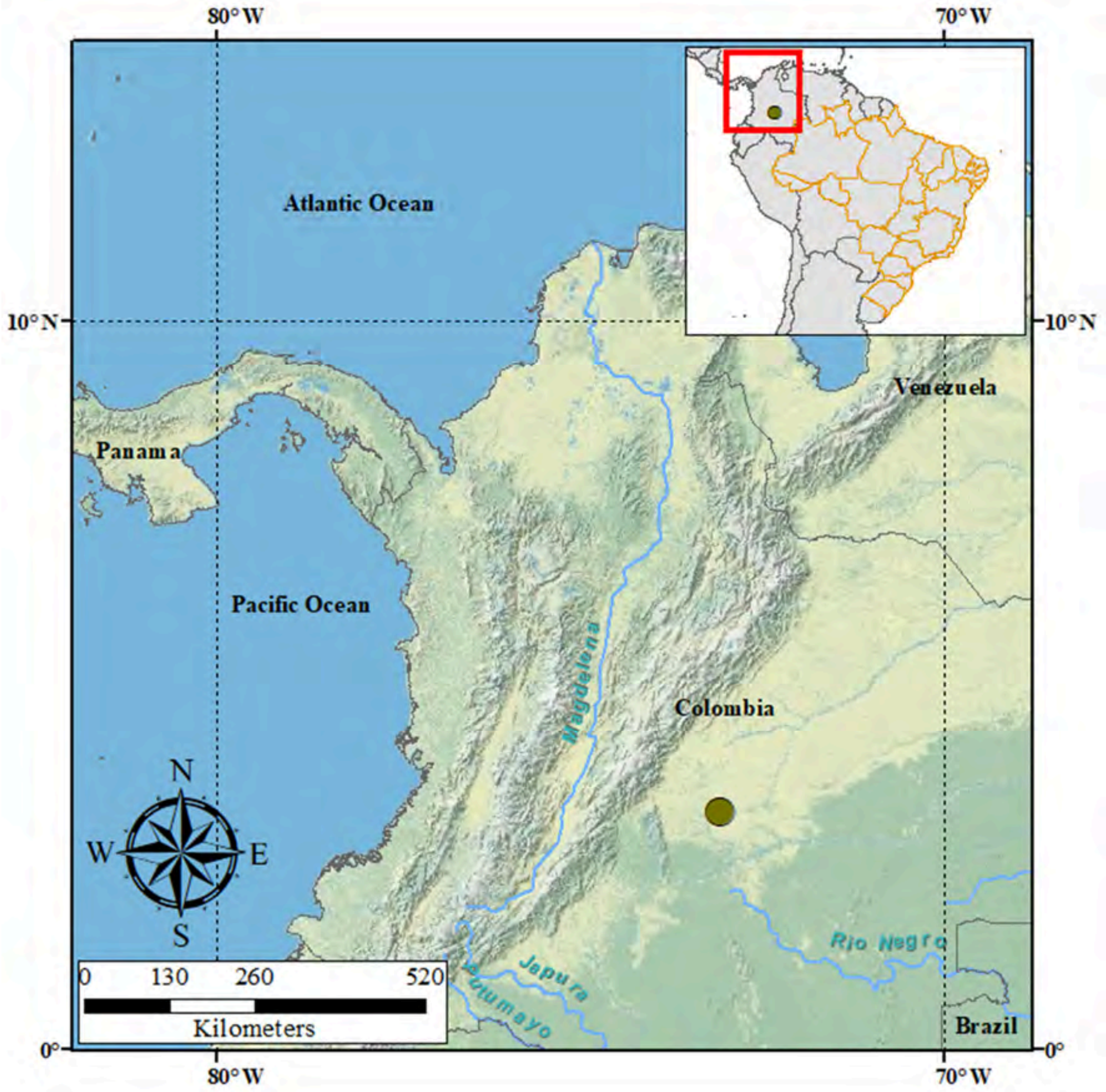


**Figure 34**. Location of the *Liotyphlops argaleus* (dot) examined in this study.

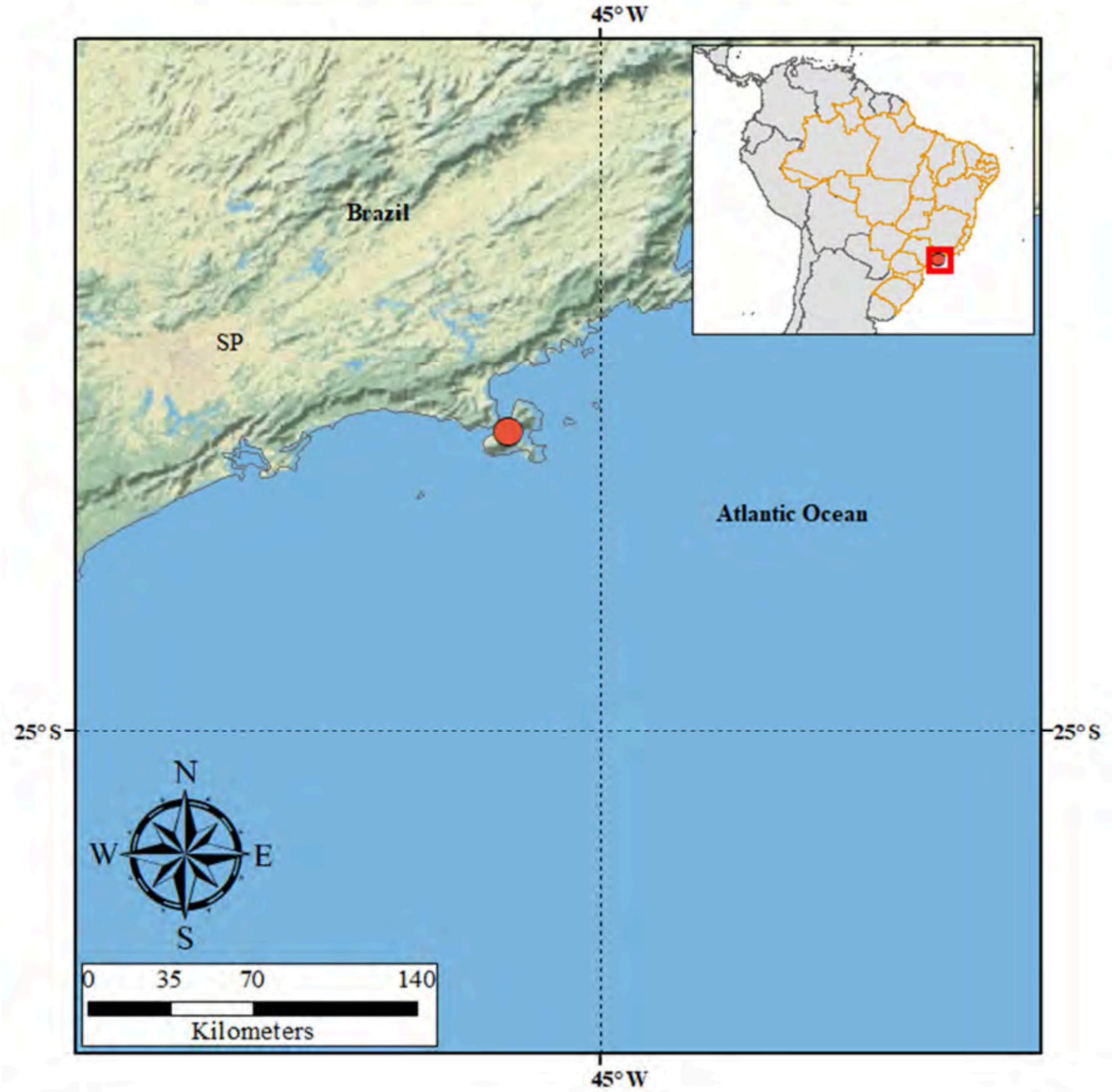


**Figure 35**. Location of the *Liotyphlops caissara* (dot) examined in this study.

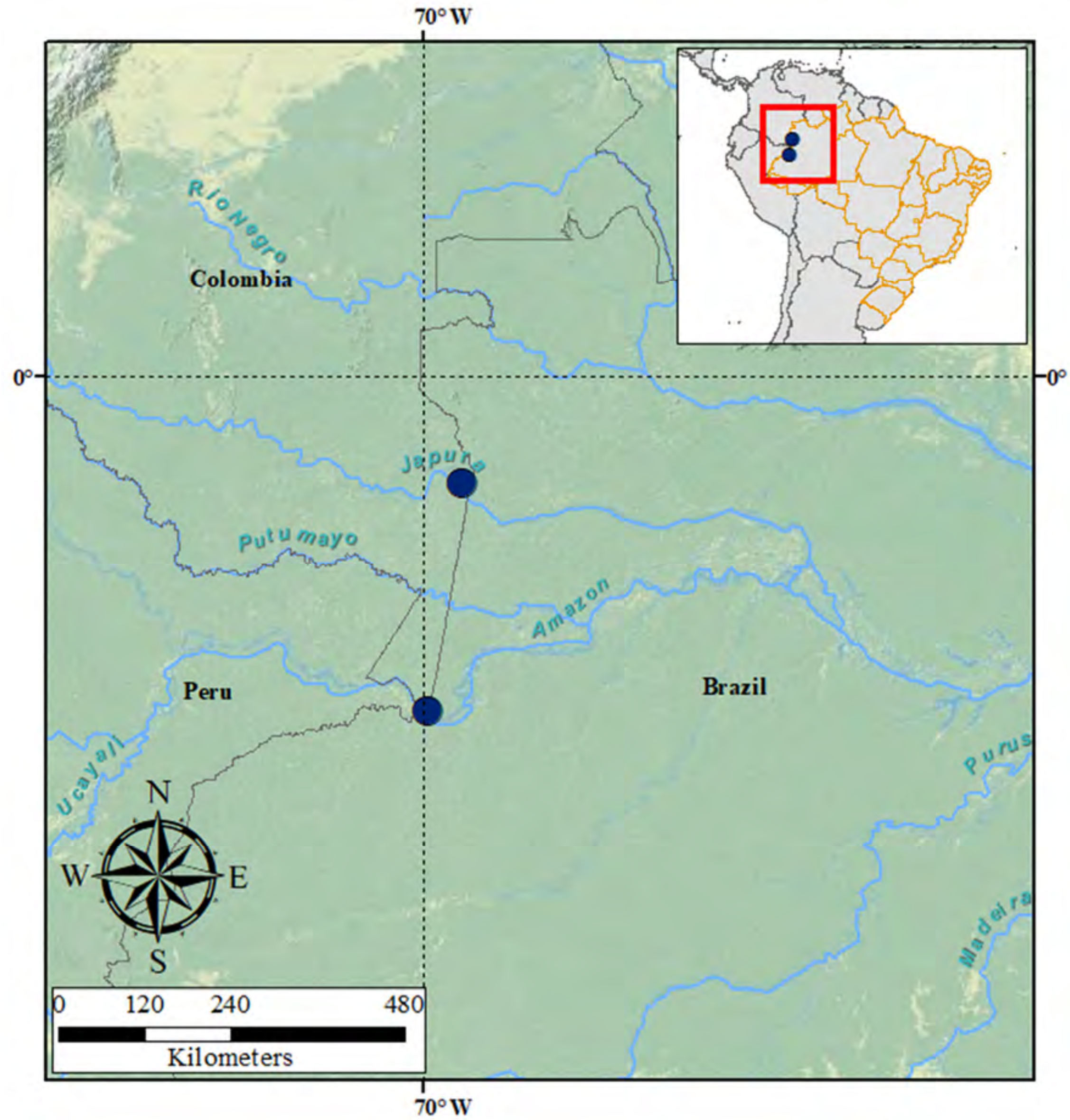


**Figure 36**. Location of the *Liotyphlops haadi* (dots) examined in this study.

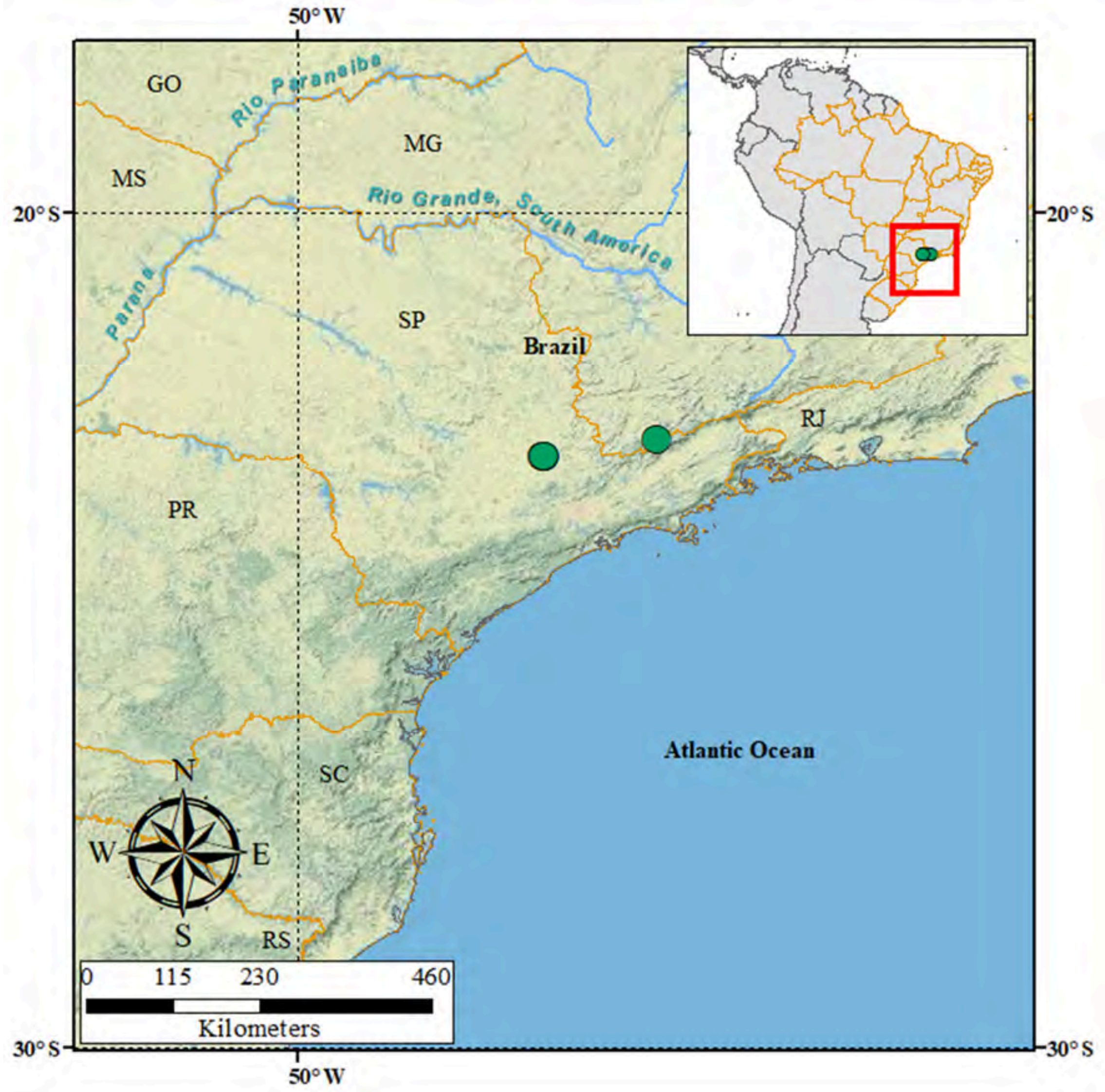


**Figure 37**. Location of the *Liotyphlops schubarti* (dots) examined in this study.

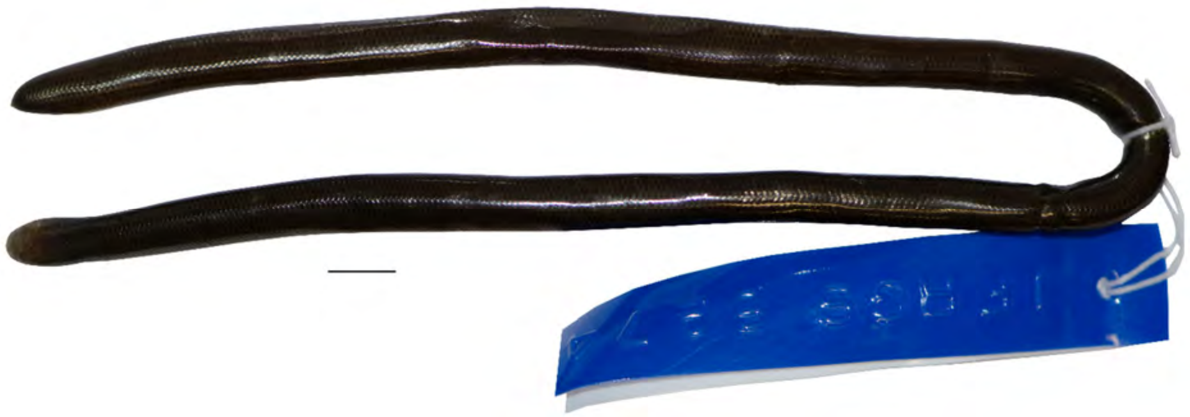

**Figure 38**. Holotype of *Liotyphlops ss* sp. nov. (UFRGS 6274, 191.4 mm SL) from Pequena Central Hidrelétrica Passos Maia, Passos Maia, Santa Catarina, Brazil. Scale bar = 5 mm.

