THE WORMSNakes (FAMILY TYPHLOPIDAE) OF THE NEOTROPICS, EXCLUSIVE OF THE ANTILLES

by

JAMES R. DIXON

and

FRED S. HENDRICKS

Texas A & M University, College of Agriculture, Dept. Wildlife and Fisheries Sciences, College Station, Texas 77843, U.S.A.

With 10 text-figures

ABSTRACT

The systematic arrangement of the worm snakes (Typhlops) from the continental western hemisphere is presented. Allocations of many names historically assigned to Central and South American Typhlops are clarified. The continental Typhlops include nine species, two of which are described as new. The intraspecific variation of all species is explored within the limitations of known specimens. Three major radiations of New World Typhlops are postulated to account for the radiations of the present species groups.

INTRODUCTION

The taxonomic status of some of the species of Typhlops occupying the mainland of South America have been thoroughly confused for about 200 years. This confusion was initiated by Linnaeus' (1758) description of Anguis reticulatus. Had Linnaeus actually seen a specimen of his species, we believe the confusion would not have existed. Scheuchzer (1735-38) gave a brief description of a “two headed” snake [paraphrased by M. Boeseman, in litt., as follows: A backwards and forwards crawling snake with black spots on a white background; more numerous spots on neck; belly yellow with black of tail interrupted by yellow (probably referring to the light colored tail ring)]. Scheuchzer also provided an illustration that was accurate enough to identify the figure as a Typhlops. Gronovius (1756) described an “amphisbaena” (= Two headed animal) that resembled Scheuchzer's illustration; gave a pertinent color description and two important squamative features, ventral scale and subcaudal numbers of 177 and 37, respectively. The number of ventral scales may well fit some species of Typhlops but there are no known typhlopids in the world that have 37 subcaudals. Gronovius' description also suggests that his specimen had a subrounded tail (no mention of a tail spine), and the animal had “rings”
of scales (Hoogmoed, in litt.). In addition, the measurements of 195 mm for total length, and 164 mm for head and body length suggests an animal that had a tail/total length ratio (15.9%), higher than any known typhlopid. He also states that the specimen had a broad tongue that was bifid at the extreme tip. The tongues of amphisbaenids are broad, while those of typhlopids are long and narrow. In our estimation (and that of M. S. Hoogmoed, in litt.), Gronovius' description was actually of an amphisbaenid and not a *Typhlops*. Linnaeus (1758) paraphrased Gronovius' (1756) description, cited Scheuchzer's (1735-38) illustration and utilized the two for his description of *Anguis reticulatus*, an amphisbaenid description with an illustration of a typhlopid!

Had Linnaeus only used the color description, Weigel (1782) would not have described *Anguis rostralis*. Weigel points out that his specimen does not fit any of Linnaeus' (1758) descriptions of *Anguis*, except perhaps in color pattern. Weigel then presents a most accurate color description of what we now recognize as *T. reticulatus*, including accurate ventral and subcaudal scale counts, and measurements. Perhaps most important is the series of events that prompted Schneider (1801) to coin a new name for Weigel's *Anguis rostralis* and Gmelin's *A. nasutus*. We indicated earlier that Weigel's description of *A. rostralis* is very good and described the salient features of *T. reticulatus* perfectly. However, Gmelin (1789) did not accept Weigel's proposed name, *rostralis*, for this species, paraphrased Weigel's description of *rostralis* and named the species *nasutus*. Schneider (1801) apparently did not recognize either of the two earlier names because they referred to a salient feature (the rostral area) that is common to the group as a whole. He then paraphrased Weigel's description of *rostralis* and named it *croco-tatus* because it described the color of the venter (saffron-yellow).

The status of *A. reticulatus* eventually assumes the role of *Typhlops* through the interpretation of Duméril & Bibron (1844), probably because Scheuchzer's figure was similar to specimens at hand and the paraphrased edition of Gronovius' (1756) description might have been in error. In any case, the poor description by Linnaeus (1758) led many later authors (Boulenger, 1893; Berg, 1898; Koslowsky, 1898; Serie, 1916, 1921, 1936; Beebe, 1946; Wehekind, 1955; Emsley, 1963; Roze, 1956) to confuse their specimens at hand with *T. reticulatus*. Indeed, we have been able to recognize as many as five species in some series of *Typhlops* loaned to us as *T. reticulatus*.

Species descriptions of *Typhlops* without adequate data and often with unreliable localities, or none given, have taken an enormous amount of time in literature review, correspondence and interlibrary loan, often without
success. Thus today, we still have five species of Typhlops that cannot be associated with any country or continent. The case by which typhlopids may be introduced into foreign lands by man, such as through potting soils of exotic plants cannot be overlooked as a major problem in understanding the taxonomy and distribution of typhlopids today.

Our interests in South American Typhlops began during a long-term study of the natural history of reptiles in the upper Amazon Basin of Peru (Dixon & Soini, 1975, 1977). A series of 18 specimens of Typhlops were accumulated over an eight year period from a few scattered localities within a 50 km radius of Iquitos, Peru. There were three recognizable forms among the 18 specimens, all of which could be identified as T. reticulatus utilizing existing taxonomic keys and descriptions. A brief survey of United States museums for holdings of South American Typhlops species convinced us that we were not alone in our taxonomic dilemma, thus began our journey through the sands of time.

**Materials and methods**

The material comprises about 385 specimens, including all available type specimens (14) of nine recognized neotropical forms. The material was either borrowed or examined at the following institutions: American Museum of Natural History, New York (AMNH); Academy of Natural Sciences, Philadelphia (ANSP); California Academy of Sciences, San Francisco (CAS); Carnegie Museum, Pittsburgh (CM); Centro Nacional Investigaciones Iologicas, Buenos Aires (CNII); Field Museum of Natural History, Chicago (FMNH); Florida State Museum, University of Florida, Gainesville (FSM); Instituto Butantan, São Paulo (IB); Instituto Miguel Lillo, Tucuman (IML); Institut Royal des Sciences Naturelles de Belgique, Brussels (MRHN); Los Angeles County Museum of Natural History (LACM); Museum National d'Histoire Naturelle, Paris (MNHP); Museum of Comparative Zoology, Harvard (MCZ); Museum of Vertebrate Zoology, Berkeley (MVZ); Museum of Natural History, University of Kansas, Lawrence (KU); Museo Argentino de Ciencias Naturales, Buenos Aires (MACN); Museo Ciencias Naturales, Caracas (MCN); Museo Civico di Storia Naturale di Milano (MSNM); Museo ed Istituto di Zoologia Sistematica, Torino (MZST); Museo Zoologia, Universidad de São Paulo (MZUSP); Rijksmuseum van Natuurlijke Historie, Leiden (RMNH); San Diego Natural History Museum (SDNHM); Texas Cooperative Wildlife Collection, College Station (TCWC); University of Illinois Museum of Natural History, Urbana (UIMNH); United States National Museum of Natural History, Washington (USNM); University of Costa
Rica, San José (UCR); University of Michigan Museum of Zoology, Ann Arbor (UMMZ); University of Texas Natural History Collection, Austin (TNHC); University of Texas, Arlington (UTA); University of Wisconsin, Department of Zoology, Madison (UWZH); Zoologisches Institut und Zoologisches Museum, Hamburg (ZIMH).

