



The status of the anomalepidid snake *Liotyphlops albirostris* and the revalidation of three taxa based on morphology and ecological niche models

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Abstract

Liotyphlops is a genus of blindsnakes distributed in Central and South America. We reviewed specimens of *Liotyphlops albirostris* along its current distribution range and, based on morphological data and ecological niche modeling analyses, we restrict the geographical range of *L. albirostris* and validate three previously described species. In this revision, we describe the morphological variation in the populations from Panama, Colombia, Ecuador, and Venezuela, and propose a new taxonomic arrangement. We revalidate three previous synonyms of *L. albirostris* to full species status, while dividing the populations from Colombia in two subspecies—one attributed to a previously recognized species from the Caribbean region, and a new one from the Andean region. The new species differs from *L. albirostris* from Panama in cephalic scale arrangements that effectively reduces the previously reported variability of these scales in *L. albirostris*. We also explore some osteological differences that are congruent with the variation observed. We hope that the recognition of these new species better represents the diversity within *Liotyphlops*, helping to bring these new species out of their cryptic status so that they will be considered in future conservation efforts.

KEYWORDS

blind snake, Colombia, morphology, osteology

1 | INTRODUCTION

Anomalepididae Taylor 1939, is a family of neotropical snakes distributed in southern Central America and South America. These snakes can reach up to 380 mm in total length, but most are smaller. Their tiny size and cryptozoic lifestyle make

them difficult to find. Anomalepididae encompasses four genera, including *Anomalepis* Jan 1860 (four spp.), *Helminthophis* Peters 1860 (three spp.), *Liotyphlops* Peters 1881 (12 spp.), and the monotypic *Typhlophis* Fitzinger 1843.

The genus *Liotyphlops* is distributed in Central and South America, from Costa Rica to Argentina. Members

of this group are characterized by the distinctive enlarged rostral scale in contact with the frontal scale, which prevents contact between the prefrontals on the dorsum of the head (Dixon & Kofron, 1983; Peters & Orejas-Miranda, 1970; Natera-Mumaw, Esqueda-Gonzalez, & Casteláin-Fernandez, 2015). The latest taxonomic revision of the genus based on external features (Dixon & Kofron, 1983), lumped 12 species into five, removed one species from synonymy, and described one new species (viz., *L. albirostris*, *L. anops*, *L. argaleus*, *L. beui*, *L. schubarti*, *L. ternetzii*, and *L. wilderi*). In the following 37 years after Dixon and Kofron's (1983) revision, the number of taxa has increased to 12 again, including *L. trefauti* (Freire, Caramaschi, & Argolo, 2007), *L. haadi* (Silva-Haad, Franco, & Maldonado, 2008), *L. caissara* (Centeno, Sawaya, & Germano, 2010), and *L. sousai* and *L. taylori* (Santos & Reis, 2018).

Liotyphlops albirostris (the type species of the genus, originally described as *Rhinyotyphlops albirostris* Peters 1858), is a small-sized blindsnake (70–223 mm, \bar{x} = 144.9 mm, Dixon & Kofron, 1983) reported in Central America and the northwest of South America, known from Costa Rica, Panama, Colombia, Venezuela, and Curacao and Ecuador (one individual from Guayas province was originally classified as *Helminthophis petersii* [Boulenger, 1889], and *L. petersii* [Dunn, 1944], but later placed within *L. albirostris* by Dixon & Kofron, 1983). Additionally, other species—including *Helminthophis bondensis* Griffin 1916, *L. cucutae* Dunn 1944, *L. caracasensis* Roze 1952, and *L. rowani* Smith and Grant 1958—have all been synonymized with *L. albirostris*, resulting in a species with high morphological variation and a wide distributional range.

Molecular data, a critical tool in taxonomy nowadays, is available only for the anomalepidids *L. albirostris* from Panama, *L. beui* and *Typhlophis squamosus*, which have been included in higher level phylogenetic analyses of snakes and squamates (e.g., Burbrink et al., 2020; Figueroa, McKelvy, Grismer, Bell, & Lailvaux, 2016; Pyron, Burbrink, & Wiens, 2013; Vidal et al., 2010). The taxonomy of these snakes hence relies strongly on morphological analyses of external characters, especially scales. However, characters such as size of the scales in proportion to the body, make it difficult to find reliable taxonomic features (Dixon and Kofron, 1983). Following the morphological species groups established by Dixon & Kofron (1983), there are three main groups within *Liotyphlops*: (a) snakes with four scales at the posterior margin of the prefrontal scale (*L. anops*, *L. argaleus*, and *L. trefauti*), (b) snakes with one scale contacting the posterior margin of the nasal, between the prefrontal and the second supralabial (*L. albirostris*, *L. caissara*, *L. haadi* and *L. wilderi*), and (c) snakes with two scales contacting

the posterior margin of the nasal, between the prefrontal and the second supralabial (*L. beui*, *L. schubarti*, and *L. ternetzii*). Nonetheless, some of the recently described species do not fit into any of these groups (Santos & Reis, 2018). In recent years, anomalepidid snakes have been re-studied using X-ray microtomography (microCT) data (Santos, 2018; Santos & Reis, 2018, 2019; Rieppel, Kley, & Maisano, 2009; Strong, Scherz, & Caldwell, 2021), offering a great opportunity to perform skull anatomy comparisons and increasing the amount of available phenotypic data for taxonomic purposes.

Individuals referred to *Liotyphlops albirostris* (Dixon & Kofron, 1983) show a light spot on the tip of the snout and reduced eyes covered by the cephalic scales (Savage, 2002). In Colombia, specimens assigned to this species have been reported in the Caribbean region, but there are now several records that extend its distribution inland, reaching well into the Andean region, and possibly extending into the equatorial Andes. Some of the earliest inland specimens were collected by the missionary and naturalist Antoine Rouhaire, also known as Hermano Niceforo María, who collected this species in the Magdalena Valley, near the locality of Honda (MCZ R-29599, 1929) and in Cúcuta, in the Cordillera Oriental near Venezuela (MLS 38 in 1936, and MCZ R-67930 on June 29, 1962). In recent years additional records have been found in the inter-Andean valleys of Colombia at elevations up to 1,620 m above sea level (MASL).

These populations have remained understudied for over 40 years, but occasionally have been collected in the northern part of Colombia; between the years 2013 and 2019, 20 specimens were collected. In the year 2002, a congregation of eight snakes was discovered in a more southern locality, near Roldanillo in the Valle del Cauca, Colombia by some of the authors (RT, DOD, JDD). Following these collections in the Valle del Cauca, several field trips led by another author (WB-G) found specimens at five additional localities in the inter-Andean valleys of Colombia. While reviewing this new material we noticed marked differences with specimens from the type locality (Panama, Veragua). To verify the status of this species, we followed three approaches: (a) reviewed previously described species now part of *L. albirostris* using museum specimens and the literature, and re-evaluated their taxonomic status; (b) compared the scale characters (meristic and morphometric) in the new material with specimens from the type locality, including the holotype of *L. albirostris*; (c) microCT scanned and compared four specimens from the new locality (Valle del Cauca, Colombia) with available osteological descriptions of *L. albirostris* (Dunn & Tihen, 1944; Haas, 1964; Rieppel et al., 2009) and published CT scan images; (d) collected geographic coordinates of museum specimens and

generated ecological niche models for all the species based on confirmed specimens. Using these sources of data we hypothesize that the northern populations from South America represent three different species, separated from *L. albirostris* from Panama; one of the South American species is also further divided into two main subspecies, all of which we describe herein.

2 | MATERIALS AND METHODS

Referred and examined material are housed in the following collections: American Museum of Natural History, New York, USA (AMNH); The Academy of Natural Sciences Drexel University, Philadelphia, USA (ANSP); California Academy of Sciences, San Francisco, USA (CAS); Carnegie Museum of Natural History, Pittsburgh, USA (CM); Colección de Prácticas Zoológicas Universidad del Valle, Cali, Colombia (CPZ-UV); Private Collection of Donald E. Hanh, Arizona, USA (DEH); Florida Museum of Natural History, Gainesville, USA (FLMNH); Field Museum of Natural History, Chicago, USA (FMNH); Colección Herpetológica Instituto Alexander von Humboldt, Villa de Leyva, Colombia (IAvH); Instituto Butantan, São Paulo, Brazil (IBSP); Kansas University Biodiversity Institute & Natural History Museum, Lawrence, USA (KU-KUH); Natural History Museum of Los Angeles County, Los Angeles, USA (LACM); Museum of Comparative Zoology, Cambridge, USA (MCZ); Museo de Historia Natural La Salle, Caracas, Venezuela (MHNLS); Museo de Herpetología Universidad de Antioquia, Medellín, Colombia (MHUA); Museo de La Salle, Bogotá, Colombia (MLS); Museum National d'Histoire Naturelle, Paris, France (MNHP); Museu Nacional Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil (MNRJ); Museu de Zoologia Universidade de São Paulo, São Paulo, Brazil (MZUSP); Museo de Zoología Pontificia Universidad Católica de Ecuador, Quito, Ecuador (QCAZ); Rijksmuseum van Natuurlijke Historie, Leiden, Netherlands (RMNH); Staatliches Museum für Naturkunde, Stuttgart, Germany (SMNS); Museum of Zoology, University of Michigan, Ann Arbor, USA (UMMZ); Smithsonian National Museum of Natural History, Washington, USA (USNM); Colección de Anfibios y Reptiles Universidad del Valle, Cali, Colombia (UVC).