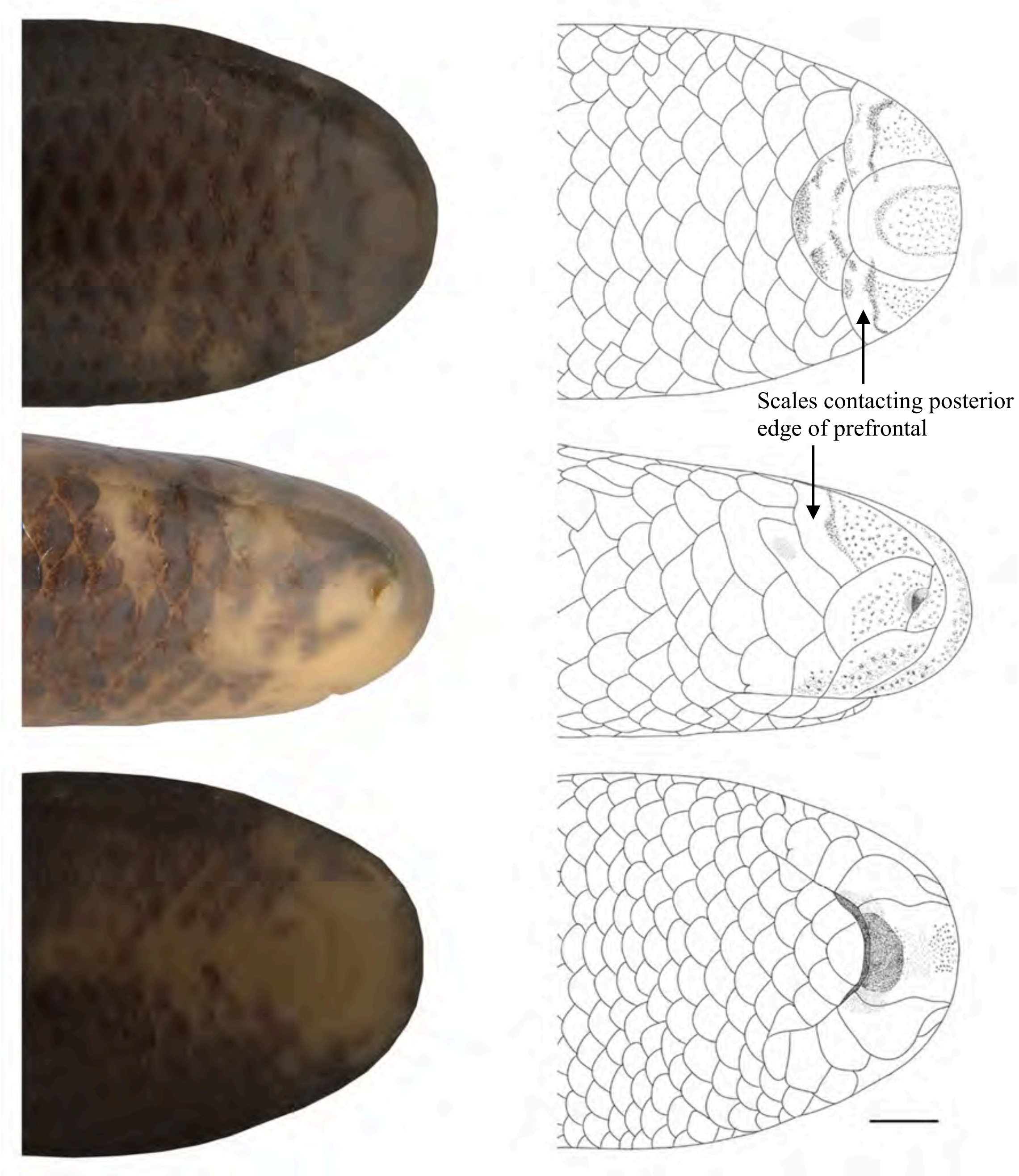


**Figure 39**. Dorsal, lateral, and ventral views of the head of *Liotyphlops ss* sp. nov. (UFRGS 6274, holotype). Scale bar = 1 mm.

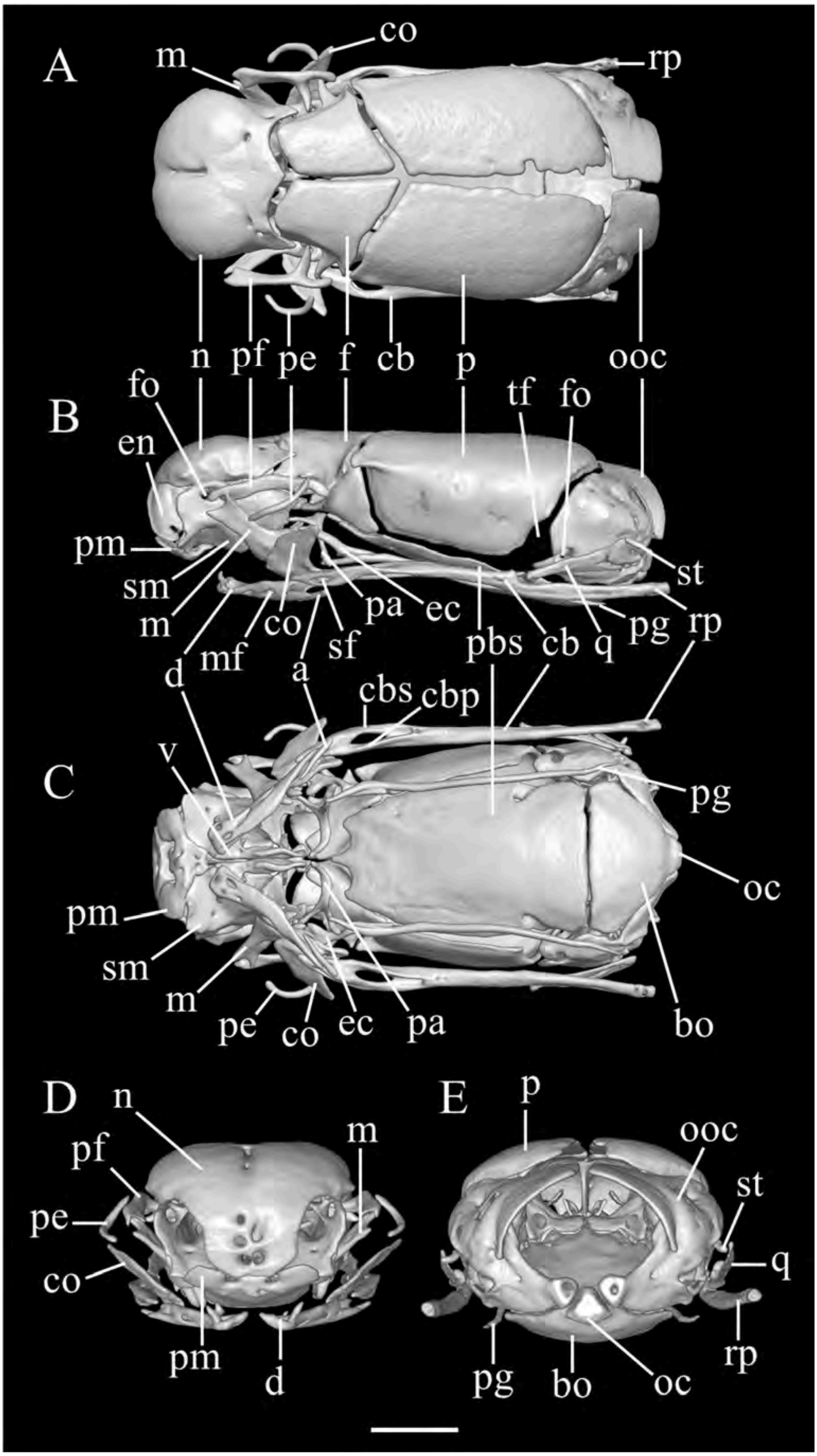


**Figure 40**. Three-dimensional reconstruction of the skull of *Liotyphlops ss* sp. nov. (UFRGS 6274, holotype) based on HRXCT data. A: Dorsal view. B: Lateral view. C: Ventral view. D: Anterior view. E:

Posterior view. Scale bar = 1 mm. Anatomical abbreviations: a, angular; bo, basioccipital; cb, compound bone; cbp, compound bone prearticular component; cbs, compound bone surangular component; co, coronoid; d, dentary; ec, ectopterygoid; en, external naris; f, frontal; fo, foramen; m, maxilla; mf, mental foramen; n, nasal; oc, occipital condyle; ooc, otico-occipital (fused prootic + opisthotic + exoccipital); p, parietal; pa, palatine; pbs, parabasisphenoid; pe, postorbital element; pf, prefrontal; pg, pterygoid; pm, premaxilla; q, quadrate; rp, retroarticular process; sm, septomaxilla; sf, surangular foramen; st, supratemporal; tf, trigeminal foramen; v, vomer.

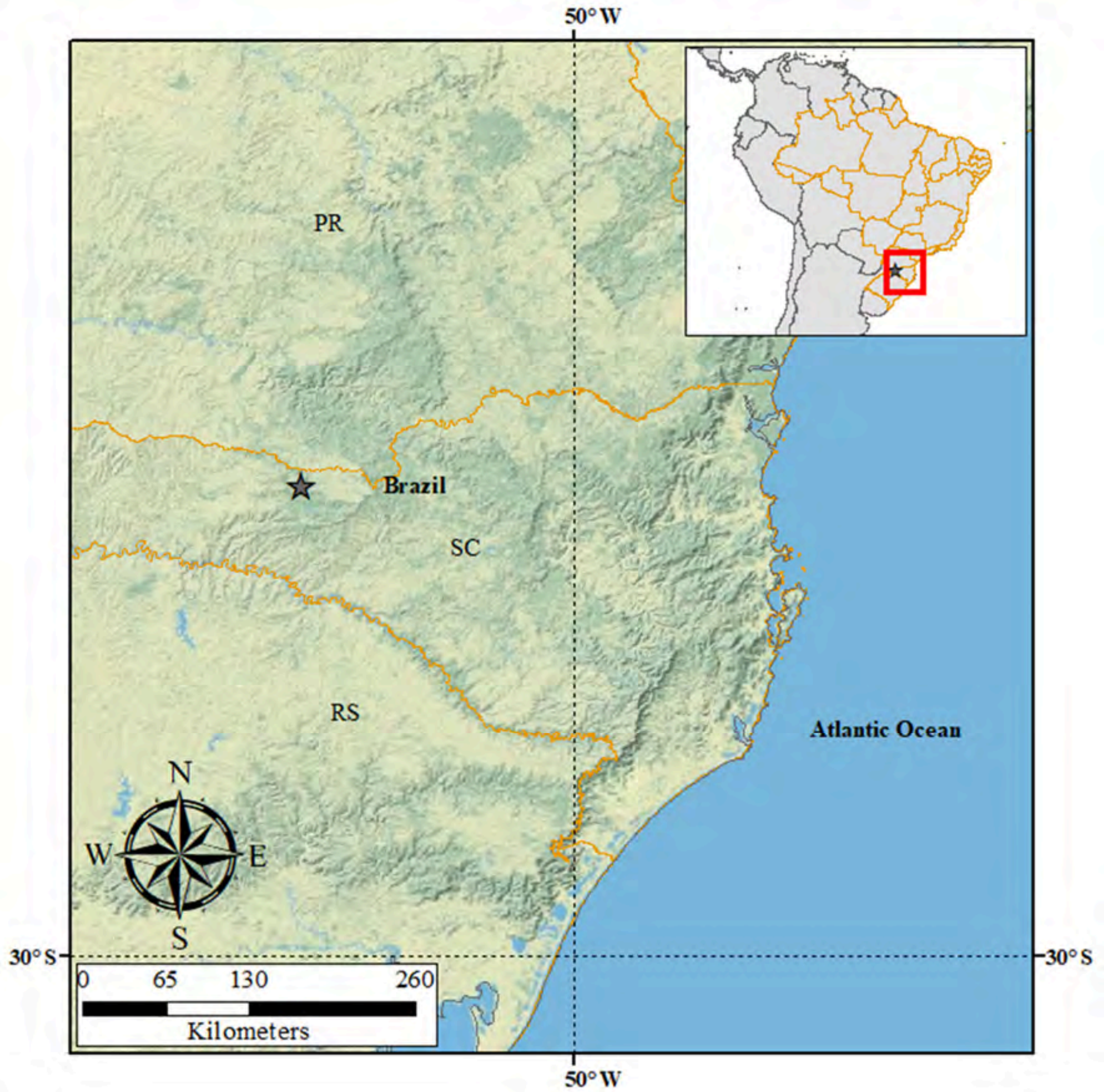


**Figure 41**. Location of type locality of *Liotyphlops ss* sp. nov. (star) from Pequena Central Hidrelétrica Passos Maia, Passos Maia, Santa Catarina, Brazil.


**Figure 42**. Holotype of *Liotyphlops tt* sp. nov. (MZUSP S-14975, 239.4 mm SL) from Estação Ecológica Serra das Araras, Porto Estrela, Mato Grosso, Brazil. Scale bar = 5 mm.

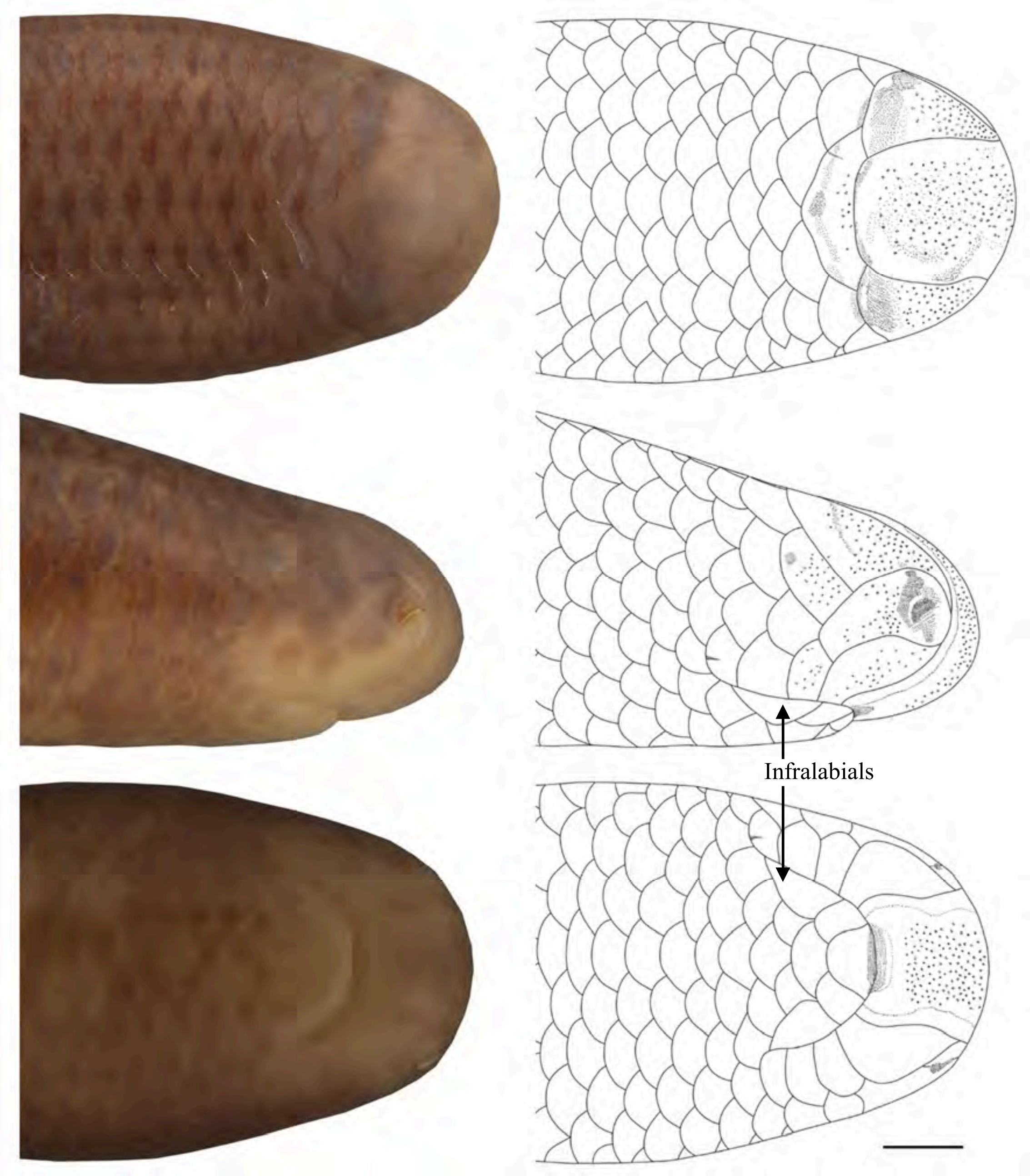


**Figure 43**. Dorsal, lateral, and ventral views of the head of *Liotyphlops tt* sp. nov. (MZUSP S-14975, holotype). Scale bar = 1 mm.