Three quantitative (total dorsals, total subcaudals, number of scale rows) and 12 mensural characters were taken for each specimen. Each mensural character was subjected to a ratio analysis, utilizing two basic characters, total length and head width. Additionally, rostral width to rostral length was utilized. Total dorsals were counted from the posterior edge of the rostral to the tail spine. Subcaudals were counted from the posterior edge of the cloacal lip to the tail spine; scale rows (SR) were counted 20 dorsals posterior to the rostral, at midbody and 20 dorsals anterior to the cloaca.

All mensural characters were either taken with vernier calipers or an ocular micrometer to the nearest tenth of a millimeter. Total length (TTL) was measured from the tip of the snout to the tip of the tail. Tail length (TL) was measured from posterior edge of the cloaca to the tail spine; head width (HW), transverse measurement at level of eyes; anterior body width (ABW), transverse measurement one head length beyond head; midbody width (MBW), at midbody; posterior body width (PBW), one head length anterior to cloaca; midtail width, (MTW) at midtail; rostral length (RL), from anterior tip of snout to posterior edge of rostral, measured parallel to axis of body; rostral width (RW), transverse measurement at greatest width of rostral, eye diameter (ED), longitudinal measurement of whatever part of the eye is visible; eye to nostril distance (EN), distance from posterior edge of nostril to pigmented portion of eye spot; interorbital distance (INORB), transverse measurement between pigmented eye spots.

Twelve ratios were utilized: TL/TTL, HW/TTL, ABW/TTL, MBW/TTL, PBW/TTL, MTW/TTL, RL/RW, RL/HW, RW/HW, ED/HW, EN/HW, INORB/HW.

The hemipenis was examined in situ, on those specimens where permission was granted for tail dissection. The tail was longitudinally slit midventrally and the hemipenis retractor muscle was excised in order that the vertically folded hemipenis could be stretched to its full length. A longitudinal slit was made the full length of the hemipenis ventrally, in order to examine the organ for microornamentation.

The analyses of intra- and interpopulational variation were based on samples that were combined according to homogeneity and geographic proximity. Standard statistical programs yielding univariate data were utilized.
Problematical species of Typhlops reported from the western hemisphere

*Typhlops leucogaster.* — The type specimen of *T. leucogaster* Wied (1825) was never preserved according to Wied’s comments following his original description. He also indicated he could not complete the notes he made in the forest because he no longer had the specimen. There are several statements made by Wied that indicate that his description is of an amphisbaenid rather than a typhlopid. The tail was almost 1/10 of the total length (actually 8.4 percent from measurements given by Wied), anus covered with large, pointed scales, and the head scale configuration described by Wied is unlike that of any typhlopid. If we translate his description of the body scales correctly, they are also unlike those of typhloids. We suspect the description to be that of a species of the amphisbaenid genus *Leposternon.* We have alerted Dr. C. Gans (in litt.) of this possibility and he may investigate it further. The type locality, Lagoa d’Ardra, near Mucuri, Bahia state, Brasil, is well within the range of four species of *Leposternon* and only one *Typhlops,* which it does not resemble in any manner.

*Typhlops longissimus.* — The holotype of *Ophthalomidion longissimum* Duméril & Bibron, 1844, is reported to be from “North America” by Smith & Taylor (1945) and that location is confirmed by Roux-Esteve (in litt.) as the catalog entry. However, Boulenger (1893) did not indicate the place of origin since Duméril & Bibron failed to include it in their description of the species. Our examination of the holotype of *T. longissimus* reveals that it is not North American and probably belongs to either of the genera *Rhinotyphlops* or *Ramphotyphlops.* *Rhinotyphlops* is African while *Ramphotyphlops* is primarily Australian. Between 1837 and 1851 the donor, F. de Castelnau, traveled widely in North and South America as French Consul. Between 1852 and 1878, he was French Consul to South Africa, Siam and Australia (Papavero, 1971). According to the dates of Castelnau’s travels, he would have sent the specimen to the Paris Museum, prior to becoming Consul to South Africa and Australia, before 1844. This suggests that his voyages between Europe, North and South America may have been routed around the horn of Africa, and he may have visited Australia at the same time. The placement of *T. longissimus* into the proper genus must await approval of the examination of its gonads. If the specimen is a male, an allocation can be made on the basis of the hemipenes being characteristic of either an Australian lineage or other more typical saurian type of hemipenes (see Robb, 1966, for discussion of typhlopid hemipenes).

*Typhlops lumbricalis.* — Thomas (1976) has revised the known species of *Typhlops* that occur on the Antillean Islands. One of these species, *T. lum-
bricalis, was the first to be applied to the genus Typhlops under the Linnaean system. Barbour & Ramsden (1919) indicated that the species not only occurred throughout the Antillean Islands but on the mainland of South America as well. The latter authors were probably reflecting the statements of Boulenger (1893), who recorded T. lumbricalis from Berbice, Guyana (see below). Thomas (1976) restricted the type locality of T. lumbricalis to New Providence Island, Bahamas, on the basis of Linnaeus' (1758) squamation data and those of his own. One specimen (AMNH 67881, William Beebe Collection) is reported from Kartabo, Guyana, but Thomas (pers. comm.) believes that Beebe probably found the specimen in the Port-au-Prince region of Haiti, when he visited there in 1927. Thomas has examined the American Museum of Natural History specimen and indicates that its squamation falls within the range of a population of T. cf. lumbricalis of the Haitian Cul de Sac. Thomas (1976) also points out that the holotype of Meditoria nasuta Gray (1845) is not T. lumbricalis as indicated by Boulenger (1893), nor is its type locality correct (Berbice, Guyana). Thomas indicates that the specimen is identical to T. jamaicensis Shaw, from Jamaica, the Antilles.

Typhlops melanocephalus. — We have examined the holotype of Catherinthus melanocephalus Duméril & Bibron (1844), reported to have come from Peru (data on Invoice), but Dr. R. Roux-Estève (pers. comm.) indicated that the locality was a lapsus calami, the actual locality data reads “origin inconnue — voyage de Péron et Lesueur”. According to Roux-Estève, Péron and Lesueur sailed from Le Havre, France, on 19 October 1800, voyaged to the Azores, around the Cape of South Africa to Mauritius, then to the west coast of Australia and finally to Timor. They returned to Le Havre, France, on 25 March 1804, following much the same route. Our data suggest that melanocephalus has close affinities to the Typhlina guentheri group of the Indonesian Archipelago, as defined by McDowell (1974).