For each species we list all the material referred to it, and in each case, we indicate with an asterisk the material reviewed (*).

External morphology: Detailed observation of the scales, including meristic and qualitative characters, were scored by inspecting specimens under a Leica EZ4 W dissecting microscope equipped with a 5 MP integrated camera, and a Keyence Digital Microscope VHX-7000 series.

Some illustrations were done using a Leica MS5 dissecting microscope equipped with a camera lucida. Nomenclature of scale variables follows Dixon and Kofron (1983), Savage (2002), Freire et al. (2007), Haad et al. (2008), Centeno et al. (2010), and Santos and Reis (2018). However, we opted for keeping the use of ocular and preocular scales, given that the eye is visible in the Colombian specimens, and in some specimens of *L. albirostris*. Additional measurements used in general for typhlopoid snakes follows Thomas and Hedges (2007). These measurements include eye diameter (ED), internarial distance (ID), interocular distance (IOD), antero-posterior length of the ocular scale (LOS), and nostril-eye distance (NE). We also included the length and width of the frontal scale (FL, FW), and the rostral-ventral width (RVW). All measurements were taken using ImageJ 1.53e (Schneider, Rasband, & Eliceiri, 2012). One specimen was scanned using the diffusible iodine-based contrast-enhanced computed tomography diceCT method (Gignac et al., 2016) and was used to observe high resolution details of the cephalic scales (Metscher, 2009) and is illustrated showing internal gland and jaw muscles in Bell et al. (2021).

Osteology: We gathered microCT data for four specimens from the new localities (CPZ-UV 7289–7292; Valle del Cauca, Colombia). Specimens were scanned at the University of Texas at Austin using a Zeiss Versa 620 scanner with the following scanning parameters: 4x objective, 80 kV, 10 W, 0.5 s acquisition time, detector 11.014 mm, source -30.035 mm, XYZ [-11, -17,975, 53], camera bin 2, angle ±180, 801 views, LE2 filter, dithering. Scans will be deposited in Morphosource.org, as part of the National Science Foundation (NSF) Outwardly Mobilizing the UTCT Vertebrate Archive for Research and Training project. We also used existing digital specimens of *L. albirostris* available online from Morphosource (www.morphosource.org): KU-KUH 116885 from Panama, FMNH 216257 also from Panama, and described in detail by Rieppel et al. (2009). Two additional specimens from Colombia—CM 44656 from Arjona, Bolívar, illustrated in Santos (2018); and UMMZ 48173, from a locality near Fundación, Bolívar (Morphosource Specimen ID 000S21195)—are also referred to the new species. Other species from the genus (*L. argaleus*, *L. beui*, *L. sousai*, *L. taylori*, *L. ternetzii*, and *L. wilderi* diceCT) are illustrated in Santos (2018) and Strong, Scherz, and Caldwell (2021). Terminology follows Cundall & Irish (2008).

Habitat and distribution: We generated species distribution models (SDM) to predict and compare potential geographic ranges of the new species and *L. albirostris* using confirmed records for both. The records were downloaded from the Global Biodiversity Information Facility (GBIF, <http://www.gbif.org>) and iDigBio (www.

idigbio.org) databases, new records not available from online databases, and published accounts (92 occurrence records in total, see Supporting Information Appendix S1). Analyses were performed in R (R Development Core Team, 2013) using the “sdm” package (Naimi & Araújo, 2016). We used a set of bioclimatic variables as model predictors, which were previously checked for collinearity by calculating the variance inflation factor (VIF; Marquardt, 1970). The quotient VIF was calculated using 19 bioclimatic variables from WorldClim (Fick & Hijmans, 2017) with the function *Vifcor*. We used nine out of 19 bioclimatic variables to produce the distribution models for *L. albirostris* and the new species, namely: bio 2 (mean diurnal range), bio 3 (isothermality), bio 4 (temperature seasonality), bio 8 (mean temperature of wettest quarter), bio 13 (precipitation of wettest month), bio 14 (precipitation of driest month), bio 15 (precipitation seasonality), bio 18 (precipitation of warmest quarter), and bio 19 (precipitation of coldest quarter). We used the MaxEnt algorithm (Phillips & Dudík, 2008) to generate the models, one of the most widely used methods for modeling of species distributions (Elith et al., 2011). For each species, the data points were randomly partitioned into two subsets (calibration and validation in a ratio of 3:1), and models were run and replicated 1,000 times. Results from the modeling prediction were posteriorly evaluated using the area under a curve (AUC; Duan, Kong, Huang, Varela, & Ji, 2016; Elith et al., 2011).

3 | RESULTS

Taxonomic statement: In this article, we apply a strict morphological definition to *L. albirostris*; this definition is narrower than the one implemented by Dixon and Kofron (1983) which allowed for large morphological variation and extensive range distributions. Our approach results in the resurrection of three previously described species that were synonymized with *L. albirostris*. In blindsnake taxonomy it is common for species with large range distributions to correspond to several lineages, and in many cases some of these lineages occur in sympatry (e.g., Ellis, 2016; Hedges & Thomas, 1991; Thomas & Hedges, 2007; Wallach, 2009). Our decision is influenced by the results of reviewing the material from Colombia, where we found a very consistent arrangement of cephalic scales. We also implement the concept of subspecies for the resurrection of *L. bondensis*. Given current evidence (morphology, and ecological niche modeling) we consider it more conservative to divide this species into two major populations. The two putative populations occupy different regions, and exhibit some important phenotypic

differences, however we prefer to retain them in the same taxon until more information is available (e.g., molecular data). Based on morphological variation, three species previously synonymized with *L. albirostris* are herein recognized as separate species. Our decision is congruent with previous observations of the large morphological variation within *L. albirostris*, which previous authors have suggested more taxonomic diversity within this species (e.g. Mijares-Urrutia & Arends 2000, La Marca & Soriano, 2000).

Liotyphlops bondensis (Griffin 1916)

General traits of *Liotyphlops bondensis*: *L. bondensis* was identified in many collections as *L. albirostris* due to the similarity with that species. For this reason, previous taxonomic revisions (Dixon & Kofron, 1983; Santos, 2018) reported large morphological variation within *L. albirostris*, but recognized all the populations as a single species. Dixon and Kofron (1983) reported large variation in the contact of the cephalic scales of *L. albirostris*, describing individuals with the prefrontal and second supralabial in contact, ocular and third or fourth supralabials in contact, frontal and ocular in contact, and even individuals with three preocular scales. In the same publication they recognized that the specimens from Colombia have a slightly higher average number of dorsal scales (377–478, \bar{x} = 424.6, vs. 370–455, \bar{x} = 413.2 in *L. albirostris* sensu stricto, Table 1) and usually exhibit contact between the third supralabial and the ocular scale (the second scale of the second vertical row). The number of dorsal scales in our sample is lower (363–449, \bar{x} = 407.7 Table 1) than the one reported by Dixon and Kofron (1983), being similar to the one reported for *L. albirostris*. Also, none of the specimens assigned here to *L. bondensis* have the third supralabial in contact with the ocular scale. Their data pose a limitation, since they only reported ranges of variation for the sample, without reporting the individual scale counts. The same limitation can be observed in the diagnosis provided by Santos (2018).