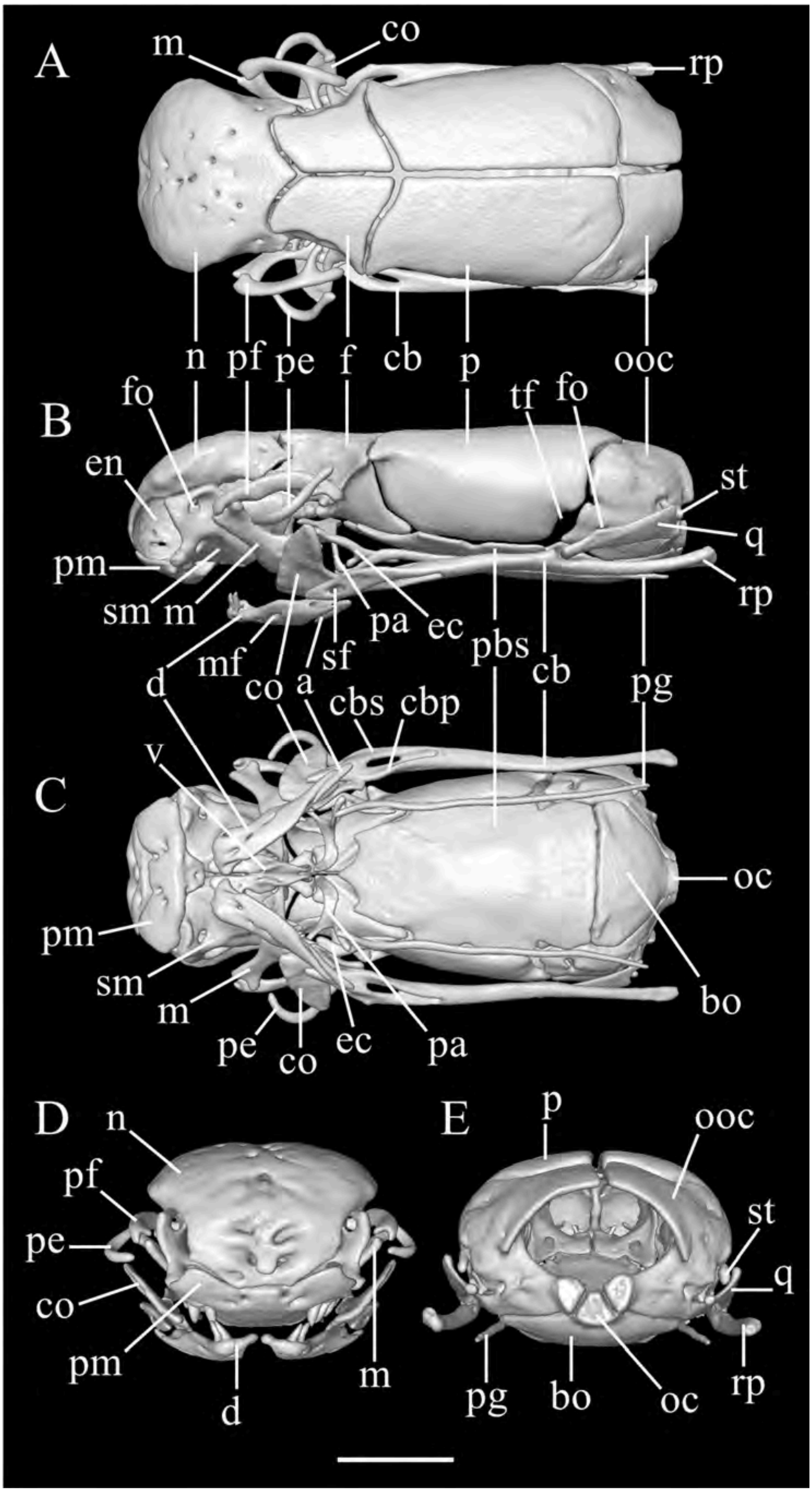


**Figure 44**. Three-dimensional reconstruction of the skull of *Liotyphlops tt* sp. nov. (MZUSP S-14975, holotype) based on HRXCT data. A: Dorsal view. B: Lateral view. C: Ventral view. D: Anterior view. E:

Posterior view. Scale bar = 1 mm. Anatomical abbreviations: a, angular; bo, basioccipital; cb, compound bone; cbp, compound bone prearticular component; cbs, compound bone surangular component; co, coronoid; d, dentary; ec, ectopterygoid; en, external naris; f, frontal; fo, foramen; m, maxilla; mf, mental foramen; n, nasal; oc, occipital condyle; ooc, otico-occipital (fused prootic + opisthotic + exoccipital); p, parietal; pa, palatine; pbs, parabasisphenoid; pe, postorbital element; pf, prefrontal; pg, pterygoid; pm, premaxilla; q, quadrate; rp, retroarticular process; sm, septomaxilla; sf, surangular foramen; st, supratemporal; tf, trigeminal foramen; v, vomer.

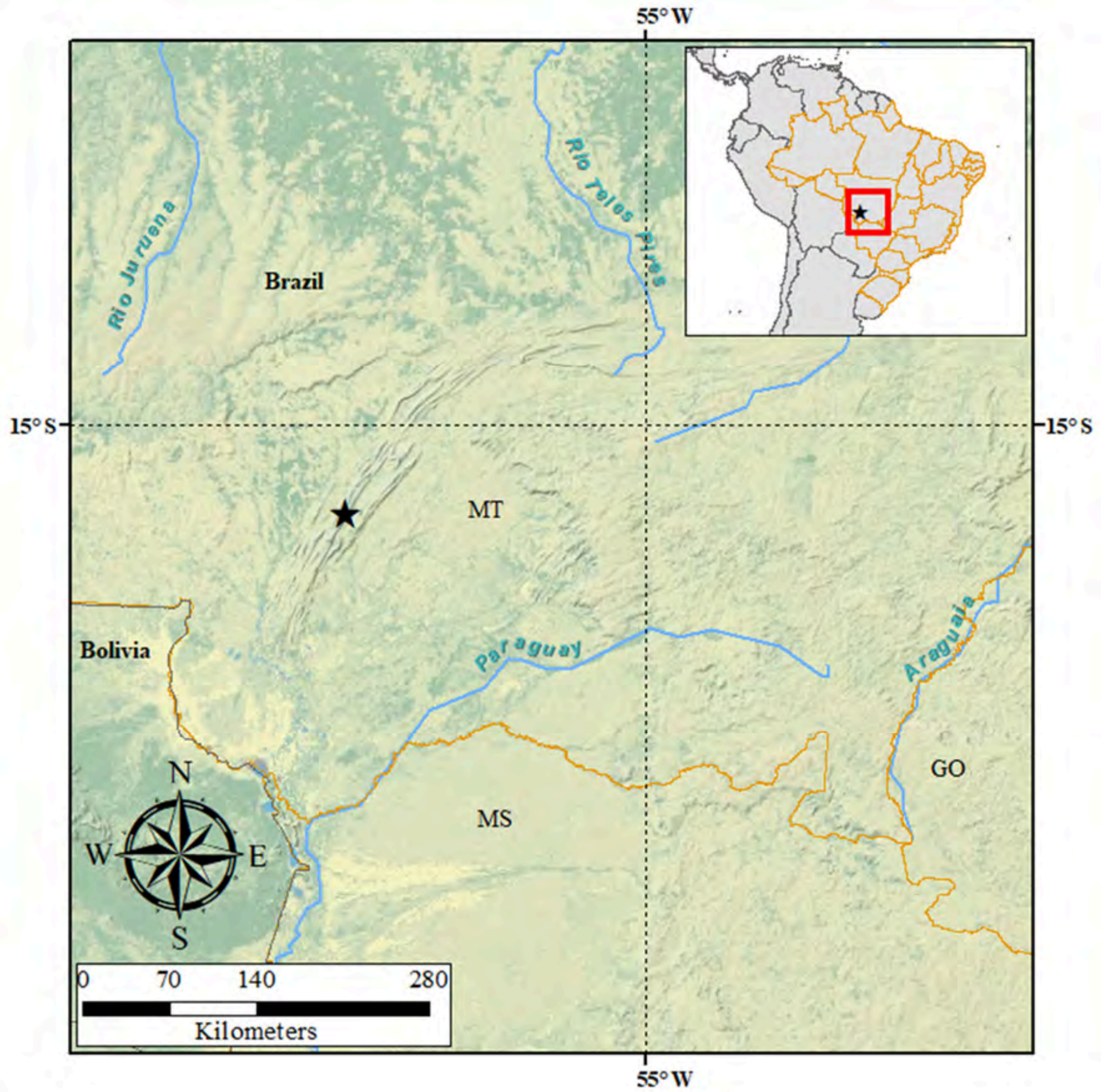


**Figure 45**. Location of type locality of *Liotyphlops tt* sp. nov. (star) from Estação Ecológica Serra das Araras, Porto Estrela, Mato Grosso, Brazil.

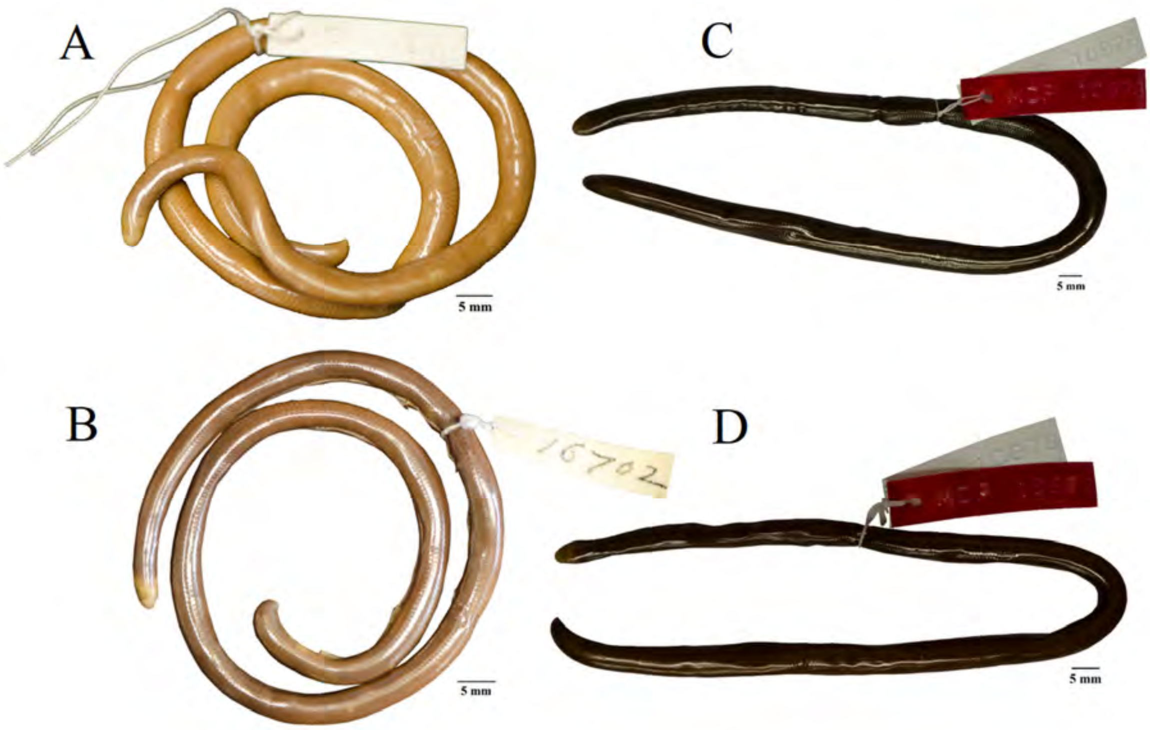


**Figure 46**. Types of *Liotyphlops ternetzii* and *Liotyphlops beui*. A: Holotype of *L. ternetzii* (BMNH 1946.1.11.77, 325.1 mm SL) from Paraguay. B: Paratype of *L. beui* (MCZ 16702, 279.2 mm SL) from Butantan, São Paulo, Brazil. C: Specimen of *L. ternetzii* (MCP 10878, 248.9 mm SL) with dark brown coloration. D: Specimen of *L. beui* (MCP 10879, 233.9 mm SL) with dark brown coloration.


**Figure 47**. A: Dorsal, lateral, and ventral views of the head of holotype *Liotyphlops ternetzii* (BMNH 1946.1.11.77), and B: dorsal, lateral, and ventral views of the head of the paratype of *Liotyphlops beui* (MCZ 16702). Scale bar = 1 mm.

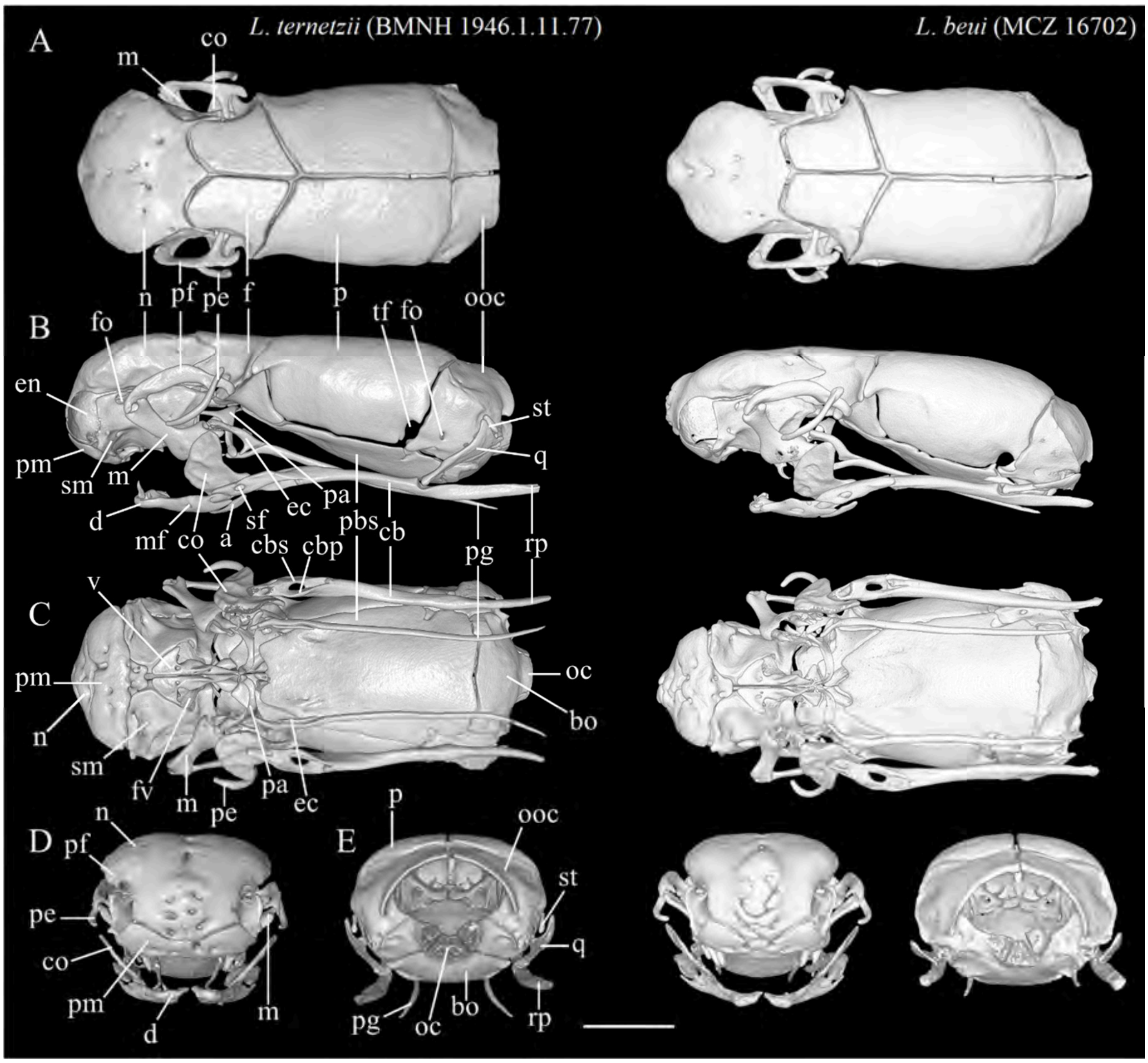


**Figure 48**. Three-dimensional reconstruction of the skull of holotype *Liotyphlops ternetzii* (BMNH 1946.1.11.77), and of the skull of the paratype of *Liotyphlops beui* (MCZ 16702) based on HRXCT data. A: Dorsal view. B: Lateral view. C: Ventral view. D: Anterior view. E: Posterior view. Scale bar = 1 mm. Anatomical abbreviations: a, angular; bo, basioccipital; cb, compound bone; cbp, compound bone prearticular component; cbs, compound bone surangular component; co, coronoid; d, dentary; ec, ectopterygoid; en, external naris; f, frontal; fo, foramen; m, maxilla; mf, mental foramen; n, nasal; oc, occipital condyle; ooc, otico-occipital (fused prootic + opisthotic + exoccipital); p, parietal; pa, palatine; pbs, parabasisphenoid; pe, postorbital element; pf, prefrontal; pg, pterygoid; pm, premaxilla; q, quadrate; rp, retroarticular process; sm, septomaxilla; sf, surangular foramen; st, supratemporal; tf, trigeminal foramen; v, vomer.

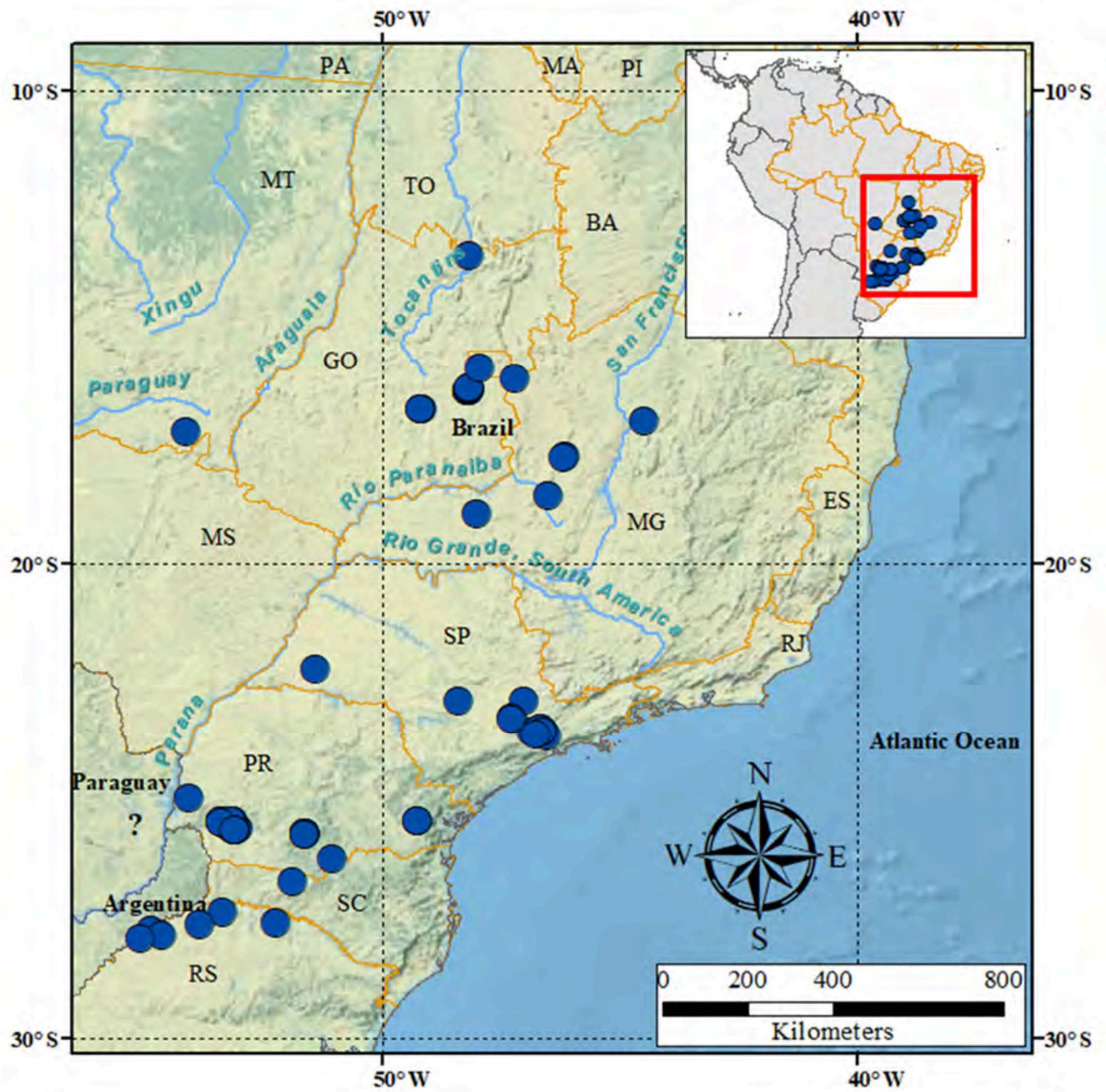


**Figure 49**. Location of the *Liotyphlops ternetzii* (dots) examined in this study. **?** = Holotype of *L. ternetzii*.