Typhlops psittacus. — The holotype of Typhlops psittacus is reported to be from Mexico, but neither the donor nor the date of capture was known at the time of its description (Werner, 1903). Taylor (1940) indicated the description suggested a relationship to old world rather than Mexican forms and questioned the “Mexico” locality label. Our examination of the holotype of psittacus and an associated specimen from Mexico at hand when Werner described the species suggests two errors were made. The first mistake was pointed out by Taylor (1940), that while Werner (1903) described psittacus as having 24 scale rows about the body, his key to the species stated that only 20 rows were present. The first error was made because Werner examined another specimen from “Mexico” that had 20 scale rows about the
body and probably inadvertently transposed the latter number into his key. The other specimen from "Mexico" represents *Typhlops brongersmianus*, known only in South America and may have been accidentally separated from a series of untagged specimens of *Typhlops brongersmianus* collected in Surinam in 1879, and currently housed in the Royal Museum in Brussels. The second error was assuming the specimen came from Mexico. The holotype belongs to either *Ramphotyphlops* or *Rhinotyphlops*. Without permission to examine its gonads, we are hesitant to place it in either genus, but its external squamation is very similar to *Rhinotyphlops caecus* of Africa.

*Typhlops unilineatus*. — One species, *Onychocephalus unilineatus* Duméril & Bibron (1844), is reportedly from Cayenne. Dr. R. Roux-Estève (pers. comm.) indicates that the specimen was sent to the Paris Museum by Madame Richard, October, 1839. She also sent specimens of frogs from the Island of Dominique, West Indies. We have no assurance that the type of *unilineatus* actually came from Cayenne. Our examination of the holotype suggests that the species is probably related to the *Typhlops diardi* group of the Indonesian Archipelago. The type is in terrible condition, extremely

### Table 1

Means and variations of traditional mensural and meristic measurements of mainland Neotropical *Typhlops*

<table>
<thead>
<tr>
<th>Species</th>
<th>Dorsals</th>
<th>Caudals</th>
<th>Anterior-Body Scale Rows</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>N</td>
<td>Mean</td>
<td>S.D.</td>
</tr>
<tr>
<td>Typhlops brongersmianus</td>
<td>126</td>
<td>243.1</td>
<td>15.9</td>
</tr>
<tr>
<td>Typhlops costaricensis</td>
<td>7</td>
<td>397.7</td>
<td>7.9</td>
</tr>
<tr>
<td>Typhlops lehneri</td>
<td>11</td>
<td>320.3</td>
<td>6.6</td>
</tr>
<tr>
<td>Typhlops minuquisquamos</td>
<td>12</td>
<td>238.8</td>
<td>13.4</td>
</tr>
<tr>
<td>Typhlops microstomus</td>
<td>34</td>
<td>530.7</td>
<td>21.0</td>
</tr>
<tr>
<td>Typhlops paucisquamos</td>
<td>2</td>
<td>179.0</td>
<td>12.7</td>
</tr>
<tr>
<td>Typhlops reticulatus</td>
<td>120</td>
<td>257.1</td>
<td>17.9</td>
</tr>
<tr>
<td>Typhlops tensis</td>
<td>21</td>
<td>396.2</td>
<td>21.0</td>
</tr>
<tr>
<td>Typhlops trinitatus</td>
<td>1</td>
<td>389</td>
<td>—</td>
</tr>
</tbody>
</table>

### Table 1

<table>
<thead>
<tr>
<th>Species</th>
<th>Mean</th>
<th>S.D.</th>
<th>Range</th>
<th>Mid-Body Scale Rows</th>
<th>Posterior Body Scale Rows</th>
<th>Pigmented Scale Rows</th>
<th>Total Length/Midbody Width</th>
</tr>
</thead>
<tbody>
<tr>
<td>T. b.</td>
<td>20</td>
<td>—</td>
<td>—</td>
<td>19.6</td>
<td>0.8</td>
<td>18-20</td>
<td>10.7</td>
</tr>
<tr>
<td>T. c.</td>
<td>20</td>
<td>—</td>
<td>—</td>
<td>19.7</td>
<td>0.5</td>
<td>19-20</td>
<td>20</td>
</tr>
<tr>
<td>T. l.</td>
<td>19.3</td>
<td>1.2</td>
<td>18-20</td>
<td>14.2</td>
<td>1.0</td>
<td>12-16</td>
<td>10.1</td>
</tr>
<tr>
<td>T. mn.</td>
<td>17.2</td>
<td>1.0</td>
<td>16-18</td>
<td>18</td>
<td>—</td>
<td>—</td>
<td>11</td>
</tr>
<tr>
<td>T. mc.</td>
<td>18</td>
<td>—</td>
<td>—</td>
<td>18</td>
<td>—</td>
<td>—</td>
<td>0</td>
</tr>
<tr>
<td>T. p.</td>
<td>20</td>
<td>—</td>
<td>—</td>
<td>18</td>
<td>—</td>
<td>—</td>
<td>14.5</td>
</tr>
<tr>
<td>T. r.</td>
<td>20</td>
<td>—</td>
<td>—</td>
<td>18.1</td>
<td>0.3</td>
<td>18-20</td>
<td>9.0</td>
</tr>
<tr>
<td>T. te.</td>
<td>18</td>
<td>—</td>
<td>—</td>
<td>18</td>
<td>—</td>
<td>—</td>
<td>8.9</td>
</tr>
<tr>
<td>T. tr.</td>
<td>20</td>
<td>—</td>
<td>—</td>
<td>20</td>
<td>—</td>
<td>—</td>
<td>11</td>
</tr>
</tbody>
</table>
soft and deteriorated and it is impossible to obtain an accurate number of dorsal scales. However, the scale row numbers, head shields and general configuration of the body suggest a relationship with Indonesian typhlopids and not with those of South America. Future workers should consider examining the holotypes of *longissimus*, *melanocephalus*, *psittacus* and *unilineatus* in any revision of Indo-Australian and African typhlopids.

**KEYS AND SPECIES ACCOUNTS**

The following key is provided to facilitate identification of *Typhlops* of the continental western hemisphere. These include species inhabiting the continental islands of northern South America, but exclude the strictly Antillean species studied by Thomas (1976). Although the key provided easily distinguishes the species of *Typhlops*, Table 1 includes a summary of distinguishing measurements, counts and proportions and their known ranges of variation.

**KEY TO THE *TYPHLOPS* OF THE CONTINENTAL WESTERN HEMISPHERE**

([Includes Ramphotyphlops (Typhlina)]

1. Nasal suture complete, contacting rostral ........................ ........................ 2
   Nasal suture incomplete, not contacting rostral ........................ 7

2. Scale rows usually 20-20-20 .................................. 3
   Scale rows usually 18-18-18 ................................ 6

3. Dorsals less than 340 .......................... 4
   Dorsals more than 380 ................................ 5

4. More or less uniform dark brown or black, nasal suture almost vertical, touching rostral near apex; tail tip and anal area white; tongue with a pair of lateral papillae. .......................................................... *Ramphotyphlops (Typhlina) braminus*
   More or less light brown or yellowish with 11 darker lines on dorsum; venter yellow or yellowish tan; head and tail spine yellow; tongue without a pair of lateral papillae. .......................................................... *Typhlops lehneri*

5. Small species, adults less than 250 mm; ground color yellow with 11 rows of dark brown or brown lines; tail yellow; dorsals 388-389. .................. *Typhlops trinitatis*
   Large species, adults more than 300 mm, ground color brown or dark brown, no indication of lineate pattern, venter only slightly lighter color than dorsum; tail brown; dorsals 392-413. ................. *Typhlops lehneri costaricensis*