Diagnosis: *Liotyphlops bondensis* can be distinguished from other *Liotyphlops* by the following combination of characters: (a) eyes always visible due to a transparent ocular scale (Figures 1–3); (b) narrow preocular scale (third scale from the first vertical row) with a marked square angle (Figures 2–4); (c) pre-subocular scale blocks the contact between the third supralabial and the ocular scales; (d) third supralabial scale taller than the rest, reaching the posterior margin of the third scale from the first vertical row (Figures 2–4 and Tables 1 and 2); (e) superior preocular scale about ½ the width of the ocular scale (Figures 2–4); (f) posterior edges of the prefrontals not extending beyond the posterior edge of the rostral (as indicated in Santos, 2018 for *L. albirostris*); (g) large frontal scale wider than longer; and (h) posterior

TABLE 1 Qualitative and meristic description of external morphological characters of species in the genus *Liotyphlops*

| | <i>L. albirostris</i> | <i>L. anops</i> | <i>L. argaleus</i> | <i>L. bondensis</i> | <i>L. beui</i> | <i>L. caissara</i> | <i>L. caracasensis</i> | <i>L. haadi</i> | <i>L. petersii</i> | <i>L. schubarti</i> | <i>L. sousai</i> | <i>L. taylora</i> | <i>L. ternetzii</i> | <i>L. trefauti</i> | <i>L. wilderi</i> |
|---|--------------------------|-----------------|--------------------------|---------------------|----------------|--------------------|------------------------|-----------------|--------------------|---------------------|------------------|-------------------|---------------------|--------------------|-------------------|
| Eyes | Little visible or absent | Absent | Little visible or absent | Evident | Little visible | Little visible | Little visible | Absent | Little visible | Little visible | Little visible | Little visible | Evident | Absent | Evident |
| Dorsal scale row | 370–478 | 547–589 | 482–533 | 363–449 | 366–532 | 326 | | 333–384 | | 372–463 | 439 | 455 | 353–539 | 520–543 | 385–402 |
| Ventral scale row | 417–453 | 531–572 | 472 | 347–434 | 348–511 | 308 | | 309–348 | | 398–451 | 427 | 441 | 341–514 | 499–531 | 371–383 |
| Anterior scales around body | 24–26 | 26 | 26 | 24 | 22–26 | 22 | 24 | 20 | 24 | 22–24 | 24 | 22 | 22–26 | 22 | 22–24 |
| Medial scales around body | 22 | 24 | 22 | 22 | 20–22 | 20 | 22 | 19–20 | 22 | 20–22 | 22 | 20 | 20–23 | 22 | 22 |
| Posterior scales around body | 22 | 24 | 22 | 22 | 20–22 | 20 | 22 | 18–20 | 22 | 20 | 20 | 20 | 20–22 | 22 | 20–21 |
| Supralabials | 4 | 4 | 4 | 4 | 4 | 3 | 4 | 4 | 4 | 4 | 4 | 4 | 4 | 4 | 4 |
| Infralabials | 3 | 3 | 3 | 3 | 3 | 3 | 3 | 3 | 3 | 3 | 3 | 2 | 3 | 4 | 3 |
| Number of scales contacting posterior edge of prefrontal | 3 | 4 | 4 | 3 | 3 | 3 | 3–4 | 3 | 3 | 3 | 4 | 3 | 3 | 4 | 3 |
| Number of scales contacting posterior edge of nasal between second supralabial and prefrontal | 1 | 2 | 1 | 1 | 2 | 1 | 1 | 1 | 1 | 2 | 2 | 2 | 2 | 1 | 1 |
| Number of scales in the first vertical row of dorsals | 4–5 | 5–6 | 4 | 4 | 5–6 | 4 | 4–5 | 4 | 4 | 5 | 6 | 5 | 5–6 | 5 | 4 |
| Subcaudals | 12–17 | 12–14 | 16 | 11–17 | 11–22 | 10 | | 11–12 | | 11–14 | 13 | 14 | 11–22 | 8 | 12–19 |
| Total length (TL) mm | 70–225.5 | 186–337 | 208.6 | 79–204 | 106–381 | 195 | 235 | 155–180 | 110 | 85–99 | 191.4 | 239.4 | 88–413 | 362–385 | 95–231 |



FIGURE 1 Live picture of the holotype of *Liotyphlops bondensis armandoi* (CPZ-UV 7288) from Roldanillo, Valle del Cauca, Colombia

edge of the scales of the first vertical row even (i.e., all with the same posterior extent, Figure 4).

Liotyphlops bondensis bondensis

Holotype: CM 216

Type locality: Bonda, Magdalena, Colombia.

Distribution: Based on examined specimens and individuals collected in the northwest of South America, this subspecies has high probability of being distributed in the Caribbean region of Colombia from the Darién Gap at the border with Panama, including the northernmost portion of the Chocó and Antioquia; also found in Córdoba, Sucre, Bolívar, Magdalena, and La Guajira. The species distribution models also project the possible presence in Venezuela, in areas surrounding Lago de Maracaibo in the Estados of Zulia, Trujillo, Mérida (especialy along the Mérida Mountain range) and Falcón. Specimens from this region need to be examined in detail to confirm this prediction.

Diagnosis: In addition to the characters mentioned above for *L. bondensis*, members of *Liotyphlops b. bondensis* can be distinguished by having: (a) rostral scale circular and (b) frontal scale width three times its length (Figure 2a–c).

Published figures: None.

Referred specimens: Colombia: Antioquia, Necoclí MHUA-R 15315*; Atlántico, Barranquilla AMNH 95927–95928; Bolívar, Arjona CM 39565*, Cartagena MZUSP 6352, USNM 61675; Córdoba, Ayapel MHUA-R 14520*, MHUA-R 15310–15311*, MHUA-R 15313*, Montelibano, MHUA-R 15376*; La Guajira, Riohacha MHUA-R 14499*; Magdalena, Bonda CM 216, Fundación UMMZ 48173*, Santa Marta USNM 5596; Sucre, San Onofre MHUA-R 14975*; Tolú LACM 114635.

Liotyphlops bondensis armandoi new subspecies (Figures 1–7)

LSID for this species: urn:lsid:zoobank.org:pub:FFFA3F6A-6674-4859-A0D5-6526010723B3

Holotype (Figures 1 and 2d–f): Colección de Prácticas Zoológicas Universidad del Valle, Cali, Colombia (CPZ-UV 7288), adult, sex undetermined, collected at the town Roldanillo, Valle del Cauca, Colombia, by WB-G in the afternoon of March 7, 2021.

Paratypes: Colección de Prácticas Zoológicas Universidad del Valle, Cali, Colombia (CPZ-UV 5304), adult, sex undetermined, collected near the town Cerrito, Valle del Cauca, Colombia, by WB-G in the morning of September 28, 2017 (3.68483, –76.31340, 990 MASL).

Type locality: Roldanillo, Valle del Cauca, Colombia (4.41638, –76.14444, 927 MASL; datum = WGS84 in all cases).

Distribution: The species distribution models projected an overlap between the distribution of *L. b. bondensis* and *L. b. armandoi* in the region of the Darién gap, including areas from the north of Chocó, Antioquia, and Córdoba, where the transition from one population to the other occurs. The distribution of this subspecies is mainly in the inter-Andean valleys of Colombia (Cauca and the Magdalena Rivers), with further predictions for its presence in the northern portion of the equatorial Andes.

Diagnosis: In addition to the characters mentioned for *L. bondensis*, members of *Liotyphlops b. armandoi* can be distinguished by having: (a) rostral scale spatulated, or rectangular with a rounded end and (b) frontal scale width four times its length (Figures 2 and 4).

Etymology: The subspecific epithet is named after our friend Armando Carabalí Vanin, who died while hiking the Puracé volcano in the year 2000. We (AH-M, WB-G, DOD, JDD), who had the opportunity to interact with Armando during his short life will always remember him for his unconditional friendship during our years as undergraduate students at Universidad del Valle. Armando is survived by his mother Oliva Vanin. Common name: Armando's blindsnake (Spanish: La culebra ciega de Armando).

Live coloration of the holotype (Figure 1): head scales (rostral, nasal, and labial scales) lighter (ivory color) than the rest of the body. The dorsal portion of the rostral and the prefrontal scales are dark gray. The head and the cervical regions are light brown (some areas seem pinkish due to underlying vascularization), being markedly different from the body color, which is glossy brown, with body scales having slightly darker (dark brown or black) anterior margins. Ocular scale translucent and a visible black eye. Anal region cream to white.

Description of the holotype: Total length 160 mm, length of the tail 3.50 mm, body diameter at the anterior (1.80 mm), middle (2.50 mm) and posterior (2.40 mm) levels, cervical region expanded (2.20 mm), diameter at the mid-tail level (1.80 mm), head width at the ocular