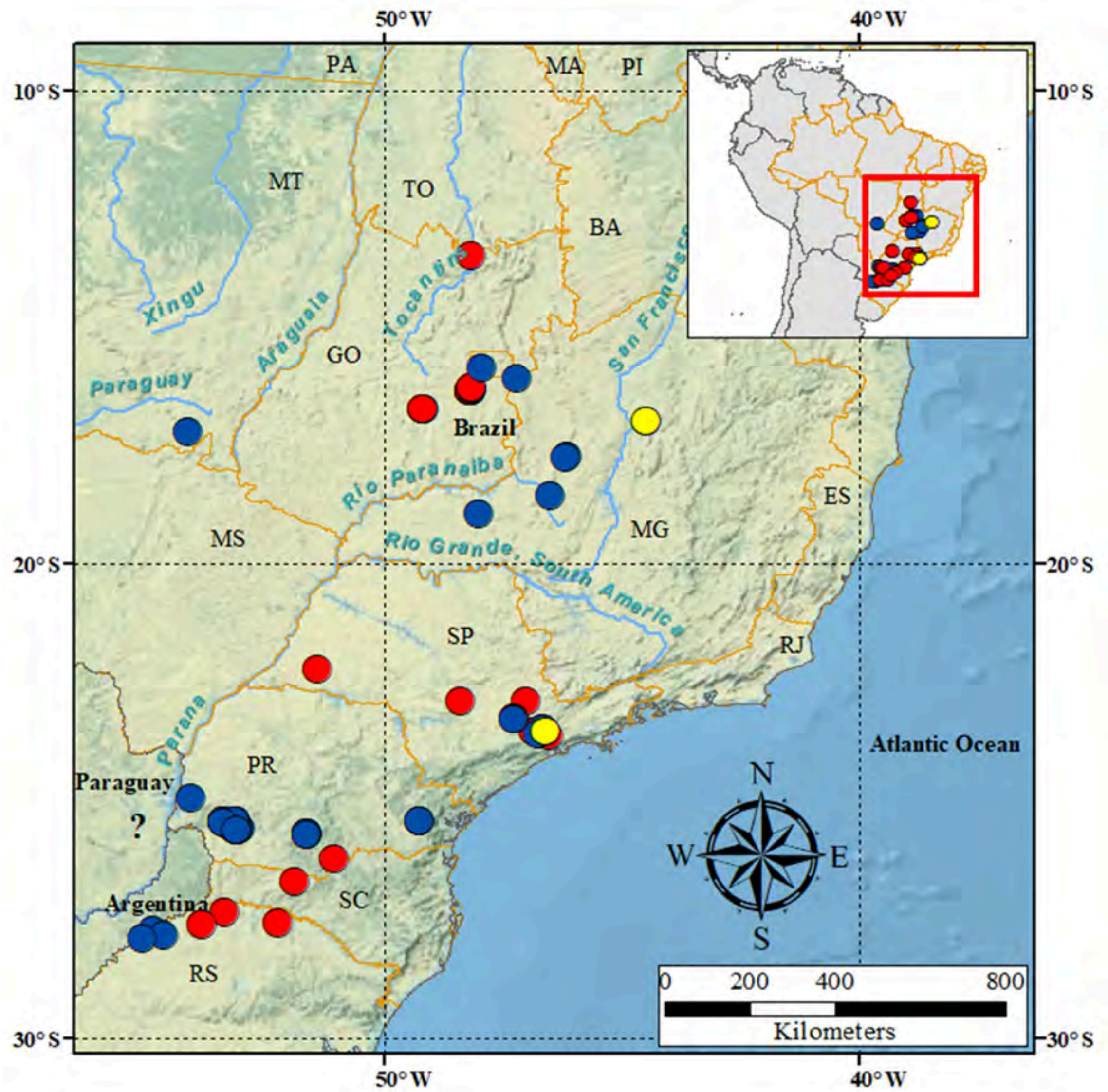


**Figure 50**. Location of the *Liotyphlops ternetzii* (blue dots), *Liotyphlops beui* (red dots), paratypes of *L. beui* (yellow dots), and holotype of *L. ternetzii* (? = undetermined type-locality) examined in this study.

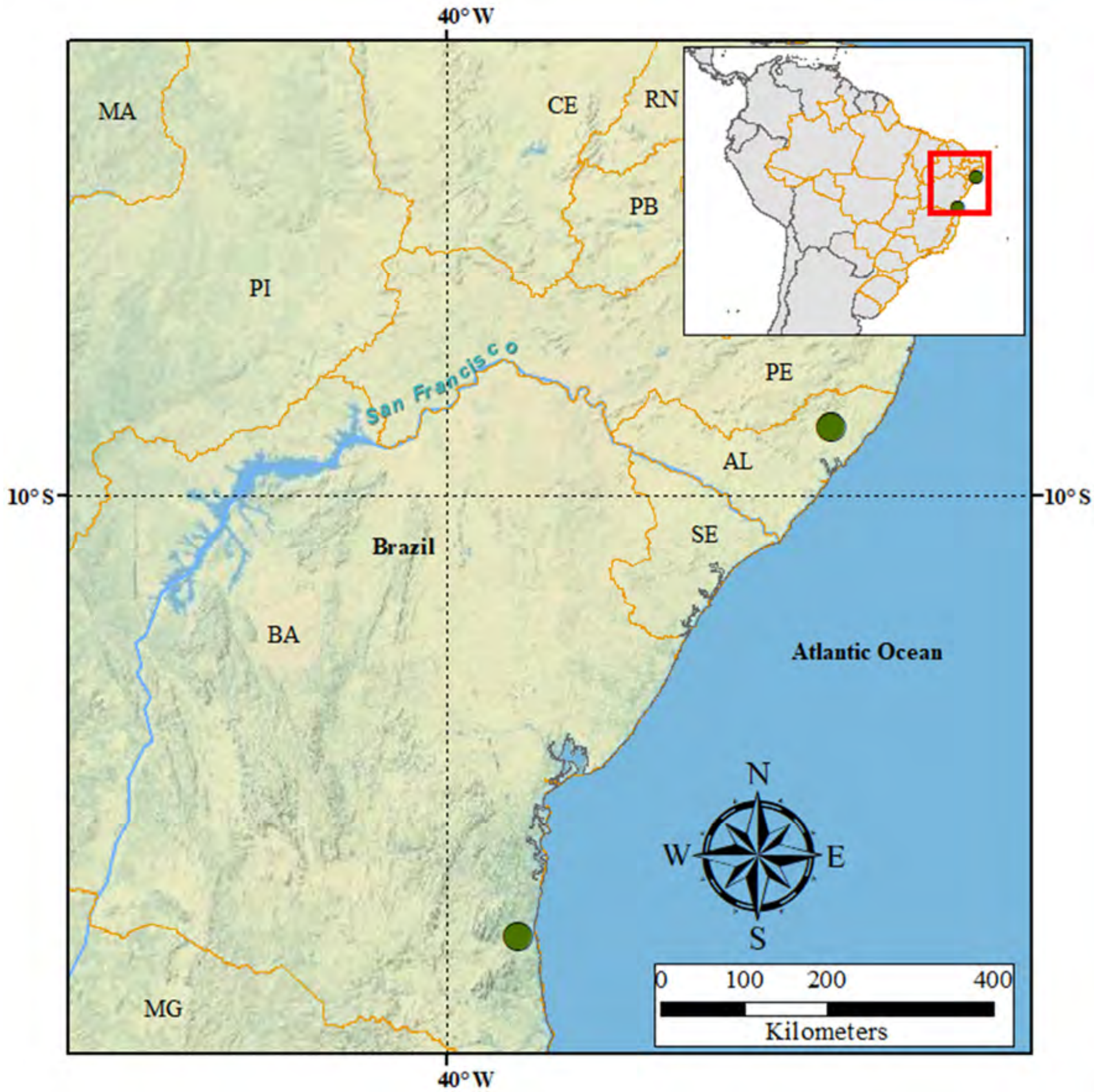


**Figure 51**. Location of the *Liotyphlops trefauti* (dots) examined in this study.

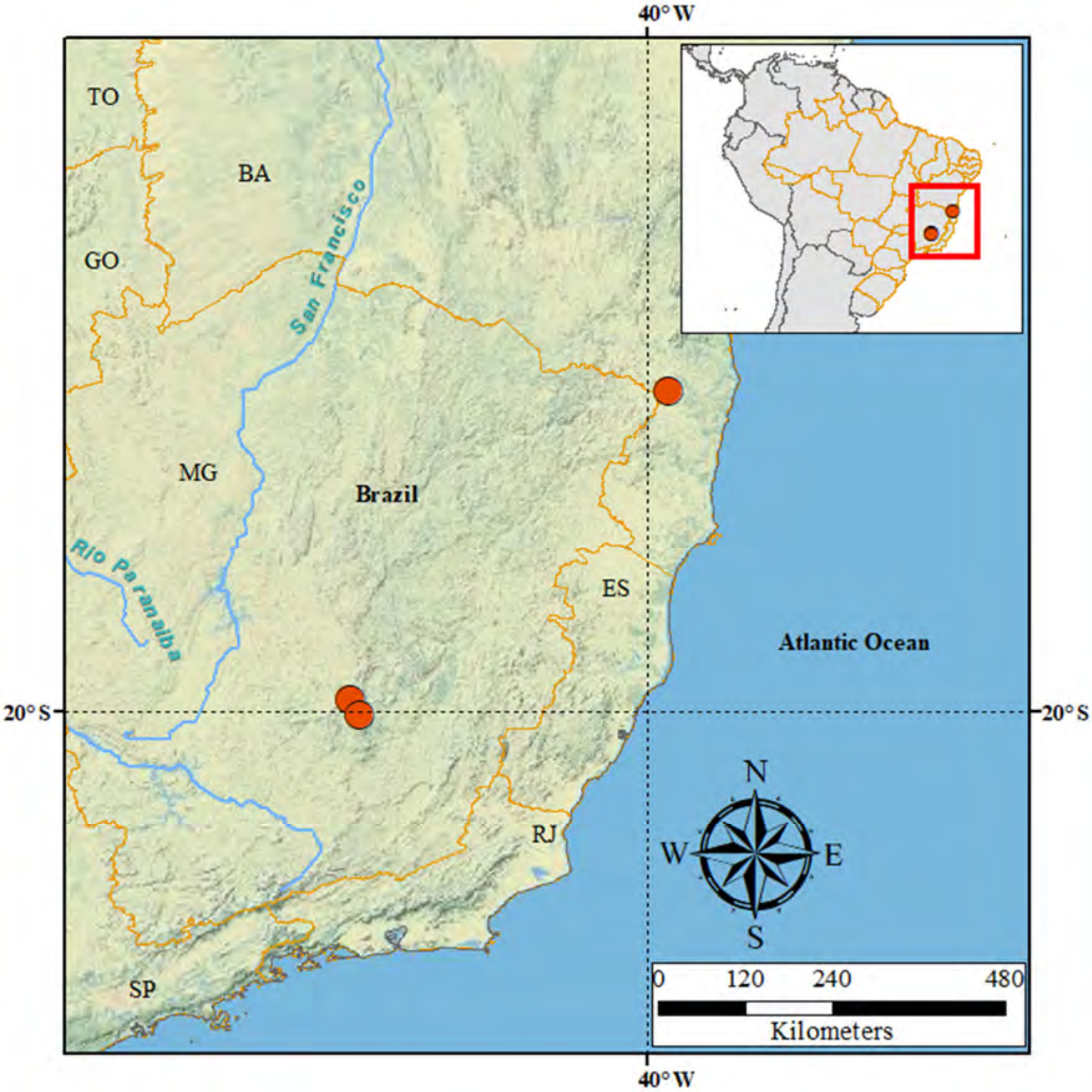


**Figure 52**. Location of the *Liotyphlops wilderi* (dots) examined in this study.

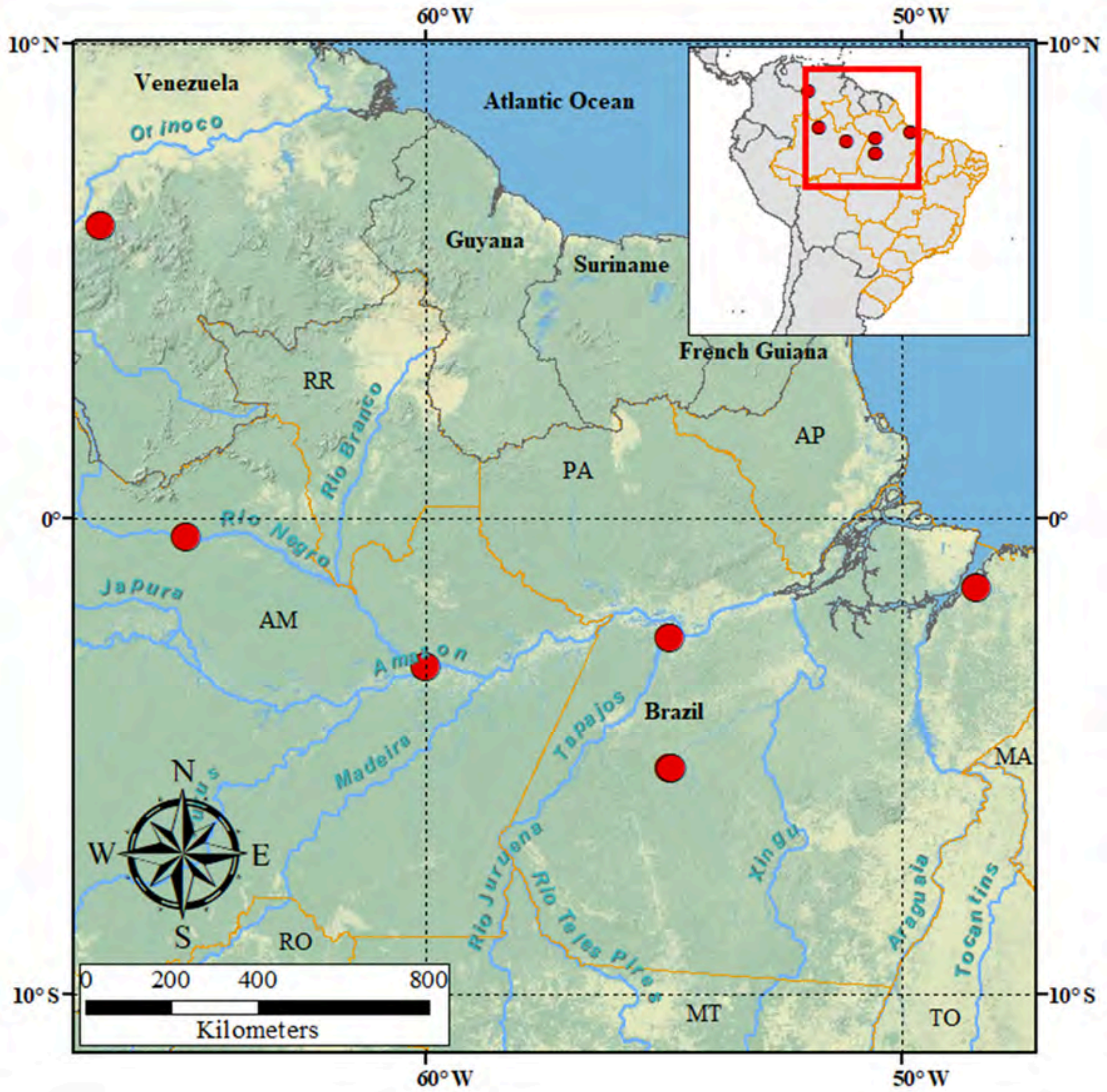


**Figure 53**. Location of the *Typhlophis squamosus* (dots) examined in this study.

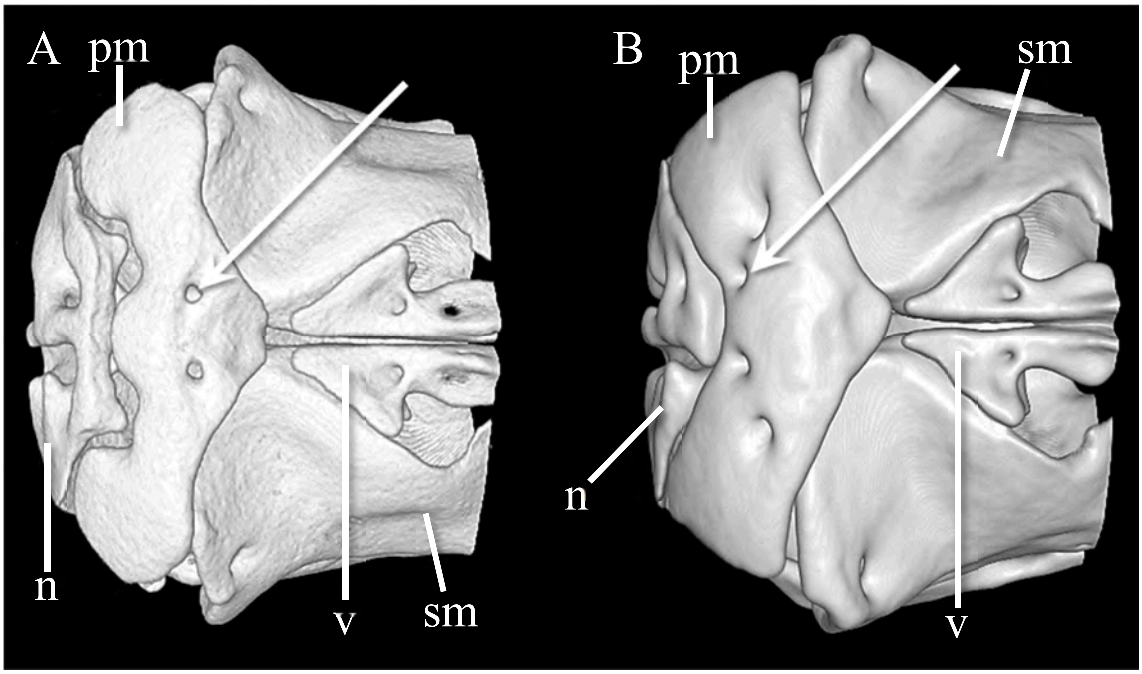


**Figure 54**. Premaxillary palatal foramina. A: State 0, paired (*Liotyphlops argaleus* MCZ R-66383, ventral view). State 1, single. B: State 2, multiple (*Liotyphlops wilderi* MNRJ 15657, ventral view). Anatomical abbreviations: n, nasal; pm, premaxilla; sm, septomaxilla; v, vomer.