6. Subocular absent, dorsals 347-429 ..................................... *Typhlops tenuis*
   Subocular present, dorsals 487-563 ................................... *Typhlops microstomus*

7. Scale rows usually 20-20-20 or 20-20-18 ................................ 8
   Scale rows usually 18-18-18, 20-18-16 or 18-16-14 .................. 9

8. White snout and white tail ring, dorsum dark brown to black; 9 dorsal rows pigmented; dorsals 225-301 .......................................................... *Typhlops reticulatus*
   No white snout or tail ring, dorsum generally yellowish brown, usually 11 dorsal rows pigmented, dorsals 195-287 .......................................................... *Typhlops brongersmanus*

9. Snout white, dorsal scale rows 20-18-16 or 18-16-14; dorsals 221-253 .......................................................... *Typhlops minusquamus*
   Snout brown or streaked, dorsal scale rows 18-18-18, dorsals 170-195 .......................................................... *Typhlops paucisquamus*
Species accounts

**Typhlops brongersmianus** Vanzolini (figs. 1c, 2c)


Diagnosis. — A slightly large species (maximum total length 325 mm) with 11 dorsal scale rows pigmented brown, yellowish brown or reddish brown, snout frequently streaked with dark brown along scale edges; dorsal pigment frequently concentrated near center of scale but occasionally diffuse, tending to appear spotted, reticulated, or lined; nasal cleft incomplete; scale rows usually without reduction (96%), 20-20-20 (rarely 20-20-19 or 20-20-18); dorsal scales from rostral to tail spine average 232.

Range. — Cis-Andean South America between 11° north and 35° south (Figure 3).

Variation. — Some 126 specimens obtained the following: TTL varies from 84-325, x 200.3; TL 2.3-8.9; x 5.5; HW 2.9-9.6; x 5.3; ABW 3.1-11.1, x 6.4; MBW 3.4-12.9, x 8.1; PBW 3.0-13.3, x 7.5; MTW 1.6-7.5, x 4.4; RL 1.5-3.8, x 2.67; RW 0.9-2.5, x 1.66; ED 0.4-1.3, x 0.58; EN 1.4-3.4, x 2.24; INORB 2.3-5.3, x 3.48. Ratios (per cent): TL/TTL 1.78-4.17, x 2.80; HW/TTL 1.82-3.93, x 2.70; ABW/TTL 2.24-4.49, x 3.32; MBW/TTL 3.21-5.10, x 4.05; PBW/TTL 2.84-4.75, x 3.71; MTW/TTL 1.38-3.06, x 2.24; RL/RW 123.5-207.7, x 162.0; RL/HW 38.5-60.0, x 50.3; RW/HW 21.7-40.0, x 31.3; ED/HW 6.8-18.8, x 11.1; EN/HW 35.0-54.8, x 42.3; INORB/HW 55.2-76.7, x 56.8. Dorsal scale rows 20-20-20 (96%), 20-20-19 or -18 (4%); dorsal scales from rostral to tail spine vary from 195-287, x 233.1; subcaudals 8-14, x 10.6.

Color pattern of spots, lines or reticulations on dorsal 7 to 13 rows (x 10.6) but nearly always 11 rows; tail and snout always without white ring or spot; snout usually brownish or light tan and usually streaked with darker brown along scale edges; ventral surface always pale yellow to straw yellow (sometimes darkened in formalin).

Geographic Variation. — The total number of dorsal scales from rostral to tail spine is the most obvious and easily available character that indicates intra- and interpopulational variation. However, we suspect that there is considerable sexual dimorphism in this character. Roux-Étève (1975) found this character varied significantly between sexes, females always being
Fig. 1. Ventral, lateral and dorsal illustrations of the head scales of the six species of *Typhlops* found in South America and its continental islands.
Fig. 2. Color pattern illustrations of midbody and anterodorsal part of the head of the six species of *Typhlops* found in South America and its continental islands.
Fig. 3. Distribution of *T. brongersmianus* in South America. Circle with star represents type locality; open circles are literature records; black circles represent localities from where specimens have been examined.
higher in number in some African species. She also found that the total number of dorsal scales varied altitudinally with the higher numbers found at higher elevations. Fortunately, the two widespread species of South America are usually found below 500 meters, and geographic and sexual variation are our primary concerns. We were unable to sex the majority of our specimens for one primary reason, absence of authority to do so from Museum curators, because many of the species are known from only a few specimens and curators did not wish to have them damaged in any way. Those we were able to sex by palpation (presence of eggs) or slitting the tail and examination of the hemipenes, parallel the conclusions of Roux-Estève. However, since we were unable to sex the majority of individuals

![Graph](image)

**T. brongersmianus**

**DORSALS**

![Bar chart](chart1)

**T. reticulatus**

![Bar chart](chart2)

Fig. 4. Variation in total number of dorsals in samples of (A) *T. brongersmianus* and (B) *T. reticulatus*. The samples are arranged in more or less linear direction from northwest to southeast. The upper samples are western and the lower samples are eastern South American.
we have utilized the data regardless of sex and by doing so, we may have biased our mean slightly higher or lower, depending upon the sex ratio present in the sample. Therefore we interpret our data as preliminary until sexual variation can be adequately determined.

Our data (fig. 4A) suggest that there are two major geographical populations. Samples from Peru, Bolivia, central Brazil, Paraguay and Argentina show increasing numbers of dorsals from the northwest to the south-east. When we extract the Rio Parana Basin sample from the re-

![Fig. 5. Ventral, lateral and dorsal illustrations of the head scales of the three species of *Typhlops* found in Central America and Mexico.](image-url)
Fig. 6. Distribution of 16 species of Amilian Typhlopidae, three Central American and Mexican species and the known distribution of the introduced wormsnake, Rhamphophis typlopus (Typhlops) braminus.
mainder, it tends to stand apart as a distinct form by having the highest number of dorsals recorded for the species. However, within those high numbers are some moderately low ones, suggesting that we may well have a large series of females with only a few males present in the sample. Therefore, we have retained the Rio Parana sample within the western population.

The second population is represented by samples from Trinidad, Venezuela, Guyana, Surinam, northeastern Brazil and extreme coastal Brazil as far south as the state of Rio Grande do Sul. This entire population is characterized by having relatively low numbers of dorsals (fig. 4A). There is no overlap between the eastern and western populations utilizing three standard errors on either side of the mean, but there are individuals that are found in intermediate zones that suggest there is populational contact and possibly gene flow between the populations. The eastern population represents the nominate form and the western population does not have an existing name. However, we do not propose to recognize the latter population because sexual dimorphism has not been properly documented and we suspect there are broad zones of overlap between the populations where only a few or no specimens have been collected.

Comment. — One specimen (USNM 73499) reported from Estancia Breyer, Patquia, La Rioja, Argentina is noticeably outside the known range of *T. brongersmanus*. Dr. John Wiest and Alan Markezich (pers. comm.) arrived at the same conclusion for specimens of two separate species that they studied. We consider the locality to be in error.

**Typhlops costaricensis** Jimenez & Savage (fig. 5a)


Type locality: Monteverde, Sierra de Tilarán, Provincia de Puntarenas, Costa Rica, 1500 m.