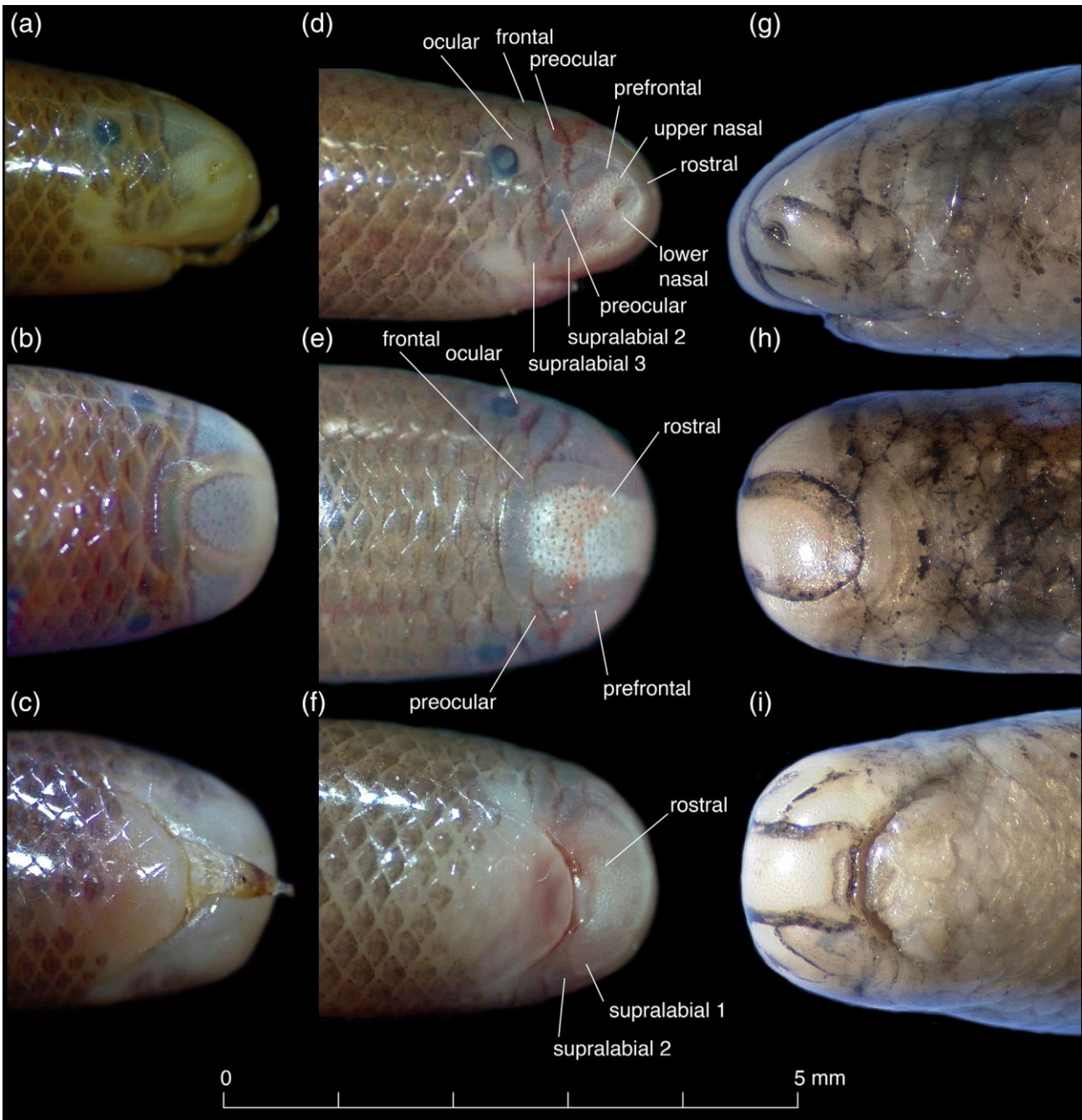


FIGURE 2 Head scales of *Liotyphlops bondensis bondensis* (MHUA-R 14975) from San Onofre, Sucre, Colombia (a–c), the holotype of *Liotyphlops b. armandoi* (CPZ-UV 7288) from Roldanillo, Valle del Cauca, Colombia (d–f), and the holotype of *L. albirostris* (MCZ R-3971) from Coclé, Panamá (g–i), in lateral (a, d, g), dorsal (b, e, h), and ventral (c, f, i) views. Source: Photographs g–i reproduced with permission from Harvard University

level (1.81 mm), head length (4.00 mm), frontal scale length (0.29 mm), frontal scale width (1.26 mm), antero-posterior eye diameter (0.27 mm), ocular scale length (0.53 mm), distance between the eyes (2.08 mm), distance from the nostril to the center of the eye (0.97 mm), rostral scale maximum breadth (0.80 mm), ventral width of the rostral scale (1.03 mm), internarial distance (1.11 mm), number of scales around the body at the anterior (24),

middle (22) and posterior (22) levels, scales smooth, cephalic scales (rostral, prefrontal, frontal, preoculars, ocular and postocular) with multiple pores for sensory receptors, number of dorsal scales in the longitudinal series (431), number of ventral scales in the longitudinal series (417), scales around the tail (22), number of sub-caudal scales to the terminal spine (11), number of supralabial scales (4), number of infralabial scales (3),

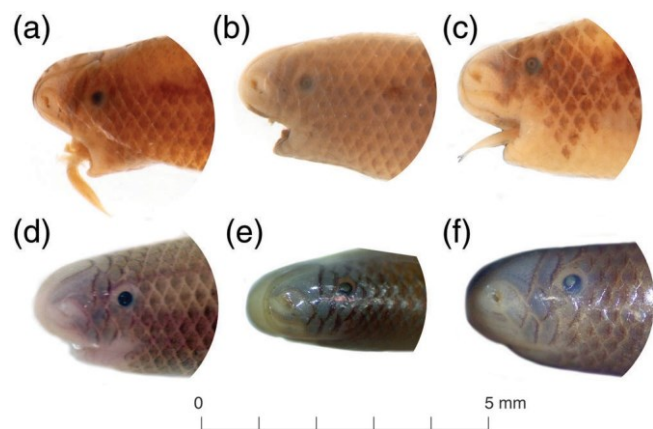


FIGURE 3 Different levels of visibility of the eye in *Liotyphlops albirostris* (a–c) and *L. bondensis armandoi* (d–f). a (AMNH R89966), b (AMNH R71667), c (AMNH R71666), d (CPZ-UV 7288), e (CPZ-UV 5583), f (MHUA-R 15233)

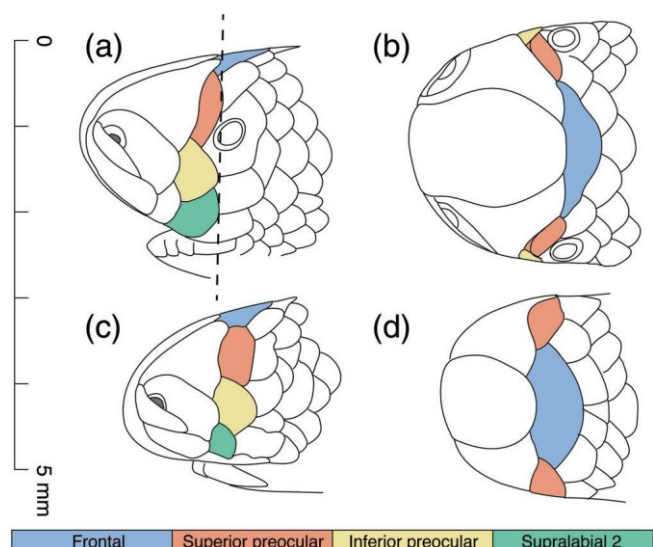


FIGURE 4 Cephalic scales of *Liotyphlops bondensis armandoi* (a–b; UVC 14029) and the holotype of *L. albirostris* (c–d; MCZ R-3971), showing the differences in the scales of the first vertical row. The dashed line shows the even posterior extent in *L. b. armandoi* “vs” uneven in *L. albirostris*

TABLE 2 Quantitative selected measurements (in mm) and proportional (in %) data for *Liotyphlops bondensis armandoi*

| n | 26 |
|-------------------------|-------------------------|
| Total length (TL) mm | 79–204 (156.23 ± 35.97) |
| Snout-vent length (SVL) | 77–200 (152.27 ± 35.33) |
| Tail length (LT) mm | 2–7 (4.08 ± 1.16) |
| Midbody diameter (MD) | 1.5–3.5 (2.49 ± 0.53) |
| MD/TL % | 1.19–2.15 |
| LT/TL % | 1.60–4.19 |
| SVL/TL % | 95.81–98.42 |

nasal scale divided into upper and lower nasal, three scales posterior to the prefrontal scale (including the frontal, and two preoculars [one superior and one inferior]), one preocular scale between the posterior margin of the upper nasal and the second supralabial, four scales in the first vertical row (frontal, 2 preoculars and second supralabial), rostral scale large and longer than its width, rostral widened in the ventral margin, contacting the supralabial laterally, the prefrontals posterolaterally, and the frontal posteriorly, second and third scales (preoculars) of the first row of vertical scales contacting the upper nasal, the lower nasal contacts the first and second supralabials and the anterior portion of the prefrontal, mental scale triangular, wider than its length and contacting the first infralabial.

Published figures: None.

Referred specimens: Colombia: Antioquia, Bello MHUA-R 14545*, Buritic, a MHUA-R 15198*, Caucasia MHUA-R 15312*, Liborina MHUA-R 15233*, Santa Fé de Antioquia MHUA-R 14836–14837*, Sonsón MHUA-R 14977, MHUA-R 15213*, Sopetr, an MHUA-R 15197*, MHUA-R 15272*, Venecia MHUA-R 15023*, MHUA-R 15226*; Caldas, Florencia CPZ-UV 2809*, CPZ-UV 3009*, CPZ-UV 4894*, La Dorada CPZ-UV 3780–3781*, CPZ-UV 3816*, CPZ-UV 3851*, CPZ-UV 3853*, CPZ-UV 3876*, CPZ-UV 4660*, CPZ-UV 6036*; Valle del Cauca, Cerrito CPZ-UV 5303–5304*, Jamundí CPZ-UV 6063*, CPZ-UV 6117*, Roldanillo CPZ-UV 7288–7292*, UVC 14029*, UVC 14031*; Toro CPZ-UV 5583*; Tolima, Honda MCZ 29599, Mariquita ANSP 25158–25159, Melgar IAvH 5471–5474.