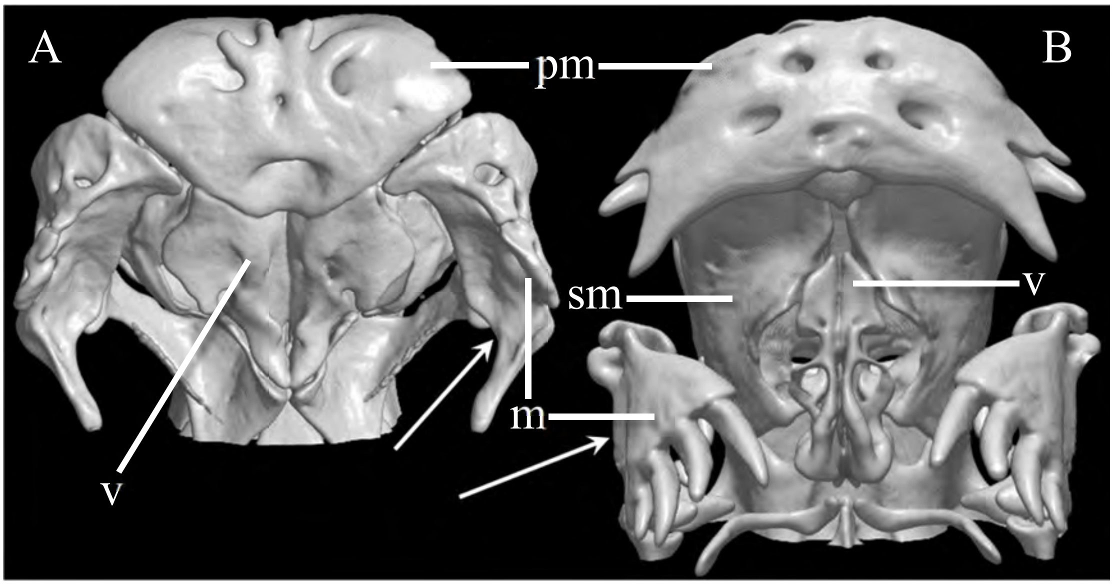


**Figure 55**. 6. Maxilla. A: State 0, alveolar (tooth) row oriented longitudinally (*Trilepida fuliginosa* MCP 4042, ventral view). B: State 1, alveolar (tooth) row oriented transversely (*Anomalepis aspinosus* CM 90254, ventral view). Anatomical abbreviations: m, maxilla; pm, premaxilla; sm, septomaxilla; v, vomer.

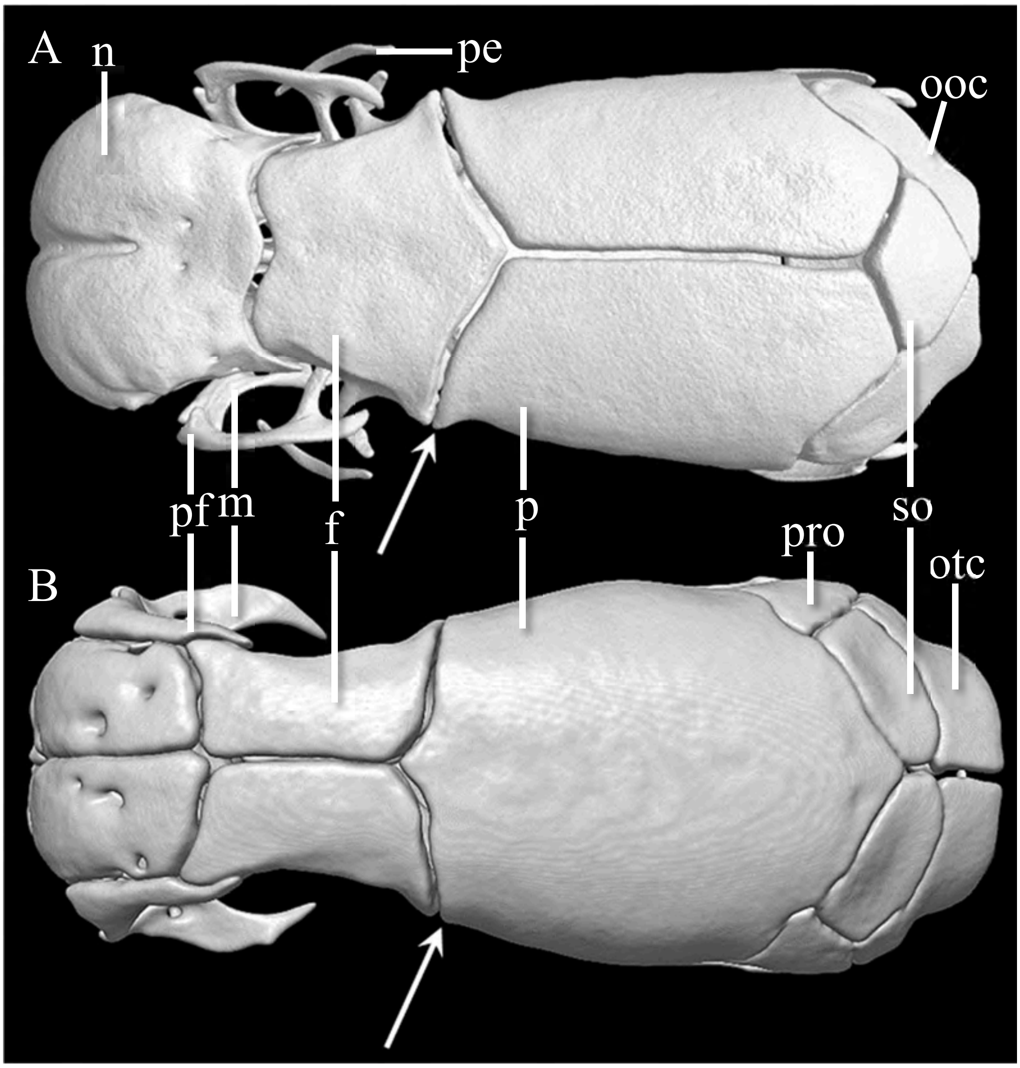


**Figure 56**. 13. Lateral process of parietal. A: State 0, lateral process distinct (*Helminthophis frontalis* MCZ R 55117, dorsal view). B: State 1, lateral process absent (*Epictia munoai* MCP 18696, dorsal view). Anatomical abbreviations: f, frontal; m, maxilla; n, nasal; ooc, otico-occipital (fused prootic + opisthotic + exoccipital); otc, otooccipital (fused exoccipital + opisthotic); p, parietal; pe, postorbital element; pf, prefrontal; pro, prootic.

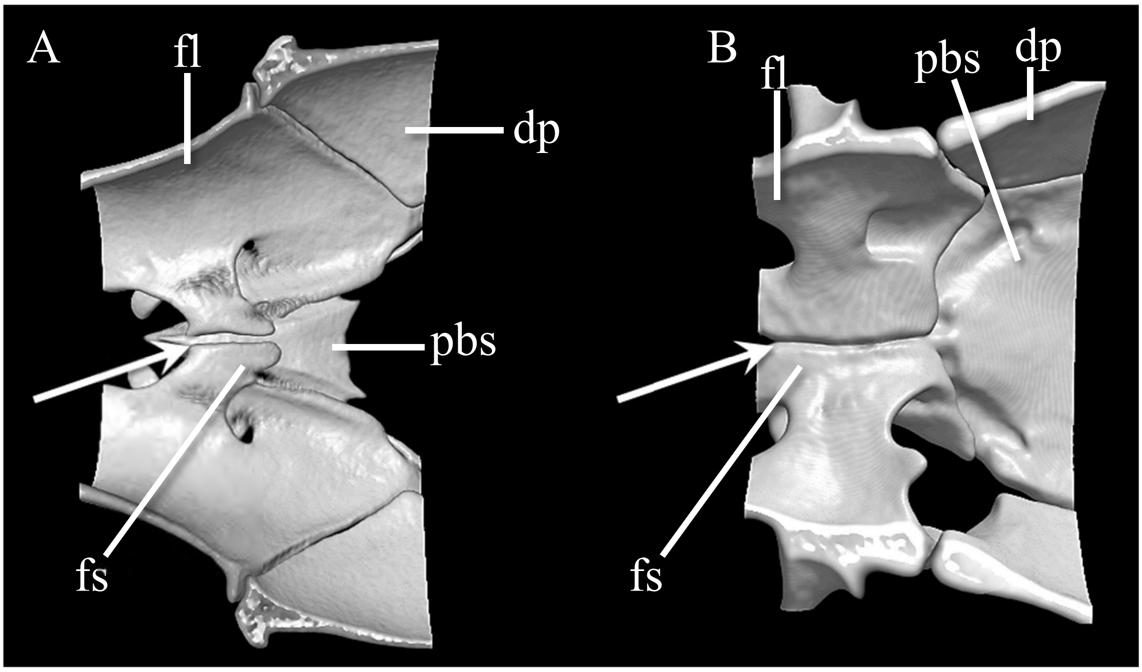


**Figure 57**. Subolfactory (lateral descending) processes of frontal. A: State 0, not contacting one another ventromedially (*Amerotyphlops reticulatus* MCP 18939, frontal axis view). B: State 1, meeting ventromedially, below medial descending processes of frontal if present (*Helminthophis flavoterminatus* AMNH R 59407, frontal axis view). Anatomical abbreviations: dp, descensus parietalis; fl, frontal laterally descending flange; fs, frontal subolfactory process; pbs, parabasisphenoid.

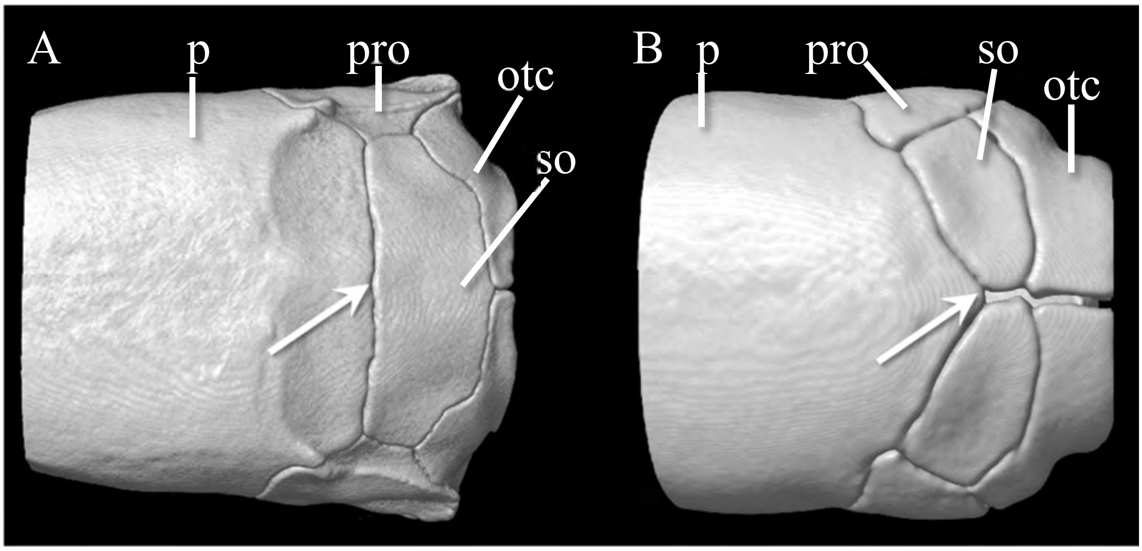


**Figure 58**. Posterior border of parietal. A: State 0, without median projection over supraoccipital (*Anomalepis flavapices* MVZ 163245, dorsal view). B: State 1, with median projection over supraoccipital (*Epictia munoai* MCP 18696, dorsal view). Anatomical abbreviations: otc, otooccipital (fused exoccipital + opisthotic); p, parietal; pro, prootic; so, supraoccipital.

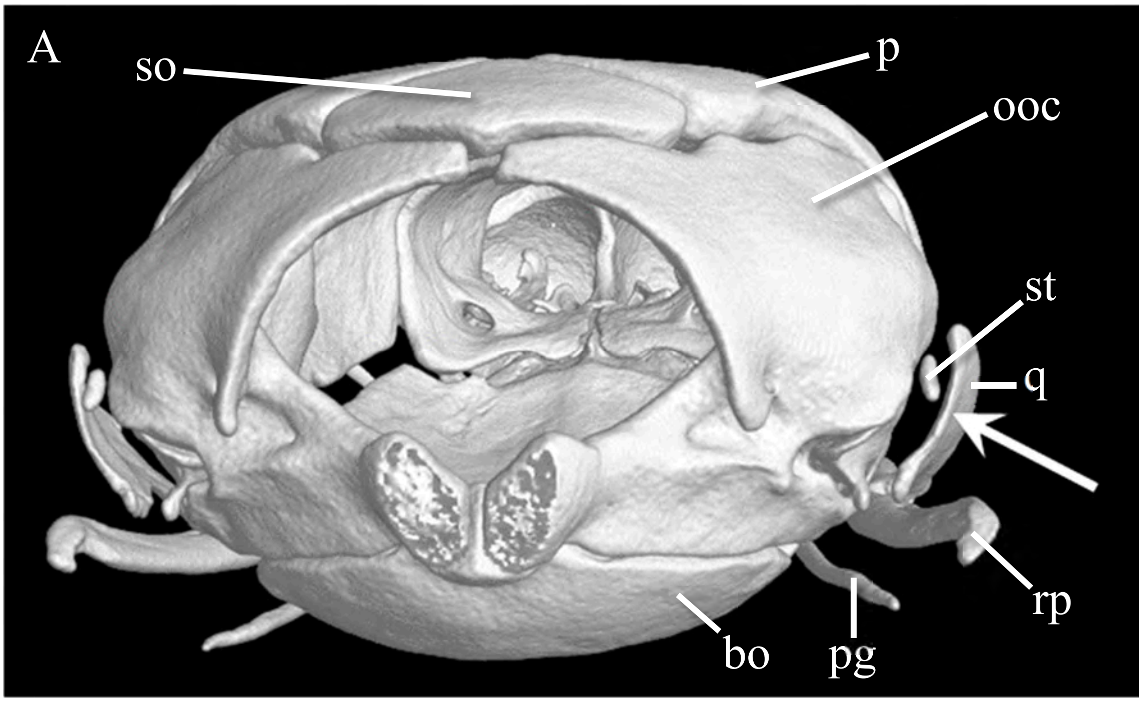


**Figure 59**. Quadrate. A: State 0, without small ossification ('stylohyal') on medial surface, contacting stapes (*Helminthophis frontalis* MCZ R 55117, posterior view). 1, with such ossification. Anatomical abbreviations: bo, basioccipital; ooc, otico-occipital (fused prootic + opisthotic + exoccipital); p, parietal; pg, pterygoid; q, quadrate; so, supraoccipital; st, supratemporal.

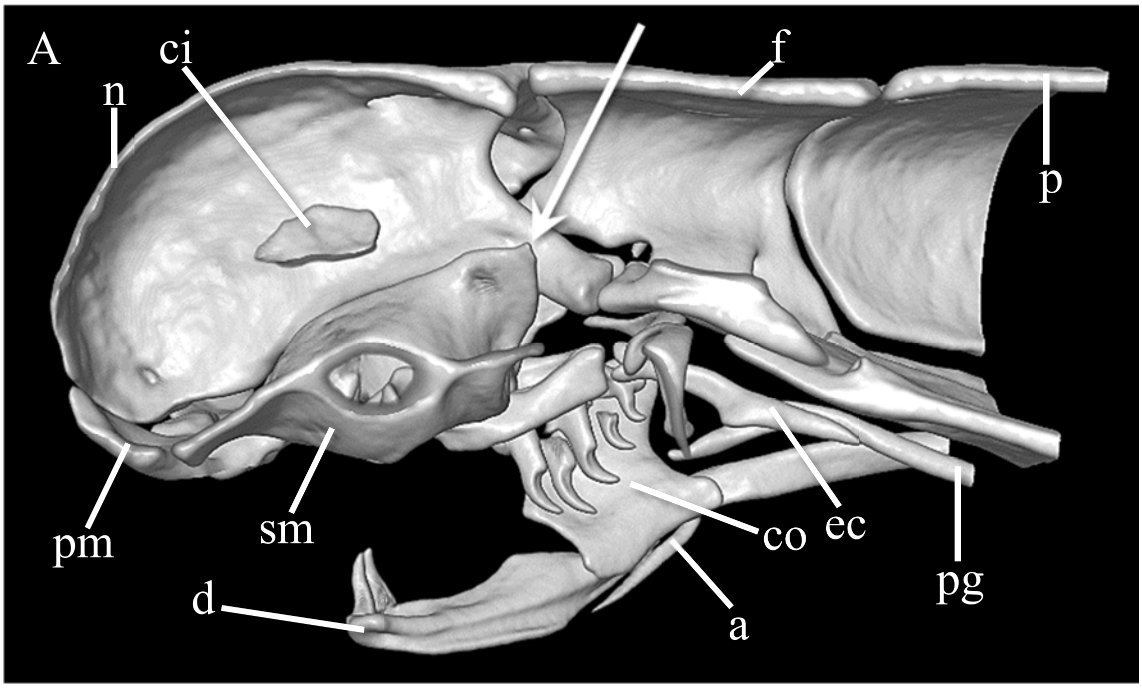


**Figure 60**. Septomaxilla-frontal contact. A: State 0, posteromedial flange of septomaxilla short, not contacting frontal (*Liotyphlops ternetzii* MCP 10881, sagittal view). 1, posteromedial flange of septomaxilla long, contacting frontal adjacent to midline on lower part of interolfactory pillar. Anatomical abbreviations: a, angular; ci, conchal invagination; co, coronoid; d, dentary; ec, ectopterygoid; f, frontal; n, nasal; p, parietal; pg, pterygoid; pm, premaxilla; sm, septomaxilla.