Diagnosis. — A moderate sized (maximum total length 360 mm) and uniformly pigmented *Typhlops* (all rows pigmented with brown) with invariably 20 scale rows about the body, a complete nasal suture, and a relatively high number of dorsal scales from rostral to tail spine (x 397.7).

Range. — Central America from Monteverde, Costa Rica, north to Matagalpa, Nicaragua (also see Villa, 1978) (fig. 6).

Variation. — The following variation is based upon seven individuals: TTL varies from 262-360, x 301.3; TL 3.9-4.8, x 4.3; HW 4.6-5.9, x 5.4; ABW 5.1-7.0, x 6.1; MBW 5.9-8.9, x 7.7; PBW 5.6-9.2, x 7.6; MTW 4.0-5.0, x 4.6; RL 2.4-3.2, x 2.8; RW 1.6-2.2, x 1.97; ED 0.2-0.4, x 0.33;
EN 2.1-2.9, ñ 2.5; INORB 3.4-4.3, ñ 3.97. Ratios (per cent): TL/TTL 1.28-1.73, ñ 1.45; HW/TTL 1.50-1.93, ñ 1.78; ABW/TTL 1.75-2.19, ñ 2.02; MBW/TTL 2.25-2.72, ñ 2.55; PBW/TTL 2.13-2.87, ñ 2.52; MTW/TTL 1.27-1.77, ñ 1.54; RL/RW 133.3-152.4, ñ 144.ι; RL/HW 47.1-56.4, ñ 52.9; RW/HW 34.8-38.9, ñ 36.7; ED/HW 3.8-8.7, ñ 6.2; EN/HW 39.6-51.8, ñ 474; INORB/HW 72.5-76.4, ñ 74.1; number of dorsals vary from 390-413, ñ 397.7; subcaudals 7-9, ñ 8.57; dorsal scale rows 20-20-20 (one with 19 posteriorly).

Typhlops lehneri Roux (figs. 1d, 2f)


Holotype. — Museum, Basle, Switzerland, no number given, collected by E. Lehner, no date given.

Diagnosis. — An attenuate and diminutive *Typhlops* with a depressed snout and invariably 20 scale rows about the body; nasal cleft complete; dorsal scales from rostral to tail spine average 320; color pattern consists of 11 (occasionally 13) olive brown to light brown lines on a yellowish ground color, pattern sharply bicolored laterally, clear yellow below lateral dark line and beneath tail; rostral and tail spine bright yellow.

Range. — Known only from El Pozon and El Pauji, Estado Falcon, Venezuela (fig. 7).

Variation. — No additional specimens of this species have been obtained since a series of 19 specimens were collected by H. G. Kugler between 1937-1945 and sent to the Museum of Comparative Zoology, Harvard. This species has been well described by Roux (1926, 1927) and comparable data presented by Shreve (1947), Richmond (1965) and Thomas (1974). Additional data on variation follow: TTL varies from 115-185, ñ 152.4; TL 1.4-2.0, ñ 1.8; HW 2.3-2.5, ñ 2.4; ABW 2.4-2.7, ñ 2.6; MBW 2.5-3.0, ñ 2.8; PBW 2.3-2.8, ñ 2.6; MTW 1.2-1.9; RL 1.3-1.6, ñ 1.5; RW 0.6-1.2, ñ 1.0; ED 0.2-0.3, ñ 0.27; EN 1.1-1.4, ñ 1.23; INORB 1.5-2.0, ñ 1.73. Ratios (per cent): TL/TTL 0.80-1.39, ñ 1.10; HW/TTL 1.6-1.75, ñ 1.68; ABW/TTL 1.70-1.88, ñ 1.82; MBW/TTL 1.72-2.10, ñ 1.96; PBW/TTL 1.63-1.96, ñ 1.84; MTW/TTL 0.85-1.33, ñ 1.05; RL/RW 125.0-216.6, ñ 158.3; RL/HW 52.0-66.6, ñ 61.3; RW/HW 24.0-52.2, ñ 42.1; ED/HW 8.69-12.5, ñ 11.1; EN/HW 47.8-56.0, ñ 51.3; INORB/HW 66.7-80.0, ñ 72.1. Number of dorsal scales from rostral to tail spine 289-337, ñ 320.3; subcaudals 7-14, ñ 9.0; dorsal scale rows invariably 20-20-20; 11 (infrequently 13) dorsal scale rows pigmented.
Fig. 7. Distribution of four species of South American *Typhlops*.
Typhlops microstomus Cope (fig. 5b)


Holotype. — United States National Museum 61064, collected by A. Schott, date unknown.

Diagnosis. — An elongate (maximum total length 366 mm) *Typhlops* with no discernable pigment, nasal suture complete, subocular scale present, scale rows invariably 18 about body, and a high number of dorsal scales from rostral to tail spine (x 530.7).

Range. — The savanna region of the horn of Central America from Merida, Mexico, south to El Paso, Guatemala (fig. 6).

Variation. — Based on 34 individuals, the following variation is obtained: TTL varies from 146-366, x 277.7; TL 1.1-4.1, x 2.59; HW 2.3-4.1, x 3.33; ABW 2.5-5.1, x 3.79; MBW 2.5-6.3, x 4.38; PBW 2.4-5.9, x 4.08; MTW 1.4-3.7, x 2.69; RL 1.2-2.3, x 1.91; RW 0.7-1.5, x 1.15; ED 0.1-0.2, x 0.17; EN 1.0-2.1, x 1.53; INORB 1.3-2.8, x 2.11. Ratios (per cent): TL/TTL 0.37-1.36, x 0.95; HW/TTL 0.95-1.61, x 1.22; ABW/TTL 1.13-1.86, x 1.38; MBW/TTL 1.29-2.00, x 1.58; PBW/TTL 1.13-2.20, x 1.48; MTW/TTL 0.71-1.53, x 0.98; RL/RW 142.8-209.1, x 168.1; RL/HW 48.1-74.2, x 57.7; RW/HW 29.3-40.0, x 34.4; ED/HW 2.56-8.68, x 5.27; EN/HW 39.0-55.6, x 45.9; INORB/HW 54.0-71.8, x 63.2. Number of dorsals vary from 487-566, x 530.7; subcaudals 5-10, x 7.82; dorsal scale rows invariably 18-18-18; scale rows pink in life, white in preservative.

Typhlops minuisquamus* sp. nov. (fig. 1b, 2b)

Holotype. — TCWC (Texas Cooperative Wildlife Collection) 39130, an adult female taken from Mishana, Loreto, Peru, on 17 March 1972 by Pekka Soini.

Paratypes. — AMNH 52411, 52867, 53776, TCWC 38148, Iquitos, Loreto, Peru; TCWC 42791 topoparatype; AMNH 98189, Kartabo, Guyana; AMNH 25050, Kamakusa, Guyana; AMNH 25087, Tacoba, Guyana; MZUSP 5233, Manaus, Brazil; UTA-R 3787, 6910, Timbo, Vaupes, Colombia.