Liotyphlops albirostris (Peters 1858)

Holotype: MCZ-R 3971 (Figure 2g–i)

Type locality: Panamá, a City, Panamá, a.

Distribution: Panamá, a.

Diagnosis: *Liotyphlops albirostris* can be distinguished from other *Liotyphlops* by: (a) the frontal being exceptionally large, where the length is half the width; (b) the posterior edge of the prefrontals passes the posterior edge of the rostral; (c) visibility of the eye variable (sometimes invisible, and sometimes poorly visible); (d) rostral scale markedly rounded in dorsal view; (e) the third scale of the first row extending beyond the posterior edge of the remaining scales of the first row; (f) posterior edge of the inferior preocular is rounded; (g) the third supralabial scale has a rounded margin; and (h) the third supralabial scale slightly higher than the second and fourth supralabials.

Published figures: Dixon and Kofron (1983, Figure 1); Pérez-Santos and Moreno (2000, Figure 4, page 47, photo 36). Also Savage (2002, Figure 11.7.b, page 545).

Referred specimens: Panamá, a: AMNH-R 71665–71666*, AMNH-R 71669*, AMNH 89967, FMNH 216257*, KU-KUH 116885*, MCZ-R 3971*; Ancón IBSP 4037; Canal Zone: AMNH-R 79044*, AMNH-R 89966*, FLMNH 43328–43329, KU 61353, MNHP 1903–1935,

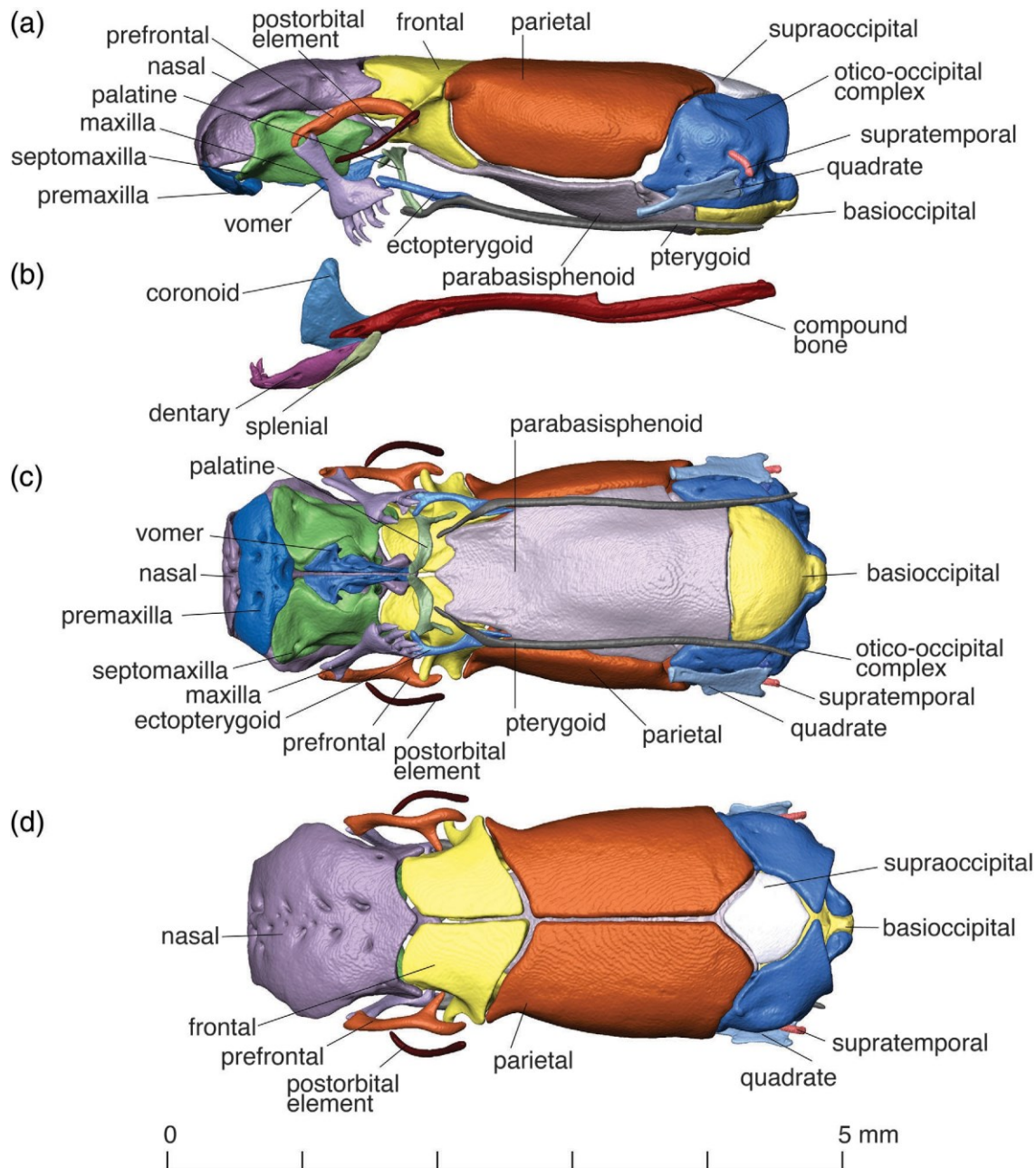


FIGURE 5 MicroCT image of the skull of *Liotyphlops bondensis armandoi* (CPZ-UV 7289). Cranium in lateral (a), ventral (c), and dorsal (d) views. (b) Lateral view of the lower jaw. Bones digitally isolated and rendered as surface elements in Avizo 2019.1 (ThermoFisher Scientific)

UMMZ 83513; Chiriquí USNM 23748; Chorrera MCZ 22221, UMMZ 95487; Coclé FLMNH 43325, KU-KUH 116894, MCZ-R 35522; Colón USNM 161155; Herrera CM 44652–44653.

Liotyphlops petersii (Dunn 1944)

Holotype: NHM 1946.1.11.26

Type locality: Guayaquil, Ecuador.

Distribution: Ecuador.

Diagnosis: *Liotyphlops petersii* is differentiated from other *Liotyphlops* in the following characteristics:

(a) width of the rostral scale equivalent to half the width of the head, (b) rostral scale extending to the interocular level, (c) third supralabial scale contacting the ocular scale, (d) prefrontal scale not in contact with the lower nasal scale.

Published figures: Peters & Orejas-Miranda (1970, Figure 7, page 181)

Referred specimens: Ecuador: SMNS 2515; Esmeraldas, Esmeraldas QCAZ-R 3855; Guayas, Guayaquil NHM 1946.1.11.26.