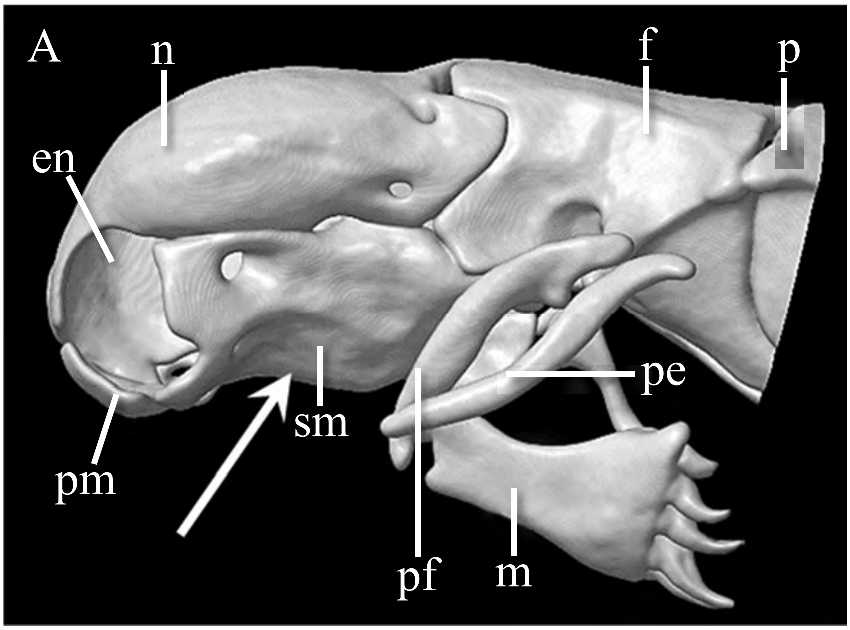


**Figure 61**. Septomaxilla. State 0, maxilla, but not septomaxilla, contributes to posterior border of the external naris. A: State 1, septomaxilla with lateral flange contributing to the posterior border of the external naris (*Helminthophis flavoterminatus* CM 90255, lateral view). Anatomical abbreviations: f, frontal; en, external naris; m, maxilla; n, nasal; p, parietal; pe, postorbital element; pf, prefrontal; pm, premaxilla; sm, septomaxilla.

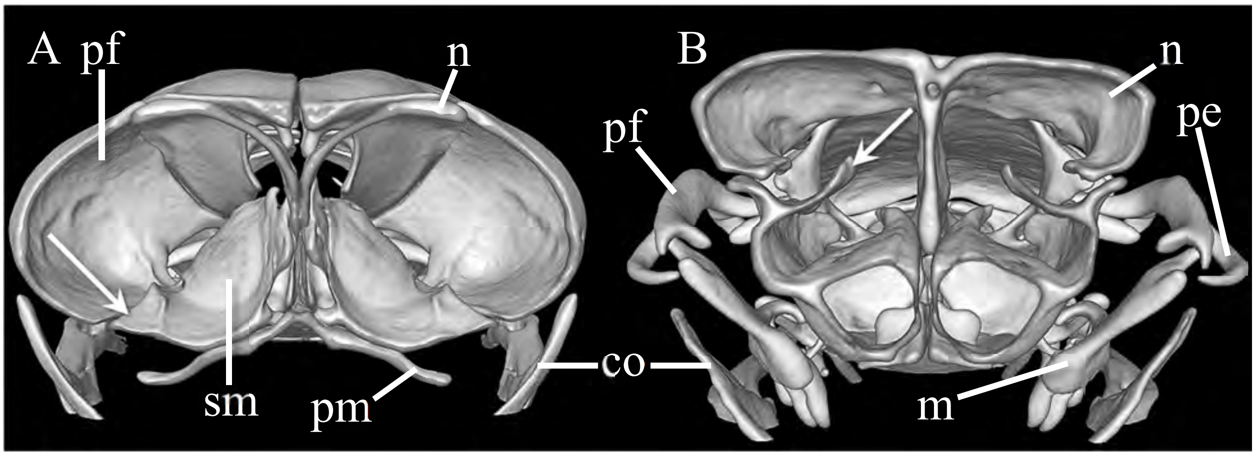


**Figure 62**. Septomaxilla lateral flange: A: State 0, absent (*Amerotyphlops reticulatus* MCP 18939, transverse view). State 1, present. B: State 2, reaches well above roof of vomeronasal organ (*Liotyphlops ternetzii* MCP 10881, transverse view). Anatomical abbreviations: co, coronoid; m, maxilla; n, nasal; pe, postorbital element; pf, prefrontal; pm, premaxilla; sm, septomaxilla.

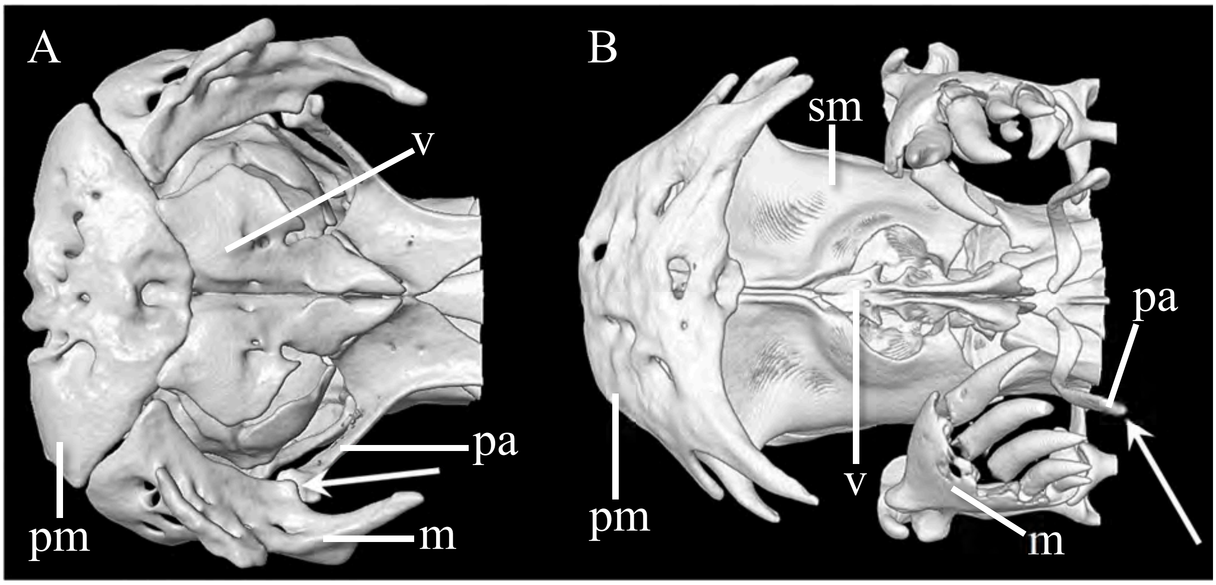


**Figure 63**. Palatine-maxilla contact. State 0, palatine sutured to maxilla. A: State 1, palatine meets maxilla in a loose joint (*Trilepida fuliginosa* MCP 8609, ventral view). B: State 2, palatine does not contact maxilla (*Anomalepis flavapices* MVZ 163245, ventral view). Anatomical abbreviations: m, maxilla; pa, palatine; pm, premaxilla; sm, septomaxilla; v, vomer.

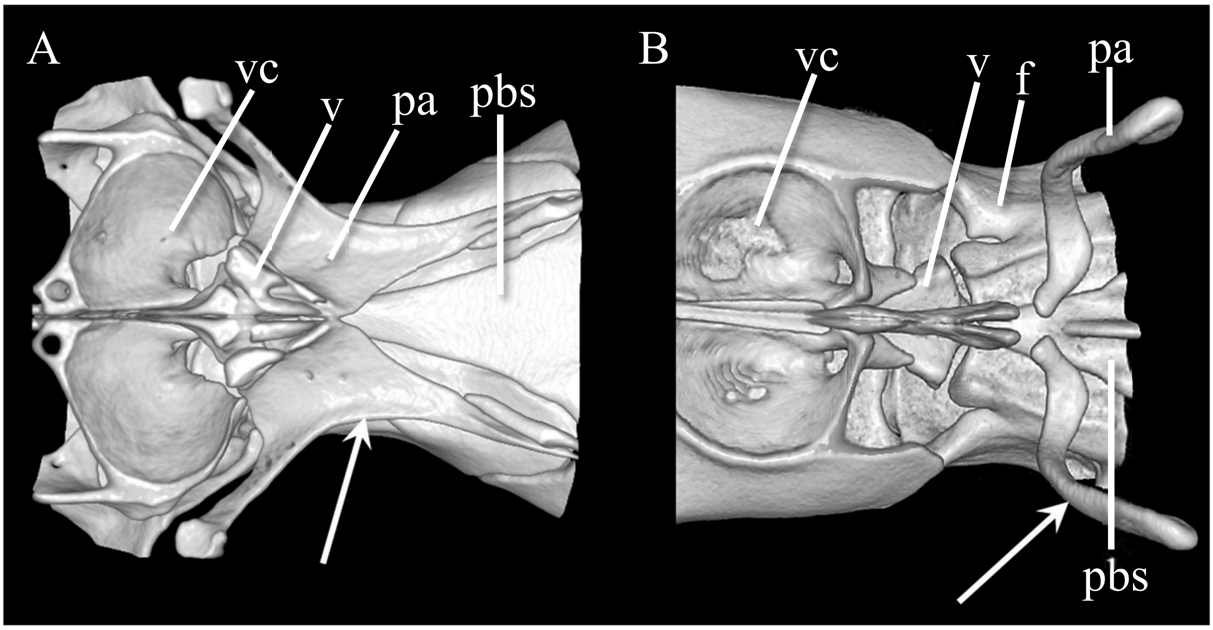


**Figure 64**. Medial (choanal or vomerine) process of palatine. A: State 0, anteroposteriorly broad plate of bone (*Trilepida fuliginosa* MCP 8609, ventral view). B: State 1, narrow finger-like process (*Anomalepis flavapices* MVZ 163245, ventral view). Anatomical abbreviations: f, frontal; pa, palatine; pbs, parabasisphenoid; v, vomer; vc, vomeronasal cupola.

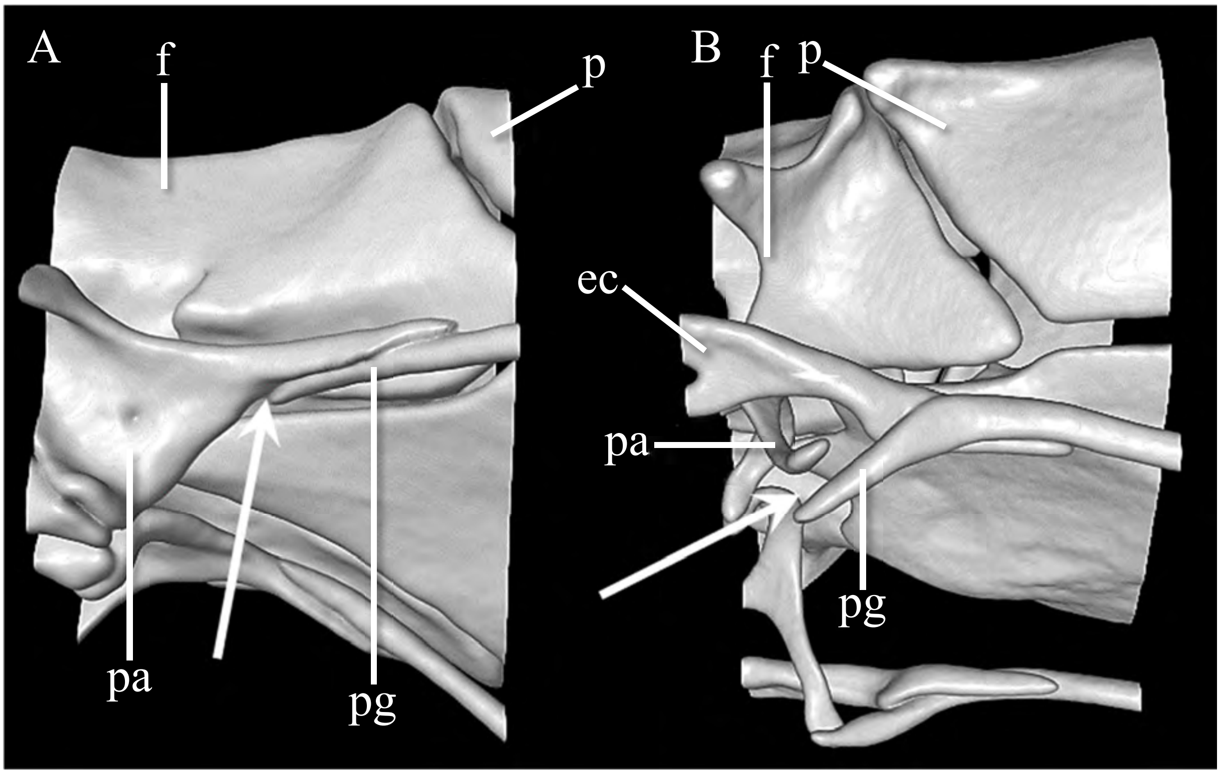


**Figure 65**. Palatine pterygoid contact[N]. A: State 0, palatine contacts pterygoid (*Epictia munoai* MCP 18696, ventrolateral view). B: State 1, palatine does not contact pterygoid (*Liotyphlops ternetzii* MCP 10881, ventrolateral view). Anatomical abbreviations: ec, ectopterygoid; f, frontal; p, parietal; pa, palatine; pg, pterygoid.

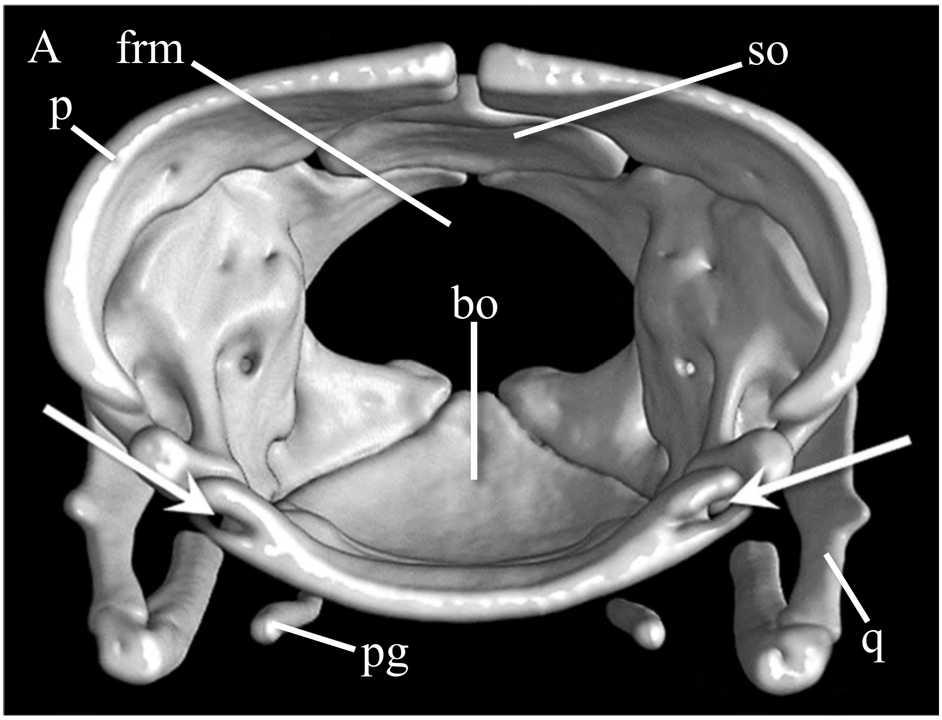


**Figure 66**. Vidian canals. A: State 0, symmetrical (*Liotyphlops albirostris* CM 39565, transverse view). State 1, asymmetrical, left larger than right or vice versa. Anatomical abbreviations: bo, basioccipital; frm, foramen magnum; p, parietal; pg, pterygoid; q, quadrate; so, supraoccipital.

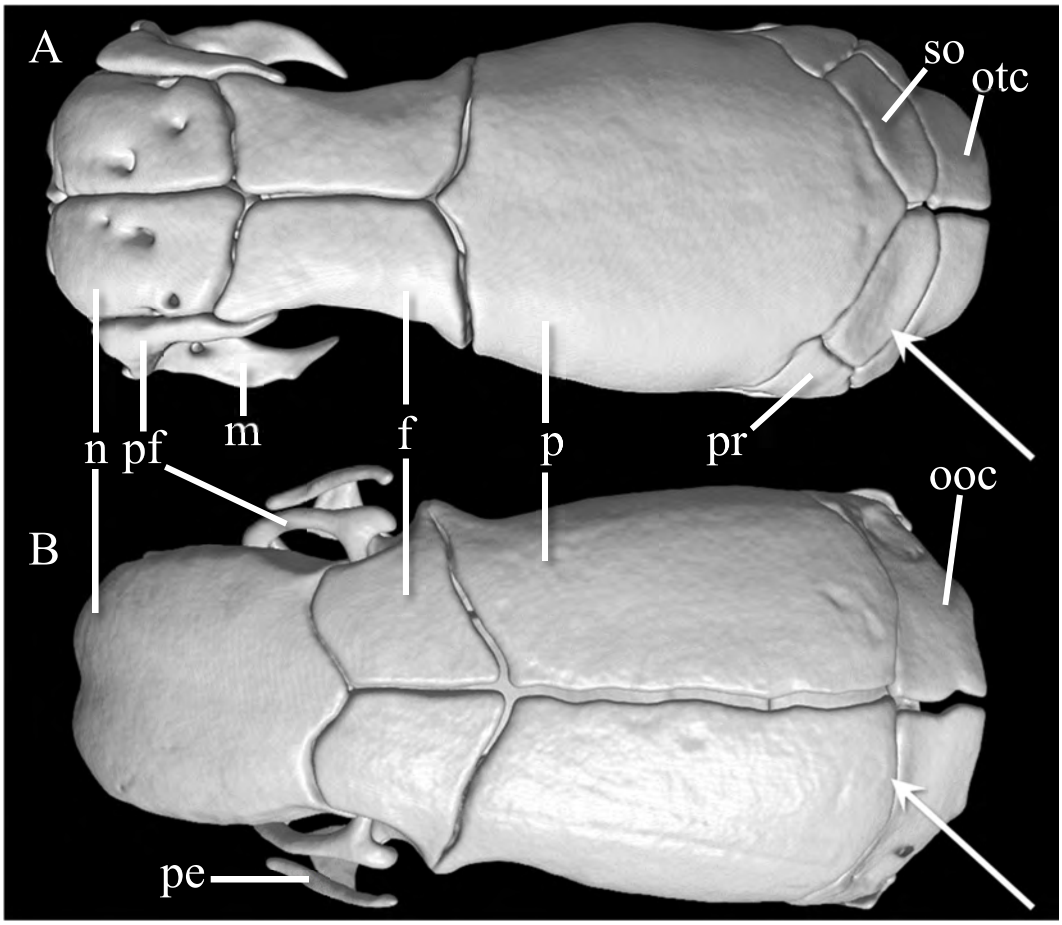


**Figure 67**. Supraoccipital[N]. A: State 0, present (*Epictia munoai* MCP 18696, dorsal view). B: State 1, absent (*Typhlophis squamosus* AMNH R 131787, dorsal view). Anatomical abbreviations: f, frontal; m, maxilla; n, nasal; ooc, otico-occipital (fused prootic + opisthotic + exoccipital); otc, otooccipital (fused exoccipital + opisthotic); p, parietal; pe, postorbital element; pf, prefrontal; so, supraoccipital.