Diagnosis. — A species of Typhlops distinguished from all other New World *Typhlops* by having a scale row reduction from 20 to 14, 18 to 14 or 18 to 12; sharply bicolored with 11 rows darkly pigmented, a white snout with or without a dark rostral spot, and the absence of a light colored tail ring.

Distribution. — This species occurs in the Amazon Basin from the vicinity of Iquitos in the west to Manaus in the east, north to Moroa, Venezuela (Roze, 1956); also along the north edge of the Guyana Shield in Guyana (fig. 7).
Description of holotype. — Total length 230 mm, tail 4.9 mm; head width at eyes 5.6 mm; anterior body width 6.7 mm; midbody width 9.5 mm; posterior body width 8.5 mm; midtail width 5.0 mm; horizontal rostral length 3.1 mm; maximum rostral width 2.2 mm; longitudinal diameter of eye 0.5 mm; least distance between eye and nostril 2.2 mm; interorbital distance 4.0 mm; middorsal scales between rostral and tail spine 229; ventrals posterior to mental 218, subcaudals 8; abbreviated scale row reduction 18(20)-110/117(16)-202/202(14)-229; postoculars 1/1; parietals 2/2, anterior parietal not exceptionally narrow, reaching a point lateral to level of eye; rostral narrowest at level of nostril; rostral gradually broadens dorsally, somewhat oval shaped in dorsal aspect; suture between nasals incomplete; preoculars much higher than wide, almost rhomboid in shape but slightly rounded on anterior edge; posterior edge of preocular passing immediately in front of eye; preocular in contact with supralabials 2 and 3; ocular about twice as wide as high, roughly triangular in shape; postocular cycloid and similar to adjacent body scales; third supralabial about twice the size of the second, its dorsal apex situated between preocular and ocular; fourth supralabial large, three times the size of the third, its dorsal apex reaching to the lower third of the ocular; anteriorly, scales in the 11 dorsalmost rows with dark pigment with each scale light bordered anteriorly, producing a zig-zag pattern of lines or spots; lateralmost pigmented row less pigmented than others, gradually fading to the 200th dorsal where only 9 dorsalmost rows are pigmented to the anus; small brownish spot in middle of rostral; preoculars and anterior dorsal edge of nasals brownish, rest of nasals and rostral white; supralabials, oculars, preoculars parietals and frontal generally darker pigmented than rest of body; dorsum of tail pigmented as body.

Variation. — Three specimens from Guyana and one from Peru have scale row reductions from 20 to 14, one from Brazil 18 to 12, and six from Colombia and Peru 18 to 14. These patterns of reduction are summarized in Table 2. The area where the 16th scale row reduction takes place varies between the 111-213 dorsals in the entire series, while the last reduction always takes place within 16-28 dorsals (x = 20.5) from the tail spine. The total number of dorsal scales from rostral to tail spine vary from 221-253 (x = 241.4); caudals 6-11 (x = 8.7). The 11 pigmented rows are usually chocolate brown to blackish brown, but may be tinged with yellowish brown in old preserved specimens. The rostral scale is white in six specimens and contains a dark pigment spot in five specimens.

Of 11 specimens, the total length varies from 152-361, x 252 mm; TL 3.8-11.0, x 6.5; HW 4.1-8.6, x 6.06; ABW 5.3-9.9, x 7.02; MBW 6.4-14.3,
Summary of the scale row formulae for *Typhlops minuisquamus*. All scale alterations encountered at each reduction site are listed with their frequencies in brackets, range in parentheses and mean number of dorsal scales over which they occur is given.

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Comparisons. — *Typhlops minuisquamus* appears to be related to *Typhlops reticulatus*. Its color pattern is very similar to that of *T. reticulatus* except for the absence of the light colored tail ring. However, there are no western hemisphere *Typhlops* that we are aware of that have extensive scale row reductions like those of *T. minuisquamus*.

Etymology. — The name *minuisquamus* is taken from the Latin, meaning diminishing scales.

Specimens examined. — (See holotype and paratypes).

**Typhlops paucisquamus** sp. nov. (figs. 1a, 2a)

Holotype. — Museum Comparative Zoology R-147336, (originally 1444b), an adult (sex unknown) taken from the state of Pernambuco, Brasil; collected by Dr. Burnet and donated to the museum Dec. 21, 1863.

Paratype. — IB (Instituto Butantan) 17219, and adult female from Recife, Pernambuco, Brazil, collected 9 April 1957, by A. R. Hoge.

Diagnosis. — A species of *Typhlops* with 18 scale rows around the body, without reduction; extremely low number of dorsal and ventral scales; all scale rows pigmented.
Distribution. — Known only from the Brazilian state of Pernambuco (fig. 7).

Description of holotype. — Total length 133 mm, tail length 5 mm; head width at eyes 4.2 mm, anterior body width 5.4 mm, midbody width 6.1 mm, posterior body width 6.0 mm, midtail width 3.8 mm, horizontal rostral length 2.2 mm, maximum rostral width 1.4 mm, longitudinal diameter of eye 0.4 mm, least distance between eye and nostril 1.8 mm, interorbital distance 2.8 mm; middorsal scales between rostral and caudal spine 170; ventrals posterior to mental 171; subcaudals 11; scale rows about body 18-18-18; postoculars 1/1, parietals 2/2; parietals about twice as long (laterad) as wide, prefrontal, frontal and postparietal scales large, twice to 2½ times larger than dorsal body scales following postparietal; anterior parietal reaching a point lateral to the eye; rostral narrowest at lower level of nostril; rostral with almost straight edges dorsally gradually tapering towards dorsal tip but rounded somewhat at dorsoposterior tip; nasals almost in medial contact behind rostral; anterior edge of preocular forming an obtuse triangle, the apex slightly above the level of the nostril but not reaching nostril; nasal sutures incomplete; lower edge of nasal suture touching second supralabial; posterior edge of nasal scale contacting second supralabial; third supralabial twice as high as second, with its dorsal apex situated between preocular and ocular shields; fourth supralabial twice as long as third, its upper edge at same level as third; postocular cycloid, similar to body scales following it; preocular in contact with second and third supralabials, but mostly with third; all scale rows pigmented (darkened by formalin?), but nine dorsalmost rows more pigmented than others; each dorsal scale with a light colored center, ventral scales with light brownish band through middle of scale, leaving anterior and posterior edges with lighter color; snout appears pale straw color with no evidence of dark pigment on trailing edge of nasals and preoculars with brownish pigment; dorsum of tail pigmented as body and without evidence of a light colored tail ring.

Variation. — The female paratype is slightly larger than the holotype (TTL = 158 mm) and contains four oviducal eggs. The female obtains 190 dorsals, 10 caudals and 188 ventrals; other squamative characters are similar to the holotype. The snout is yellowish, without dark pigment, from tip of snout to posterodorsal edge of rostral; a dark streak is present in the dorsalmost segment of the preocular and nasal shields; body with nine, plus two partial dorsal rows of scales with dark pigment, midbody with 11 complete and posteriorly with 11 complete plus two partially complete pigmented rows of dorsals.

Comparisons. — *Typhlops paucisquamus* does not appear related to any
Caribbean Island or mainland South American species. As far as we can determine, there are no typhlopids in the world with so few dorsal scales.