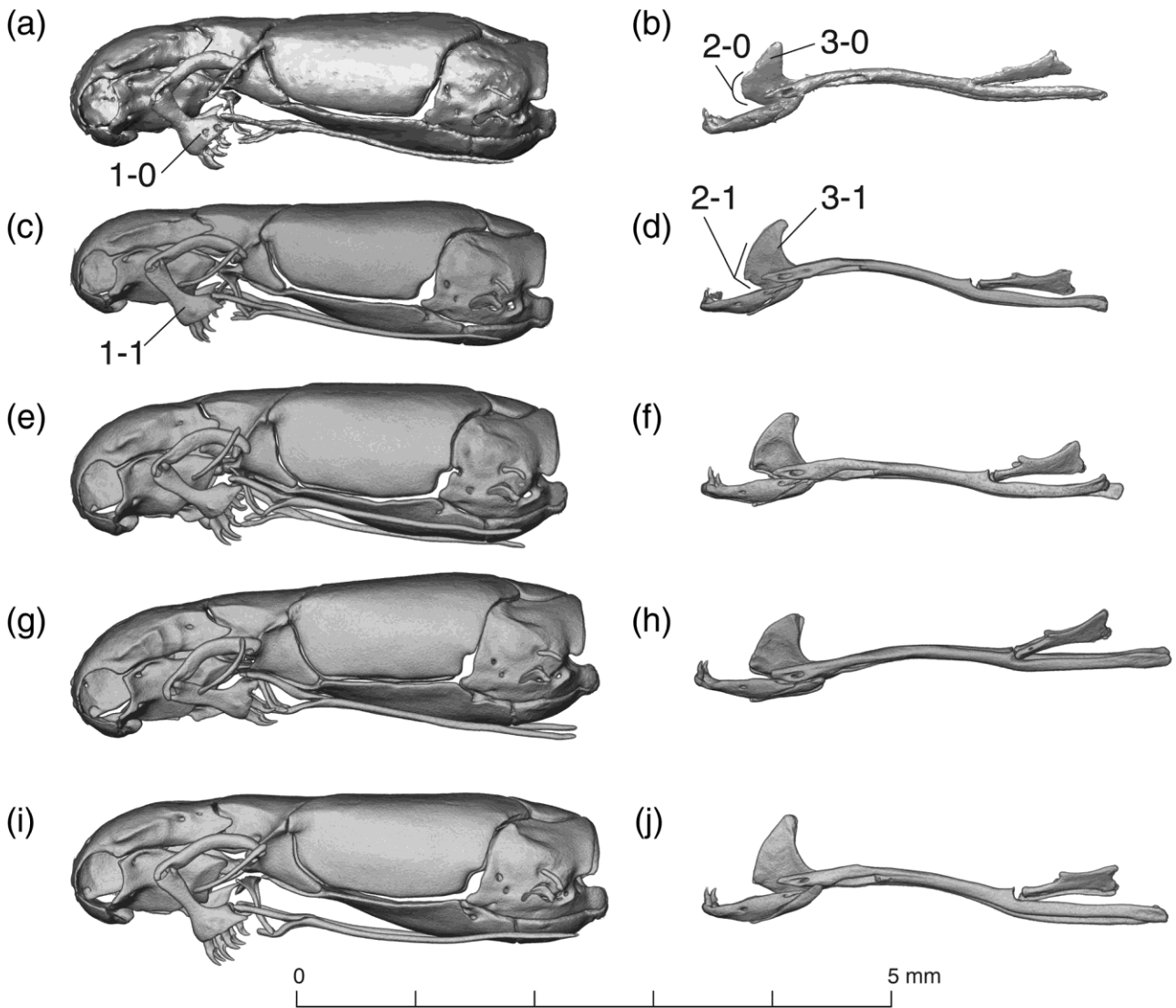


FIGURE 6 Lateral views of cranium (left) and lower jaw (right) for specimens of *Liotyphlops albirostris* (a, b) and *L. bondensis armandoi* (c–j). (a, b), surface model of specimen FMNH 216257 (see also http://digimorph.org/specimens/Liotyphlops_albirostris/). Volume renderings of *L. b. armandoi* specimens organized from smallest to largest: CPZ-UV 7292 (c, d), CPZ-UV 7290 (e, f), CPZ-UV 7291 (g, h), CPZ-UV 7289 (i, j). Variable characters: (1) maxillary foramina: present (0), absent (1); (2) Anterior margin of coronoid: rounded (0), right angle (1); and (3) Coronoid shape: triangular (0), claw-shaped (1)

Liotyphlops caracasensis (Roze 1952)

Holotype: MHNLS 514

Type locality: Cuartel Urdaneta, Caracas D. F., Venezuela.

Distribution: Venezuela in the vicinity of Caracas and the Estado de Miranda, also in Mérida and Curaçao.

Diagnosis: The original description of *L. caracasensis* is congruent with the specimens from Colombia, however, in the recent review of *L. albirostris* which used specimens from Venezuela and Colombia, two diagnostic characters are reported: (a) five or four scales in the first vertical row of dorsal scales, (b) preocular scales absent, (c) ocular scales in contact with prefrontals. An additional character reported by Santos (2018) includes the

posterior edge of the prefrontal scale extending beyond the posterior edge of the rostral scale. In his revision, Santos (2018) listed specimens from Venezuela (CM 90256, MHNLS 514, MHNLS 11824) and from Colombia (CM 39565), but not from Panam,a. Since the second character is not present in any of the specimens from Colombia, it is possible that this character is present in *L. caracasensis* or that Santos (2018) was referring to a character that is present in *Liotyphlops albirostris* from Panam,a.

Published figures: Roze (1952, Figures 1 and 2, page 151, SCN 4327); Roze (1966, Figure 2, page 33); Dixon and Kofron (1983, Figure 2, page 250, NHM 1904.6.30.1, NHM 1905.5.31.61, NHM 1903.4.28.11). Also

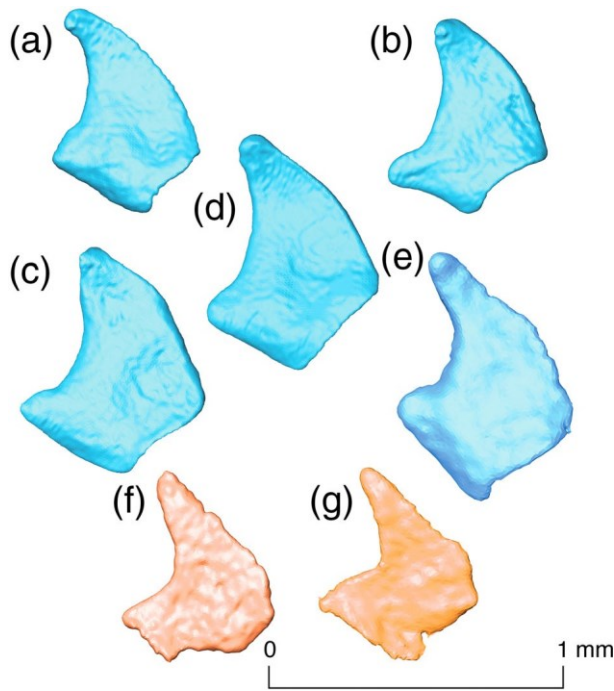


FIGURE 7 Medial view of the isolated left coronoids of *Liotyphlops bondensis armandoi* CPZ-UV 7292 (a), CPZ-UV 7290 (b), CPZ-UV 7291 (c), CPZ-UV 7289 (d); *Liotyphlops b. bondensis* UMMZ 48173 (e); and *L. albirostris* FMNH 216257 (f), and KU-KUH 116885 (g). Note the anterior right angle and more “squarish” bone in *L. b. armandoi*, compared with the rounded anterior margin in *L. albirostris*

see Natera-Mumaw, Esqueda-Gonzalez and Castelaín-Fernández (2015, Figure 335, 336, page 270).

Referred specimens: Venezuela: Caracas CAS 94619–94620, CM 7345, CM 90256, DEH 10458, DEH 10740, DEH 12096, IBSP 25802, MCZ-R 50747, MHNLS 514, MNRJ 7854, NHM 1976.101, UMMZ 117273; Mérida MNHP 1903–1935, NHM 1903.4.28.11, NHM 1904.6.30.1, NHM 1905.5.31.61; Miranda: MHNLS 514, MHNLS 11824, MHNLS 15550. Curaçao: RMNH 7851, RMNH 19215.

Note on *Liotyphlops cucutae* (Dunn, 1944). This species was described based on material from Cúcuta, Norte de Santander, Colombia. Other specimens have been assigned to this species from other regions. *L. cucutae* was also synonymized with *L. albirostris* (Dixon & Kofron, 1983); however, the description of this morphotype, and examination of photographs of the holotype available from the Museo de La Salle in Bogotá, reveal an unusual character, which is not present in any of the material from *L. bondensis* nor *L. albirostris*: (a) Contact between the third supralabial and the ocular scale. Given our strict definition of the species in this article, we consider it convenient to maintain the taxonomic status of *L. cucutae* as *insertae sedis*. Besides the holotype of this “species” from Cúcuta (MLS 038), there are at least two

more specimens from Colombia assigned to this taxon (Santander, Puerto Wilches AMNH 91798; Norte de Santander, Cúcuta MCZ 67939). Specimen AMNH 91798 lacks the contact between the third supralabial and the ocular, having a pre-subocular scale, resembling more the cephalic scales of *L. b. bondensis*. Unfortunately, the ecological niche models of *L. b. bondensis* and *L. b. armandoi* have low probabilities for Cúcuta, therefore we cannot use this argument to resolve its taxonomic placement.

Osteology: There is an extensive morphological background available for *L. albirostris*, described from anatomical and histological preparations (Dunn & Tihen, 1944; Haas, 1964), illustrated in List (1966), and recently using microCT data (Rieppel et al., 2009). For this reason, a detailed description of the skull is not included herein. The microCT data of *L. b. armandoi* was compared with previous descriptions, and with additional images and microCT data available for *L. albirostris* (CM 39565), *L. argaleus* (MCZ R-66383), *L. beui* (MCZ R-16702), *L. sousai* (UFRGS 6274), *L. taylori* (MZUSP-S 14975), *L. ternetzii* (MCP 10878, 10881), and *L. wilderi* (MNRJ 15657) listed in Santos (2018). The skull of *L. bondensis* shares with *L. albirostris* and *L. argaleus* the presence of a discrete supraoccipital element. In the case of *L. bondensis* and *L. albirostris*, this bone is roughly hexagonal (Figure 5), while in *L. argaleus* it is more fan-shaped. The presence of a discrete supraoccipital is a distinct feature of the Central American and northern South American members of *Liotyphlops*, which is not present in the southern members of this genus. Another variable character is the fenestration of the nasal bone—*L. bondensis* and *L. albirostris* have extensive fenestration concentrated in the midline of the nasal bone. In the other species for which data is available, the nasal was either poorly fenestrated (*L. beui*, *L. wilderi*), or with scattered fenestration not particularly concentrated in the midline (e.g., *L. ternetzii*).