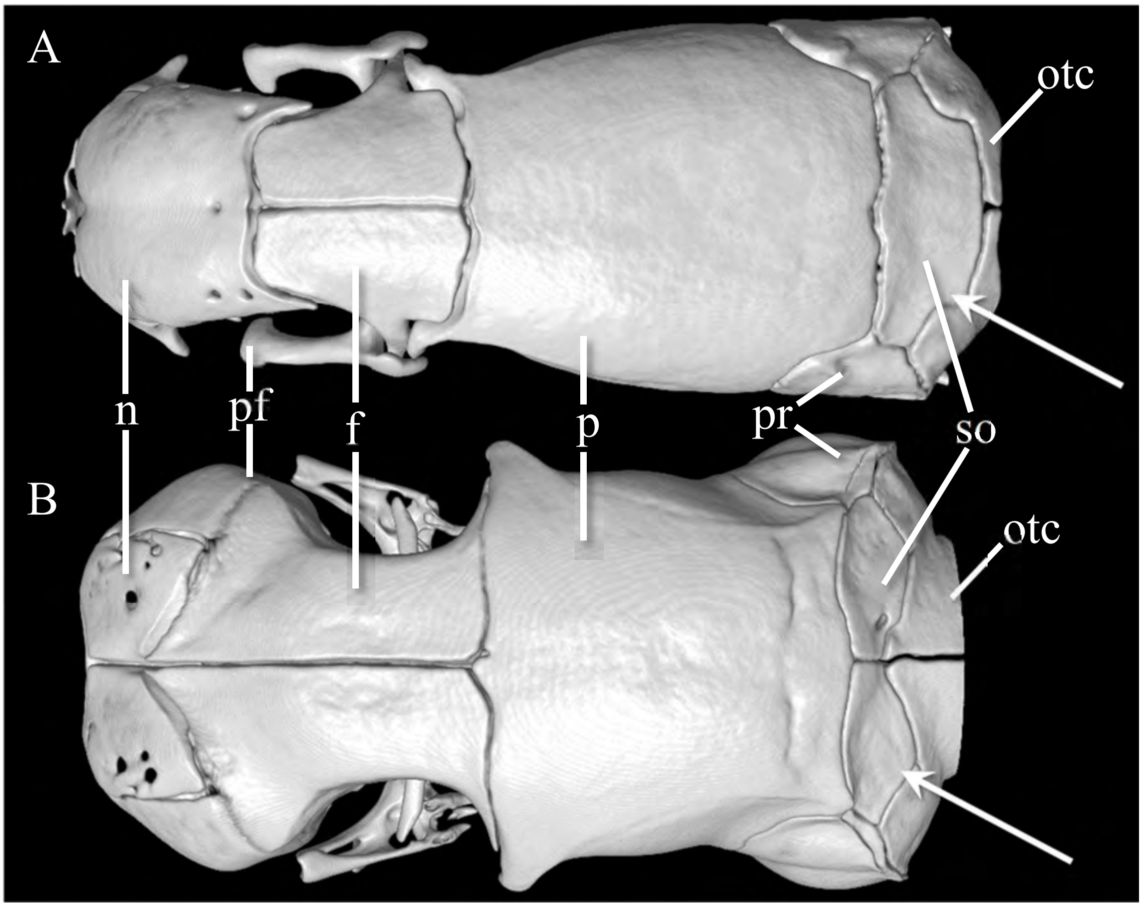


**Figure 68**. Supraoccipital. A: State 0, single (*Anomalepis aspinosus* CM 90254, dorsal view). B: State 1, double (*Amerotyphlops brongersmianus* MCP 19088, dorsal view). Anatomical abbreviations: f, frontal; n, nasal; otc, otooccipital (fused exoccipital + opisthotic); p, parietal; pf, prefrontal; pr, prootic; so, supraoccipital.

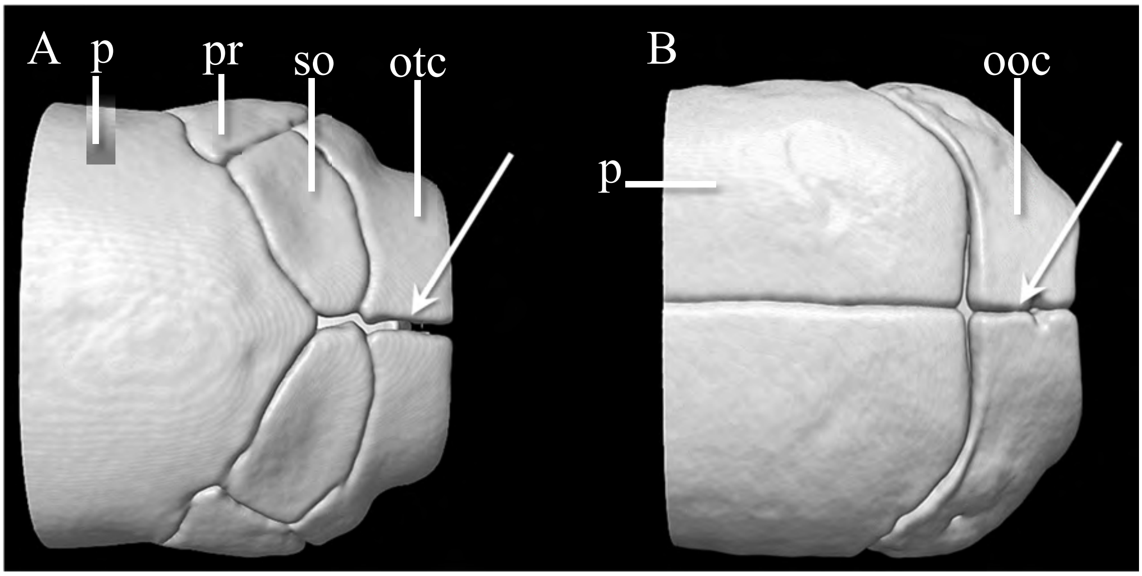


**Figure 69**. Exoccipital separation dorsal to foramen magnum. State 0, exoccipitals widely separated above foramen magnum. A: State 1, exoccipitals narrowly separated above foramen magnum[N] (*Epictia munoai* MCP 18696, dorsal view). State 2, exoccipitals with point contact above foramen magnum. B: State 3, exoccipitals in extensive median contact above foramen magnum (*Helminthophis flavoterminatus* CM 90255, dorsal view). Anatomical abbreviations: ooc, otico-occipital (fused prootic + opisthotic + exoccipital); otc, otooccipital (fused exoccipital + opisthotic); p, parietal; pr, prootic; so, supraoccipital.

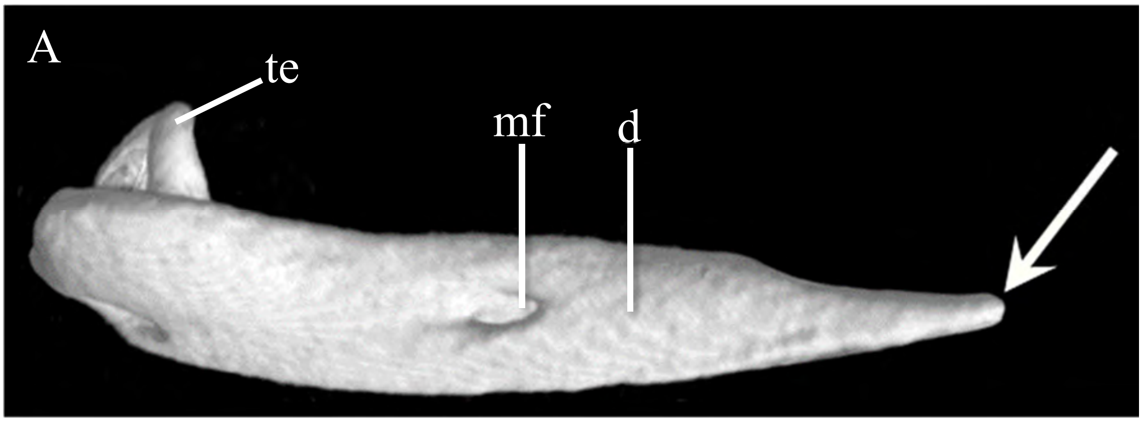


**Figure 70**. Posterolateral margin of dentary. A: State 0, notch absent, posterolateral margin of dentary straight or slightly concave, dorsoposterior and ventroposterior processes indistinct *(Liotyphlops argaleus* MCZ R 66383, lateral view). State 1, with shallow notch, processes short. State 2, with deep notch, processes long. Anatomical abbreviations: d, dentary; mf, mental foramen; te, teeth.

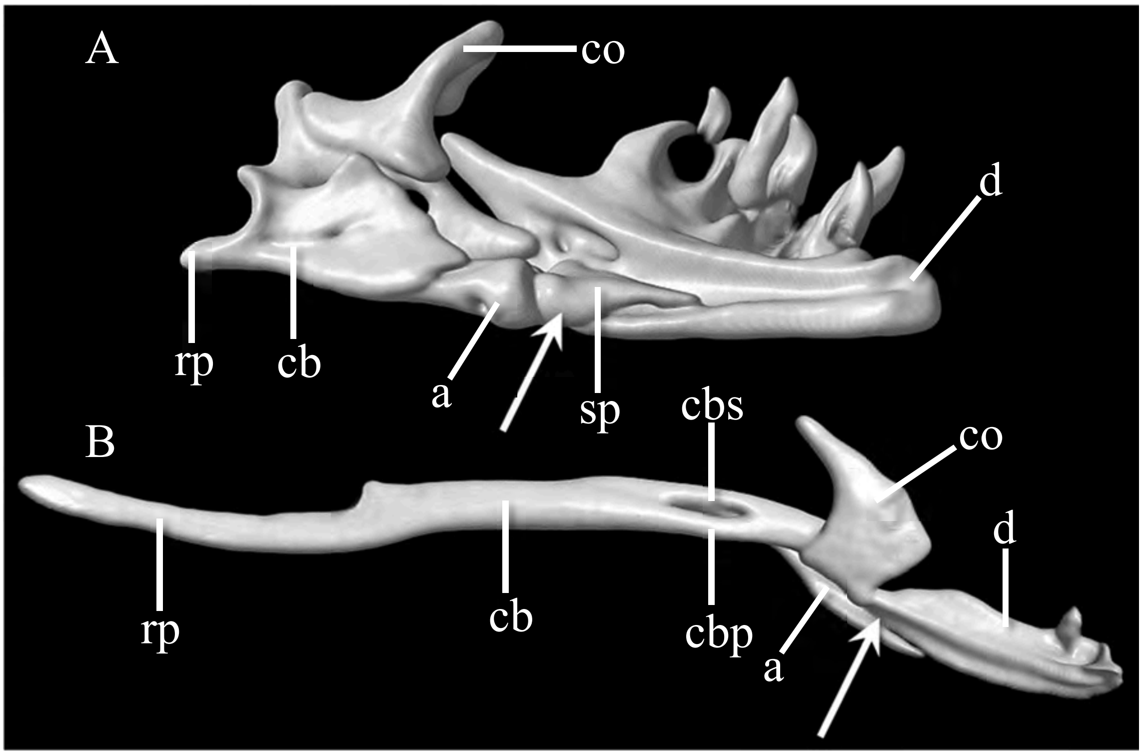


**Figure 71**. Splenial. A: State 0, splenial present as discrete element (*Epictia munoai* MCP 18696, lateral view of mandible). B: State 1, splenial not present as discrete element (*Helminthophis praeocularis* AMNH R 62942, lateral view of mandible). Anatomical abbreviations: a, angular; cb, compound bone; cbp, compound bone prearticular component; cbs, compound bone surangular component; co, coronoid; d, dentary; rp, retroarticular process; sp, splenial.

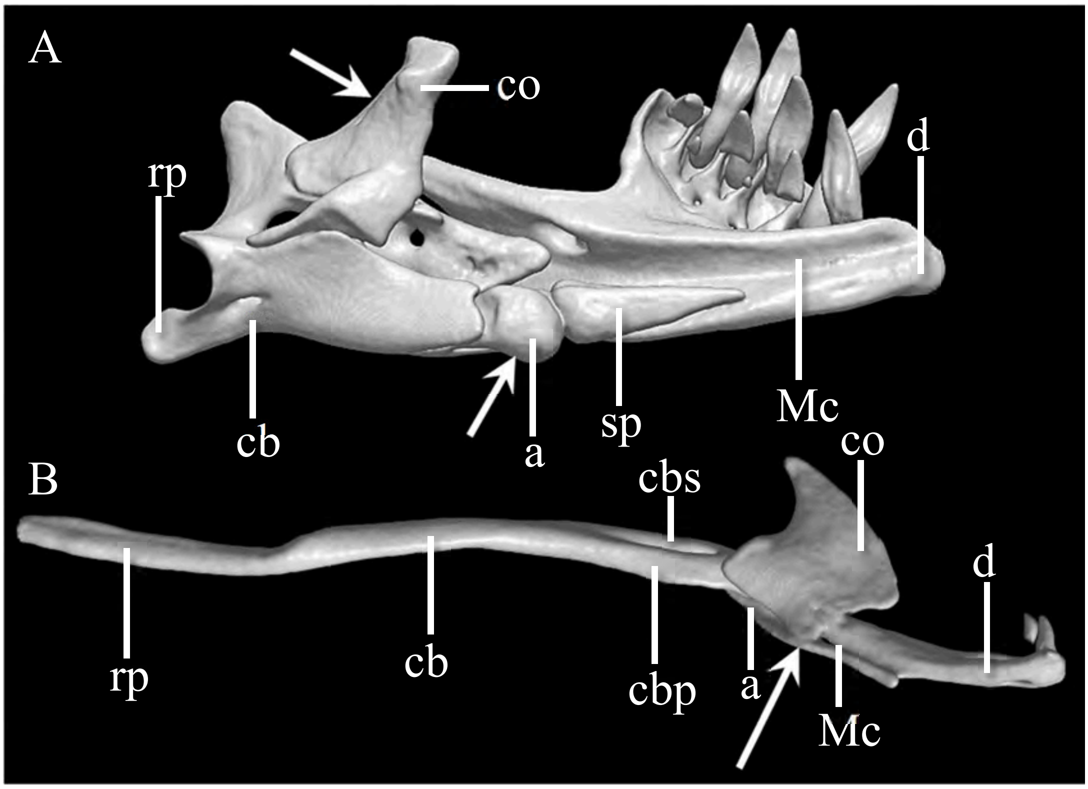


**Figure 72**. Coronoid-angular contact. A: State 0, coronoid and angular separated by prearticular, or prearticular portion of compound bone (*Trilepida fuliginosa* MCP 8609, lateral view of mandible). B: State 1, coronoid contacts angular (*Typhlophis squamosus* AMNH R 131787, lateral view of mandible). Anatomical abbreviations: a, angular; cb, compound bone; cbp, compound bone prearticular component; cbs, compound bone surangular component; co, coronoid; d, dentary; Mc, Meckel's canal; rp, retroarticular process; sp, splenial.

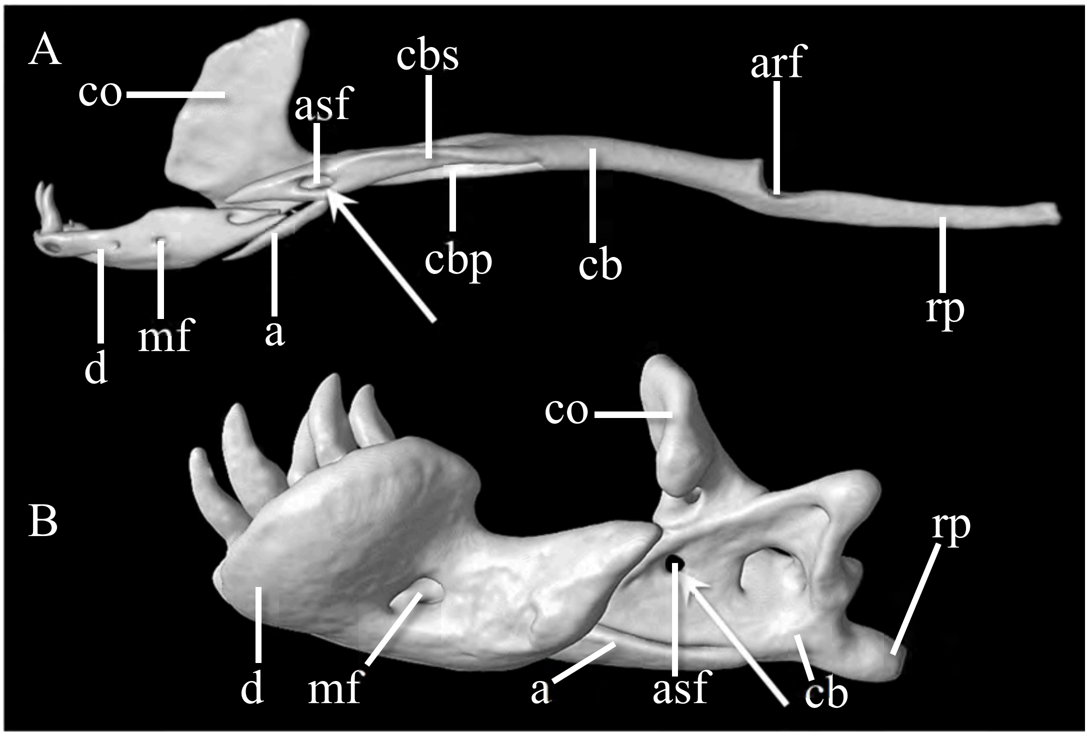


**Figure 73**. Anterior surangular foramen. A: State 0, situated posteriorly, below apex of coronoid process or more posterior (*Liotyphlops ternetzii* MCP 10881, lateral view of mandible). B: State 1, situated anteriorly, between apex and anterior limit of coronoid process (*Trilepida fuliginosa* MCP 4042, lateral view of mandible). 2, situated far anteriorly, in front of anterior limit of coronoid process. Anatomical abbreviations: a, angular; arf, articular fossa; asf, anterior surangular foramen; cb, compound bone; cbp, compound bone prearticular component; cbs, compound bone surangular component; co, coronoid; d, dentary; mf, mental foramen; rp, retroarticular process.