Etymology. — The name _paucisquamus_ is taken from the Latin, meaning few scales.

Specimens examined. — Only the holotype and paratype.

**Typhlops reticulatus** (Linnaeus) (figs. 2c, 2d)

_Anguis reticulata_ Linnaeus, 1758, Systema Naturae, Ed. 10, 1: 228. Type locality: America (no holotype designated).


_Anguis nasutus_ Gmelin, 1789, Systema Natuarae, Ed. 13, 1 (3): 1120. Type locality: unknown.

_Anguis crocotatus_ Schneider, 1801, Hist. Amphib., 2: 340. Type locality: none given.


_Tortrix reticulata_, Merrem, 1820, Tent. System. Amphib.: 82.


_Argyrophis reticulatus_, Gray, 1845, Cat. Lizards: 202. Type locality: unknown.

_Typhlops reticulatus troscheli_ Jan, 1864, Icon. Gen. Ophidiens, livr. 4: pl. 6 fig. c. Type locality: none given.

_Typhlops reticulatus nigrolacta_ Jan, 1864, Icon. Gen. Ophidiens, livr. 4: pl. 6 fig. d. Type locality: none given.


Holotype. — None designated (Linnaeus' 1758 reference to Scheuchzer's (1735-38) figure suggests that this represents the iconotype). We select Rijksmuseum van Natuurlijke Historie (RMNH) 7660 as the neotype, a subadult male taken at Paramaribo, Surinam, on 3 April 1939, and donated to the museum by H. W. C. Cossee.

Diagnosis. — A relatively large species (maximum total length 522 mm) of _Typhlops_ distinguished from all other western hemisphere forms by having a white snout and white tail ring; 9 dark pigmented rows of dorsal scales that vary from brown to black; scale rows 20-20-18 in 99% of samples examined, with the reduction taking place at the posterior (87.7% of total dorsals) end of the body.

Range. — Cis-andean South America between 12°N and 14°S latitudes, except for one specimen from coastal Ecuador (fig. 8).

Description of neotype. — Total length 211 mm, tail length 6.9 mm, head width at eyes 6.6 mm, anterior body width 8.3 mm, midbody width 10.9 mm, posterior body width 10.0 mm, midtail width 6.4 mm, horizontal rostral length 3.2 mm, maximum rostral width 1.9 mm, longitudinal diameter of eye 0.6 mm, least diameter between eye and nostril 2.5 mm, interorbital distance 4.5 mm; 234 middorsal scales between rostral and tail spine; subcaudals 11;
Fig. 8. Distribution of *T. reticulatus* in South America. See fig. 3 for explanation of symbols.
scale row reduction 20(20) — 187/194 (18) — 234; postoculars 1, parietals 2, supralabials 4, 9 dark brown pigmented rows of dorsal scales, remainder yellowish; white snout and white tail ring.

Fig. 9. In situ illustration of the left hemipenis of *T. reticulatus*. Note the single row of spines along the asulcate surface.

**Variation.** — Of 120 specimens total length varies from 121-522, $\bar{x}$ 290.2; TL 3.4-15.7, $\bar{x}$ 7.7; HW 3.9-13.0, $\bar{x}$ 7.3; ABW 4.7-16.2, $\bar{x}$ 9.0; MBW 5.0-23.9, $\bar{x}$ 11.8; PBW 4.7-23.5, $\bar{x}$ 11.4; MTW 3.0-14.0, $\bar{x}$ 7.2; RL 2.4-7.3, $\bar{x}$ 4.1; RW 1.3-5.5, $\bar{x}$ 2.5; ED 0.4-1.9, $\bar{x}$ 0.97; EN 1.7-4.8, $\bar{x}$ 2.9; INORB 2.4-8.0, $\bar{x}$ 5.0. Ratios (per cent): TL/TTL 1.6-4.3, $\bar{x}$ 2.7; HW/TTL 2.0-3.8, $\bar{x}$ 2.6; ABW/TTL 2.3-4.3, $\bar{x}$ 3.2; MBW/TTL 3.0-5.7, $\bar{x}$ 4.1; PBW/TTL 2.9-5.4, $\bar{x}$ 3.9; MTW/TTL 1.7-3.6, $\bar{x}$ 2.5; RL/RW 118.2-240.9, $\bar{x}$ 163.7; RL/HW 41.9-71.7, $\bar{x}$ 55.9; RW/HW 26.2-47.8, $\bar{x}$ 34.4; ED/HW 7.5-26.4, $\bar{x}$ 13.3; EN/HW 26.2-48.4, $\bar{x}$ 39.5; INORB/HW 60.0-79.3, $\bar{x}$ 67.8. The number of dorsal scale rows varies from 20-20-20 (2%) to 20-20-18 (98%); number of dorsal scales from rostral to tail spine 223-301, $\bar{x}$ 258.4; subcaudals 7-15, $\bar{x}$ 10.6. All specimens have white snouts and white tail rings, but the white ring on the tail is infrequently confined to a dorsal blotch or smaller spot; invariably nine dorsal rows of scales are pigmented bluish black, brownish black, chocolate, or brown (except when faded by exposure to preservative and sunlight); venter may be white, flesh, pale yellow or deep yellow; occasionally seven rows of dorsal scales are pigmented near the tail and occasionally the 11th row near midbody may have a few scales with pigment (less than 2%).

Comments. — *T. reticulatus* is unique among mainland South American *Typhlops* in having a row of 7-9 spines on the asulcate surface of the hemipenes (fig. 9).

**Geographic Variation.** — The total number of dorsal scales from rostral to tail spine is the most variable character in this species and also shows
the greatest amount of geographic variation. However, as discussed earlier in the geographic variation section for *T. brongersmianus*, strong sexual dimorphism is suspected in *T. reticulatus* also, therefore our analysis is preliminary.

*Typhlops reticulatus* follows the same geographic variation pattern seen in *T. brongersmianus* (fig. 4b). Samples from Colombia, Ecuador, Peru and west central Brazil have very high numbers of dorsals and show an increase in total numbers from the northwest to the southeast. The numbers of dorsals are relatively low in samples from eastern Venezuela, Guyana, Surinam, French Guyana and extreme northeastern Brazil. They show a similar cline, increasing in number from the northwest to the southeast. As with *T. brongersmianus*, there is a relatively sharp differentiation between eastern and western populations. Because of sexual dimorphism, we do not wish to formally recognize subspecies, however, if one chose to do so, the eastern population is the nominate form. Most synonyms are associated with the eastern population (i.e., *rostralis*, *crassum*, *troscheli*, *nigrolacta*), but one (*crocotatus*) cannot be assigned to either population until the type specimen is rediscovered and the number of dorsal scales determined.

**Typhlops tenuis** Salvin (fig. 5c)


Holotype. — British Museum Natural History 1946.1.11.71 (formerly 64.1.26.47), collected by Osbert Salvin, date unknown (type locality listed above).

Diagnosis. — A moderate sized *Typhlops* (maximum total length 326 mm) with an average of 395 dorsal scales from rostral to tail spine, scale rows about body invariably 18, without reduction; complete nasal suture; diameter of midbody contained in total length 45 to 58 times; usually 9 (infrequently 7 or 11) pigmented rows of dorsal scales, pigment frequently diffuse, usually not covering margin of scale and giving an appearance of large rows of spots on dorsum.