There are several clear osteological differences between *L. bondensis* and *L. albirostris* from Panama (Figures 6 and 7), including the presence of a claw-shaped coronoid with an anterior margin forming an almost right angle (Figure 7), and the posterior margin being markedly concave. In all the available specimens of *L. albirostris*, the anterior margin of the coronoid is more rounded, and the overall shape of the bone is triangular (Figure 7, see also illustration by List, 1966 of specimen USNM 61989 from Panama). Unfortunately, Santos (2018) did not include an image of the jaw to allow for examination of the coronoid, however none of the specimens examined in that study are from the Andean region.

Another potential difference is the lack of a maxillary foramina in *L. bondensis*. These foramina are visible in the microCT models of two specimens of *L. albirostris* from Panama, the one described by Rieppel et al. (2009),

and specimen KU-KUH 116885 (Morphosource specimen ID000S22449). In another specimen listed as *L. albirostris* from Colombia (CM 39565), Arjona town, Departamento

de Bolívar; Santos (2018) shows a maxilla without the foramina, but this specimen is now assignable now to *L. b. bondensis*. The specimens of *L. albirostris* are relatively small and the CT scans are of lower quality, which can affect the rendering of the bone surface. However, using different visualization methods (surface rendering and volume rendering), these foramina were consistently visible in both specimens of *L. albirostris* (See also Rieppel et al., 2009).

Niche modeling: Based on the species distribution models (SDMs) there are different adaptive peaks (based on the environmental variables), suggesting that the two species, *L. bondensis* and *L. albirostris*, have discrete distributions, separated in the Chocó biogeographic region (Figure 8). The predicted distributions suggest that the Chocó Darién Gap is a potential isolation barrier for these two species, especially considering the extreme rainfall levels which make this region the second rainiest place on earth (annual mean precipitation 3,000–11,700 mm; Banerjee, Rai, Sarma, & Joshi, 2012; Pérez-Escobar et al., 2019) and one of the wettest (Gentry, 1986). This high humidity certainly would pose a constraint for these snakes due to their cryptozoic habitat. The SDMs for *L. b. bondensis* and *L. b. armandoi* also show two different adaptive peaks, and a projected transition zone in the North of the Colombian Andes. The type localities of *L. caracasensis*, *L. petersii*, and *L. cucutae* are in areas of low probability for the presence of *L. b. bondensis* and *L. b. armandoi*.

Combination of SDMs and morphological data support the resurrection of three lineages, which have remained covered by the umbrella of *L. albirostris*.

Implications for conservation: To date, the conservation status of anomalepidids *L. albirostris*, *L. beui*, *L. caissara*, *L. ternetzii*, *L. wilderi*, *Helminthophis flavoterminalis* and *T. squamosus*, remains as least concern (LC). With the taxonomic rearrangement of *L. albirostris*, some of the resulting species are data deficient (DD) according to the International Union for Conservation of Nature (IUCN, 2021; <https://www.iucnredlist.org>) categories. The status of *L. b. armandoi* which seems to have a narrow distribution in the inter-Andean valleys of Colombia, especially as these population are now confined to small

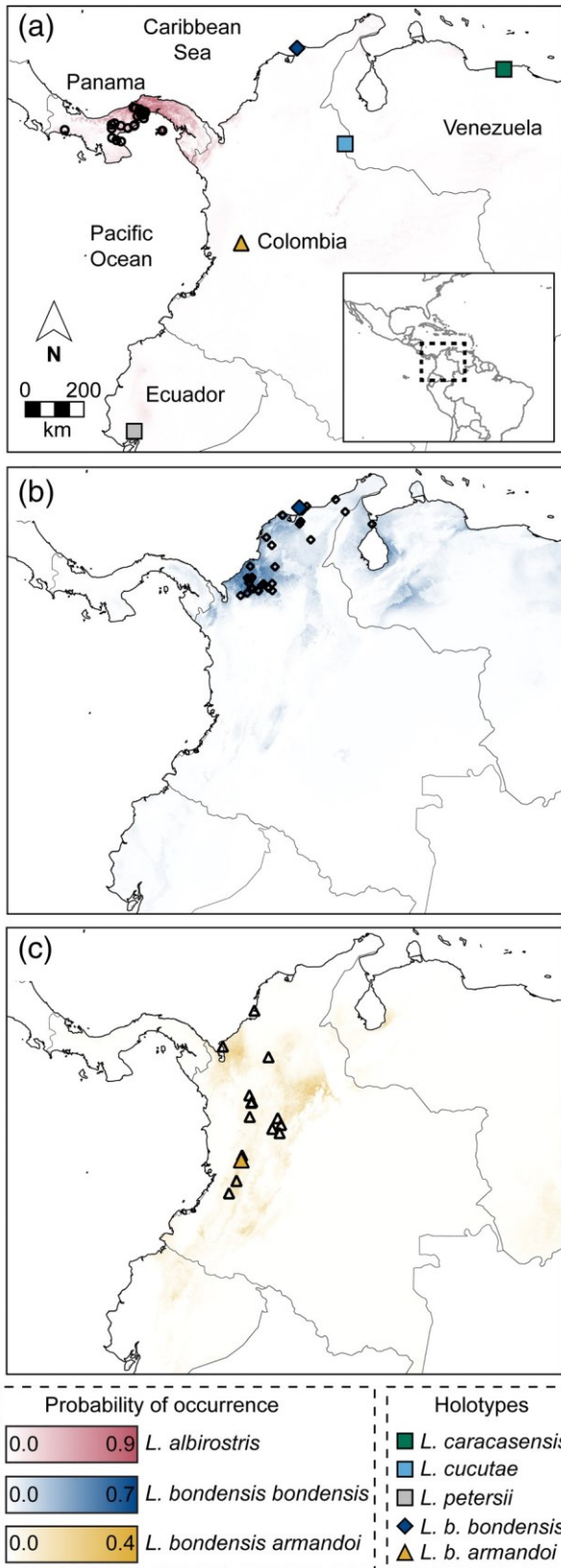


FIGURE 8 Species distribution models for *Liotyphlops albirostris* (red), *L. b. bondensis* (blue), and *L. b. armandoi* (yellow). The colors represent areas with a 50% probability that either species is present, based on the MaxEnt species distribution modeling estimation. The inset shows the location of the modeled area in South America. Open symbols indicate the localities used to calculate the models. Type localities of relevant species are shown as colored symbols



FIGURE 9 Type locality of *Liotyphlops bondensis armandoi* in Roldanillo, Valle del Cauca, Colombia

patches of natural habitat along highly cultivated or urbanized areas (Figure 9). An assessment of the validated species is needed, especially their inclusion in future conservation planning.

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AUTHOR CONTRIBUTION

Camilo Linares-Vargas: Conceptualization (equal); data curation (equal); formal analysis (equal); investigation (equal); methodology (equal); writing - original draft (equal); writing-review & editing (equal). Wilmar Bolívar-García: Conceptualization (equal); data curation (equal); formal analysis (equal); funding acquisition (equal); investigation (equal); methodology (equal); software (equal); supervision (equal); visualization (equal); writing - original draft (equal); writing-review & editing (equal). Alexandra Herrera-Martínez: Formal analysis; investigation; methodology; resources (equal); software; writing - original draft; writing-review & editing. Daniel Osorio-Domínguez: Data curation; formal analysis; investigation; methodology; software; visualization; writing - original draft; writing-review & editing. Oscar E. Ospina: Data curation; formal analysis; investigation; methodology; software; visualization; writing - original draft; writing-review & editing. Richard Thomas: Conceptualization; formal analysis; investigation; methodology; resources; visualization; writing - original draft; writing-review & editing. Juan D. Daza: Conceptualization; formal analysis; funding acquisition; investigation;