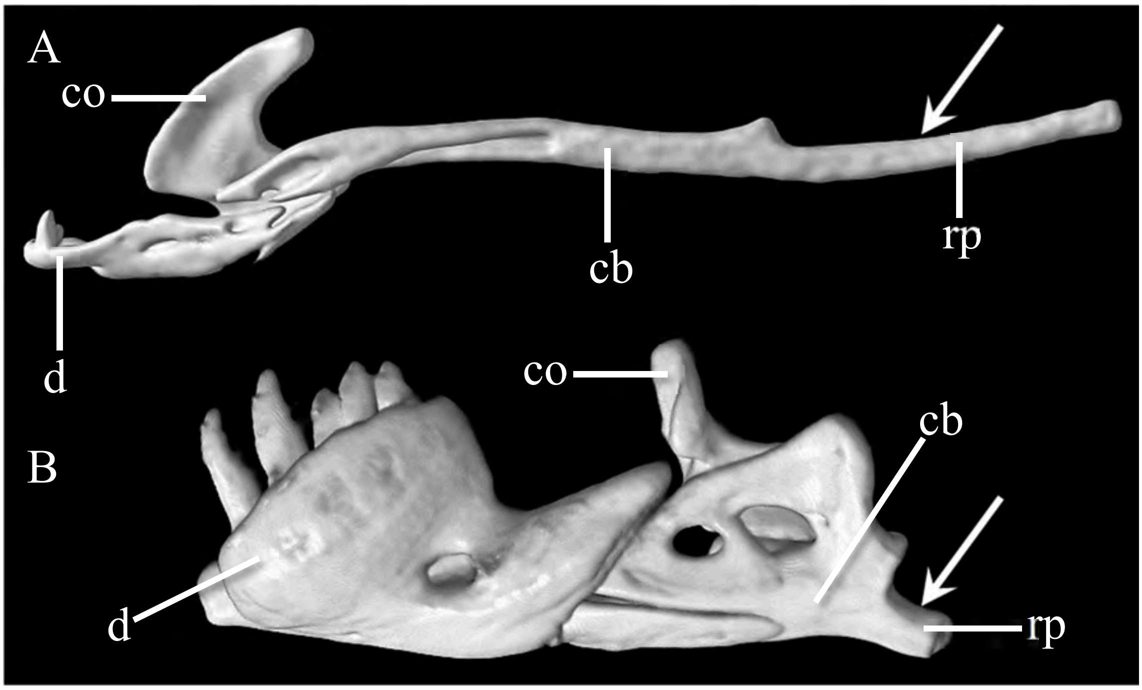


**Figure 74**. Retroarticular process length. A: State 0, long, longer than articular facet (*Liotyphlops schubarti* ZUEC REP 2278, lateral view of mandible). B: State 1, short, not longer than articular facet (*Trilepida koppesi* MCP 19227, latera view of mandible). Anatomical abbreviations: cb, compound bone; co, coronoid; d, dentary; rp, retroarticular process.

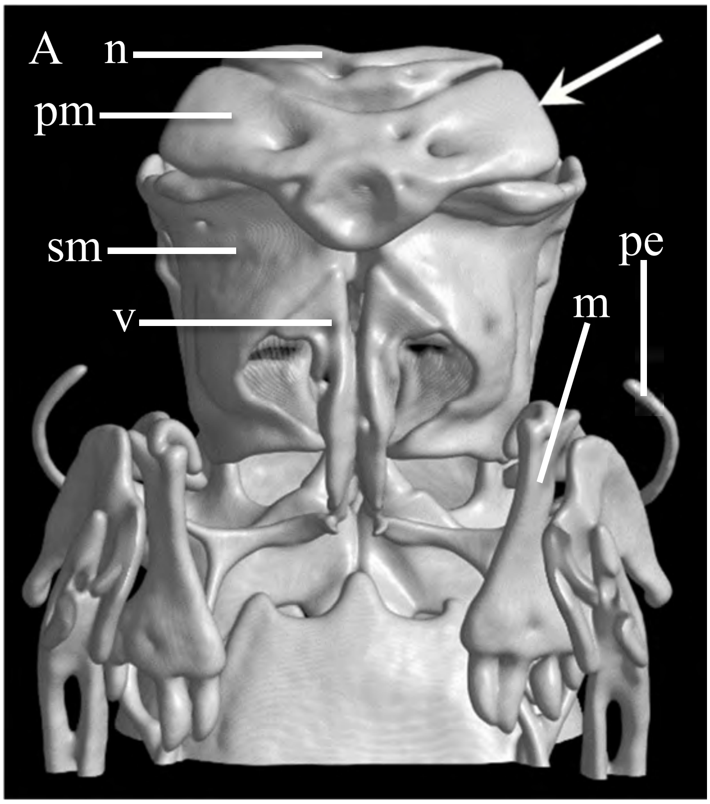


**Figure 75**. Premaxillary teeth. State 0, present. A: State 1, absent (*Liotyphlops schubarti* ZUEC REP 2278, ventral view). Anatomical abbreviations: m, maxilla; n, nasal; pe, postorbital element; pm, premaxilla; sm, septomaxilla; v, vomer.

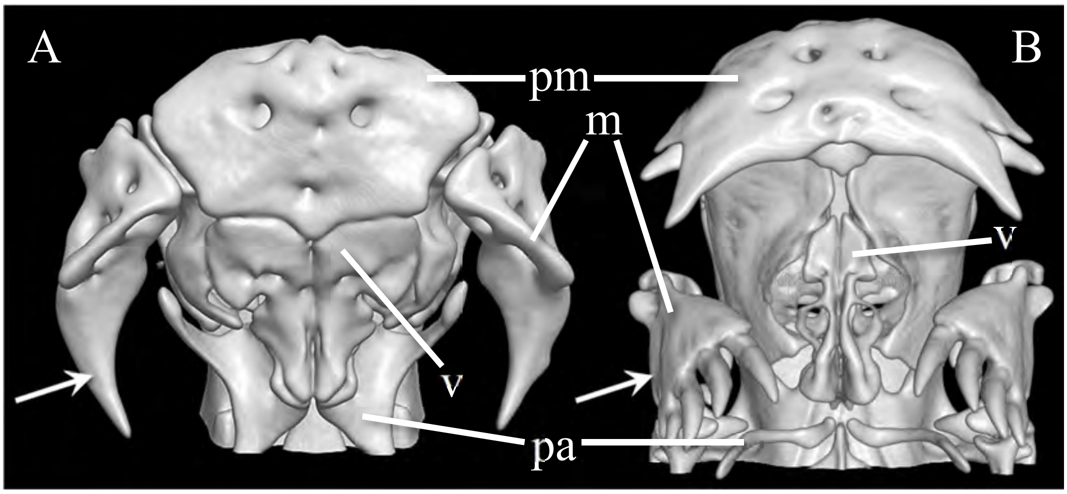


**Figure 76**. Maxillary teeth. A: State 0, ausent (*Epictia munoai* MCP 18696, ventral view). B: State 1, present (*Anomalepis aspinosus* CM 90254, ventral view). Modified. Anatomical abbreviations: m, maxilla; pa, palatine; pm, premaxilla; v, vomer.


**Figure 77**. Dentary teeth. A: State 0, present (*Helminthophis frontalis* MCZ R 55117, lateral view of mandible). B: State 1, absent (Amerotyphlops reticulatus MCP 18939, lateral view of mandible). Modified. Anatomical abbreviations: d, dentary; mf, mental foramen.

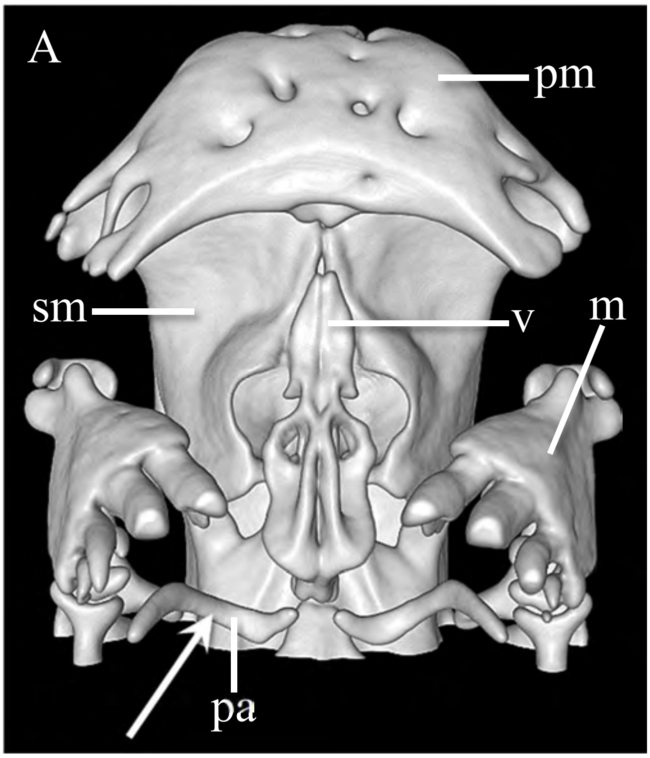


**Figure 78**. Palatine teeth. A: State 0, absent (*Anomalepis mexicanus* AMNH R 119069, ventral view). State 1, present. Anatomical abbreviations: m, maxilla; pa, palatine; pm, premaxilla; sm, septomaxilla; v, vomer.

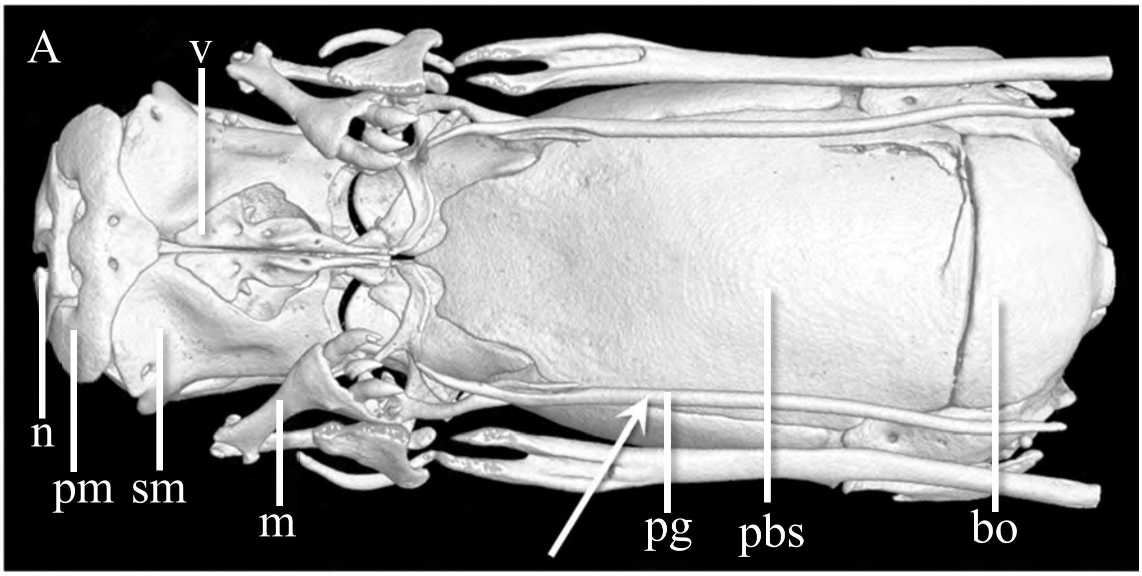


**Figure 79**. Pterygoid teeth. State 0, present. A: State 1, absent (*Liotyphlops argaleus* MCZ R 66383, ventral view). Anatomical abbreviations: bo, basioccipital; m, maxilla; n, nasal; pbs, parabasisphenoid; pg, pterygoid; pm, premaxilla; sm, septomaxilla; v, vomer.

A

**Figure 80**. Midventral scales. A: State 0, undifferentiated (*Liotyphlops ternetzii* MCP 10878, ventral view). State 1, slightly expanded transversely, remaining much narrower than body width. State 2, greatly expanded transversely, approaching body width.

A

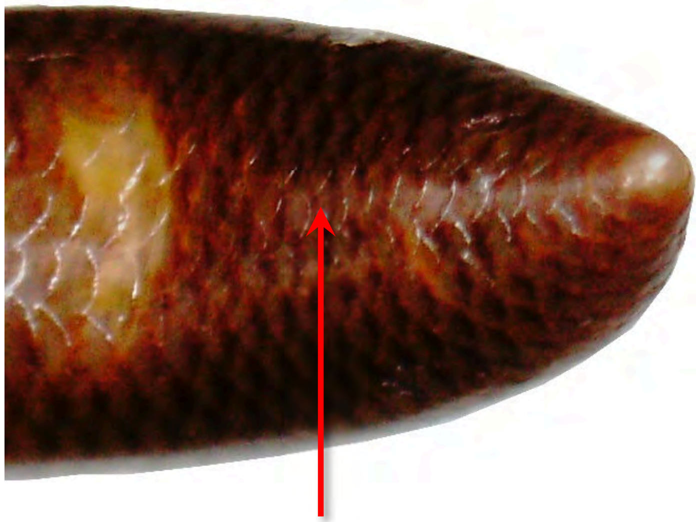

**Figure 81**. Subcaudals. A: State 0, undifferentiated (*Liotyphlops argaleus* MCZ R-66383 paratype, ventral view). State 1, single row. State 2, paired row.

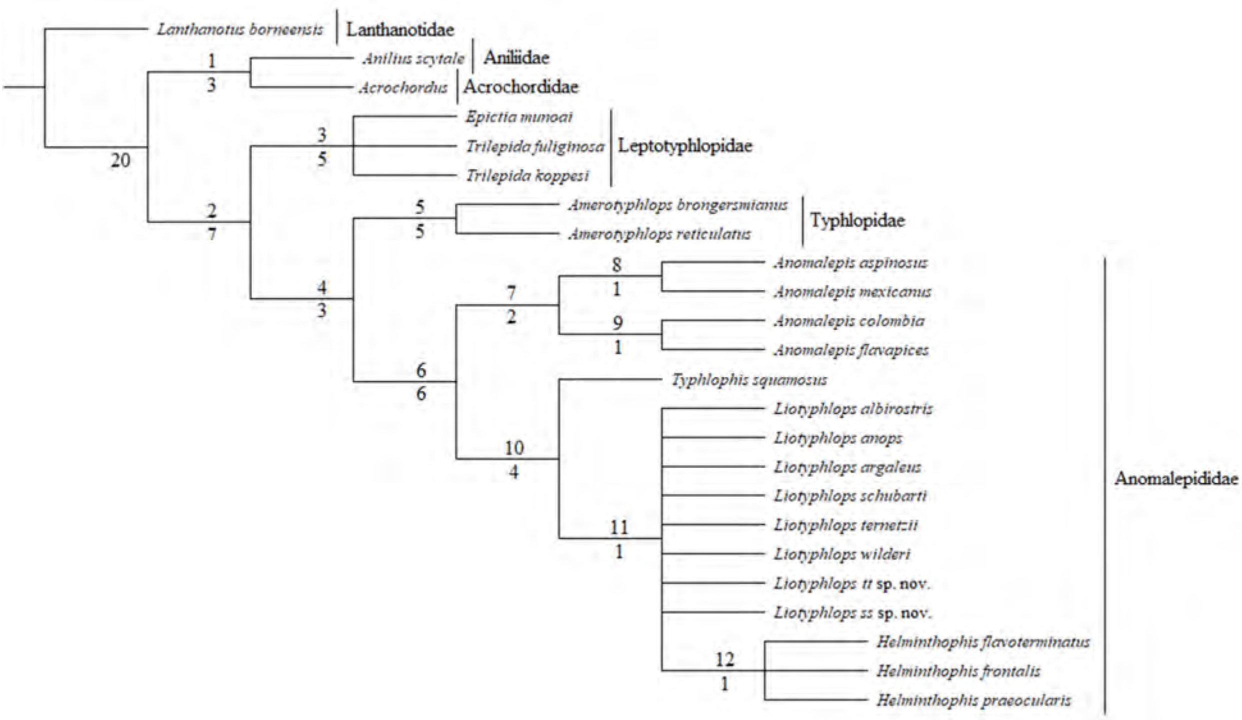


**Figure 82**. Strict consensus tree showing phylogenetic relationships among the species of Anomalepididae. Numbers above branches are node numbers (see Appendix I for transformations in each node). Values below branches are Bremer support. Length = 134 steps, Ci = 0.64, and Ri = 0.78.

MARISTA PUCRS

Pontifícia Universidade Católica do Rio Grande do Sul
Pró-Reitoria de Graduação
Av. Ipiranga, 6681 - Prédio 1 - 3º. andar
Porto Alegre - RS - Brasil
Fone: (51) 3320-3500 - Fax: (51) 3339-1564
E-mail: prograd@pucrs.br
Site: www.pucrs.br