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REFERENCES

- Banerjee, S., Rai, S., Sarma, B., & Joshi, S. (2012). Bacterial biofilm on water bodies of Cherrapunjee: The rainiest place on planet earth. *Advances in Microbiology*, 2, 465–475.
- Bell, C. J., Daza, J. D., Stanley, E. L., & Laver, R. J. (2021). Unveiling the elusive: X-rays bring scolecophidian snakes out of the dark. *The Anatomical Record*.
- Boulenger, G. A. (1889). Descriptions of new Typhlopidae in the British museum. *Annals and Magazine of Natural History*, 4, 360–363.
- Burbrink, F. T., Grazziotin, F. G., Pyron, R. A., Cundall, D., Donnellan, S., Irish, F., ... Zaher, H. (2020). Interrogating genomic-scale data for Squamata (lizards, snakes, and amphisbaenians) shows no support for key traditional morphological relationships. *Systematic Biology*, 69, 502–520.
- Centeno, F. C., Sawaya, R. J., & Germano, V. J. (2010). A new species of *Liotyphlops* (Serpentes: Anomalepididae) from the Atlantic Coastal Forest Southeastern Brazil. *Herpetologica*, 66, 86–91.
- Cundall, D., & Irish, F. (2008). The snake skull. In C. Gans, A. S. Gaunt, & K. Adler (Eds.), *Biology of the reptilia. Morphology H. The skull of Lepidosauria* (Vol. 20, pp. 349–692). Ithaca: Society for the Study of Amphibians and Reptiles.
- Dixon, J. R., & Kofron, C. P. (1983). The Central and South American anomalepid snakes of the genus *Liotyphlops*. *Amphibia-Reptilia*, 4, 241–264.
- Duan, R. Y., Kong, X. Q., Huang, M. Y., Varela, S., & Ji, X. (2016). The potential effects of climate change on amphibian distribution, range fragmentation and turnover in China. *PeerJ*, 4, e2185.
- Dunn, E. R., & Tihen, J. A. (1944). The skeletal anatomy of *Liotyphlops albirostris*. *Journal of Morphology*, 74, 287–295.
- Elith, J., Phillips, S. J., Hastie, T., Dudík, M., Chee, Y. E., & Yates, C. J. (2011). A statistical explanation of MaxEnt for ecologists. *Diversity and Distributions*, 17, 43–57.
- Ellis, R. J. (2016). A new species of blindsnake (Scolecoptidia: Typhlopidae: *Anilios*) from the Kimberley region of Western Australia. *Herpetologica*, 72, 271–278.
- Fick, S. E., & Hijmans, R. J. (2017). WorldClim 2: New 1km spatial resolution climate surfaces for global land areas. *International Journal of Climatology*, 37, 4302–4315.
- Figuroa, 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, e0161070.
- Freire, E. M. X., Caramaschi, U., & Argolo, A. J. S. (2007). A new species of *Liotyphlops* (Serpentes: Anomalepididae) from the Atlantic Rain Forest of Northeastern Brazil. *Zootaxa*, 1396, 19–23.
- Gentry, A. H. (1986). Species richness and floristic composition of Choco, region plant communities. *Caldasia*, 15, 71–75.
- Gignac, P. M., Kley, N. J., Clarke, J. A., Colbert, M. W., Morhardt, A. C., Cerio, D., ... Witmer, L. M. (2016). Diffusible iodine-based contrast-enhanced computed tomography (diceCT): An emerging tool for rapid, high-resolution, 3-D imaging of metazoan soft tissues. *Journal of Anatomy*, 228, 889–909.
- Haad, J. J. S., Franco, F. L., & Maldonado, J. (2008). Una nueva especie de *Liotyphlops* Peters, 1881 (Serpentes, Scolecophidia, Anomalepididae) del sur de la Amazonia Colombiana. *Biota Colombiana*, 9, 295–300.
- Haas, G. (1964). Anatomical observations on the head of *Liotyphlops albirostris* (Typhlopidae, Ophidia). *Acta Zoologica*, 45, 1–62.
- Hedges, S. B., & Thomas, R. (1991). Cryptic species of snakes (Typhlopidae: Typhlops) from the Puerto Rico Bank detected by protein electrophoresis. *Herpetologica*, 47, 448–459.
- IUCN. (2021). *The IUCN red List of threatened species*. Version 2021-1.
- La Marca, E., & Soriano, P. (2004). *Reptiles de los Andes de Venezuela* (p. 171). Mérida Venezuela: Fundación Polar, Conservación Internacional, CODEPRE-ULA, Fundación Mérida, BIOGEOSS.
- List, J. C. (1966). Comparative osteology of the snake families Typhlopidae and Leptotyphlopidae. *Illinois Biological Monographs*, 36, [6]+112.
- Marquardt, D. W. (1970). Generalized inverses, ridge regression, biased linear estimation, and nonlinear estimation. *Technometrics*, 12, 591–612.
- Metscher, B. D. (2009). MicroCT for comparative morphology: Simple staining methods allow high-contrast 3D imaging of diverse non-mineralized animal tissues. *BMC Physiology*, 9, 1–14.
- Mijares-Urrutia, A., & Arends, A. (2000). Herpetofauna of estado Falcón, Northwestern Venezuela: A checklist with geographical and ecological data. *Smithsonian Herpetological Information Service*, 123, 1–30.
- Naimi, B., & Araújo, M. B. (2016). Sdm: A reproducible and extensible R platform for species distribution modelling. *Ecography*, 39, 368–375.
- Natera Mumaw, M., Esqueda González, L. F., & Castelaín Fernández, M. (2015). *Atlas serpientes de Venezuela: Una visión actual a su diversidad* (pp. i-xii + 1–441). Santiago de Chile, Chile: Dimacofi Negocios Avanzados S.A.
- Pérez-Santos, C., & Moreno, A. G. (1991). *Serpientes de Ecuador* (p. 47). Torino, Italia: Museo Regionale di Scienze Naturali.
- Pérez-Escobar, O. A., Lucas, E., Jaramillo, C., Monro, A., Morris, S. K., Bogarín, D., ... Antonelli, A. (2019). The origin and diversification of the hyperdiverse flora in the Choco, biogeographic region. *Frontiers in Plant Science*, 10, 1328.
- Peters, J. A., & Orejas-Miranda, B. (1970). Catalogue of the Neotropical Squamata. Part I: Snakes. *United States National Museum Bulletin*, 297, vii + 1–347.

- Phillips, S. J., & Dudík, M. (2008). Modeling of species distribution with Maxent: New extensions and a comprehensive evaluation. *Ecography*, *31*, 161–175.
- Pyron, R. A., Burbrink, F. T., & Wiens, J. J. (2013). A phylogeny and revised classification of Squamata, including 4161 species of lizards and snakes. *BMC Evolutionary Biology*, *13*, 1–54.
- R Development Core Team. (2013). *R: A language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing. Retrieved from <http://www.r-project.org>
- Rieppel, O., Kley, N. J., & Maisano, J. A. (2009). Morphology of the skull of the white-nosed blindsnake, *Liotyphlops albirostris* (Scoleophidia: Anomalepididae). *Journal of Morphology*, *270*, 536–557.
- Roze, J. A. (1952) Contribución al conocimiento de los ofidios de las familias Typhlopidae y Leptotyphlopidae en Venezuela. *Memorias de la Sociedad de Ciencias Naturales La Salle*, *12*, 143–158.
- Roze, J. A. (1966). *La taxonomía y zoogeografía de los ofidios de Venezuela* (p. 362). Caracas: Imprenta Universitaria de la Universidad Central de Venezuela.
- Santos, F. J. M. (2018). A revision of the small snakes of the family Anomalepididae (Reptilia: Squamata: Serpentes), using high resolution computerized tomography (PhD dissertation, p. 164). Pontificia Universidade Católica do Rio Grande do Sul, Brasil, Porto Alegre.
- Santos, F. J. M., & Reis, R. E. (2018). Two new blind snake species of the genus *Liotyphlops* (Serpentes: Anomalepididae), from central and South Brazil. *Copeia*, *106*, 507–514.
- Santos, F. J. M., & Reis, R. E. (2019). Redescription of the blind snake *Anomalepis Colombia* (Serpentes: Anomalepididae) using high-resolution x-ray computed tomography. *Copeia*, *107*, 239–243.
- Savage, J. (2002). *The amphibians and reptiles of Costa Rica* (p. xx +934). Chicago: University of Chicago Press.
- Schneider, C. A., Rasband, W. S., & Eliceiri, K. W. (2012). NIH Image to ImageJ: 25 years of image analysis. *Nature Methods*, *9*, 671–675.
- Strong, C. R. C., Scherz, M. D., & Caldwell, M. W. (2021). Deconstructing the gestalt: New concepts and tests of homology, as exemplified by a re-conceptualization of “microstomy” in squamates. *The Anatomical Record*, *2021*, 1–49. <https://doi.org/10.1002/ar.24630>
- Thomas, R., & Hedges, S. B. (2007). Eleven new species of snakes of the genus *Typhlops* (Serpentes: Typhlopidae) from Hispaniola and Cuba. *Zootaxa*, *1400*, 1–26.
- Vidal, N., Marin, J., Morini, M., Donnellan, S., Branch, W. R., Thomas, R., ... Hedges, S. B. (2010). Blindsnake evolutionary tree reveals long history on Gondwana. *Biology Letters*, *6*, 558–561.
- Wallach, V. (2009). *Ramphotyphlops braminus* (Daudin): A synopsis or morphology, taxonomy, nomenclature and distribution (Serpentes: Typhlopidae). *Hamadryad*, *34*, 34–61.

SUPPORTING INFORMATION

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