Range. — East and north facing slopes of mountains (coffee belt) from Xico, Veracruz, Mexico, south, southeast to Subirana Valley, Honduras (fig. 6).
Variation. — Twenty one specimens reveal the following variation: TTL varies from 112-326, x 243.6; TL 2.0-5.6, x 3.59; HW 2.5-4.8, x 3.65; ABW 2.3-5.6, x 4.01; MBW 2.3-6.5, x 4.56; PBW 2.2-6.3, x 4.33; MTW 1.6-4.5, x 3.13; RL 1.2-2.7, x 1.96; RW 0.8-1.7, x 1.33; ED 0.1-0.3, x 0.18; EN 1.3-2.2, x 1.77; INORB 1.8-3.6, x 2.90. Ratios (per cent): TL/TTL 1.09-2.37, x 1.54; HW/TTL 1.23-2.41, x 1.58; ABW/TTL 1.16-2.50, x 1.72; MBW/TTL 1.35-2.94, x 1.95; PBW/TTL 1.33-2.86, x 1.84; MTW/TTL 1.06-1.87, x 1.33; RL/RW 116.7-176.9, x 140.5; RL/HW 44.4-64.3, x 53.4; RW/HW 29.6-41.5, x 36.6; ED/HW 2.38-8.00, x 4.97; EN/HW 35.4-55.3, x 48.76; INORB/HW 59.5-80.9, x 68.55. Number of dorsal scales vary from 347-429, x 396.2; subcaudals 7-11, x 9.0; dorsal scale rows about body invariably 18-18-18; pigmented scale rows vary from 7-11, x 8.9.

Typhlops trinitatus Richmond (figs. 1e, 2e)


Holotype. — American Museum Natural History 89820, collected 1 April 1956 by J. A. Oliver and J. Tee-Van.

Diagnosis. — An attenuate and diminutive species with a depressed snout and invariably 20 rows of scales about the body; nasal cleft complete, dorsals from rostral to tail spine 388-389 (in two known specimens), subcaudals 10; color pattern of 11 brown to dark brown lines on a yellow ground color, pattern sharply bicolored, yellow below, snout and tail spine bright yellow.

Range. — Known only from the island of Trinidad, West Indies (fig. 7).

Variation. — The species is adequately described by Richmond (1965) and compared to its nearest relatives by Thomas (1974). Additional specimens have not been found and the only useful data to be added to the above papers follow: TTL 240; TL 3; HW 3.9; ABW 4.4; MBW 4.8; PBW 4.8; MTW 2.8; RL 2.3; RW 1.7; ED 0.3; EN 1.7; INORB 2.6. Ratios (per cent): TL/TTL 1.3; HW/TTL 1.6; ABW/TTL 1.8; MBW/TTL 2.0; PBW/TTL 2.0; MTW/TTL 1.2; RL/RW 135.3; RL/HW 59.0; RW/HW 43.6; ED/HW 7.7; EN/HW 43.6; INORB/HW 66.7.

Ranphotyphlops (Typhlina) braminus (Daudin)


_Typhlops braminus_, Cuvier, 1829, Le regne animal...: 73.

_Typhlina braminus_, McDowell, 1974, J. Herp., 8:22, fig. 6.


Diagnosis. — A small, relatively short parthenogenic (McDowell, 1974) species with an almost vertical suture between the nasal opening and the rostral, the upper end of the cleft contacting the rostral near its apex; scale rows about body invariably 20; color black or dark brown ventrally and dorsally with tip of tail and anal area white; tongue with single pair of narrow and strongly pointed papillae on lateral edge.

Range. — Perhaps originally India but widely distributed on many islands and continents of the world through accidental introductions.

Variation. — For a very adequate description and illustration of the species see McDowell (1974: 22-25). Only total length measurements were taken of this form, and only data on dorsal scales were taken from Western hemisphere samples of the species. Little variation was noted in the number of dorsal scales from rostral to tail spine. In Mexico, the number of dorsals of a Sinaloan sample of 9 individuals varies from 314-335, \(\bar{x}\) 320.9; a Guerrero coastal sample of 10 individuals, 300-328, \(\bar{x}\) 315.5; Guerrero inland sample of 26 individuals 305-337, \(\bar{x}\) 322.5; a Hawaiian sample of 5 individuals 328-338, \(\bar{x}\) 331.1. No variation was noted in color pattern and the largest individual measured was 173 mm in total length.

Comments. — McDowell (1974) points out that *R. braminus* may be parthenogenic because of 114 individuals examined for sex, all were females. Since the hemipenial structure is used to distinguish between *Typhlops* and *Ramphotyphlops* (Robb, 1966), McDowell found it difficult to place *braminus* in the proper genus. However, most *Ramphotyphlops* (*Typhlina*) species have a single pair of lateral papillae behind the terminal fork of the tongue, no *Typhlops* examined have an almost vertical cleft between the nostril and rostral (except for *T. acutus* which is quite dissimilar in head shape, number of dorsals and scale rows, size and color). McDowell (1974) placed *braminus* in the genus *Typhlina*. Recently, Stimson, Robb & Underwood (1977) have shown that the use of *Typhlina* is incorrect and *Ramphotyphlops* should be the correct name for the genus. Since the issue is not settled and no males of the species have yet been found, we include *braminus* in our accounts, but not as *Typhlops*.

**Evolutionary relationships**

Thomas (1976) has postulated the evolutionary relationships of Antillean *Typhlops*. He emphasizes two major groups, the Biminiensis Group (including *caymanensis*) and the Major Antillean Radiation Group (MAR) that includes all other Antillean species except *tasymicris*. There are certain squamative features (that also reflect constant differences in head scale proportions) that are relatively constant within each group, as follows:
(Biminiensis Group contrasted to the MAR group) second and third supra­labials always contacting preocular rather than only the third; anterior section of nasal shield less flared; anterior nasal shield has less contact with second supralabial; lower portion of posterior nasal broader; preocular angle greater (broadly rounded vs angulate); lower portion of preocular broader; third supralabial shorter and higher; fourth supralabial longer and in more horizontal contact with ocular. The majority of these features are qualitative, but for the most part, separate the two groups.

Two southeastern Antillean island species, *T. tasymicris* and *T. trinitatus*, and all Central and South American species share several traits with the Biminiensis Group and practically none with the MAR Group. The second and third supralabials contacting the preocular, and the broadly curved anterior part of the preocular, are the most obvious features shared, while neither of these are found in the MAR Group [except one species which Thomas (1976) considered secondarily derived].

Of the northeastern South American species and all of the Central American species, only *T. lehneri* shows a relationship to southeastern Antillean island species *tasymicris* and *trinitatus*. These three species are closely related showing similar scale row numbers, somewhat similar color patterns, very similar head scale configurations, with the main difference being between the total number of transverse dorsal scales from rostral to the tip of the tail.

Of the Central American species, *T. costaricensis* is very similar to *caymanensis* of the Biminiensis Group. They share the number of dorsal scale rows, transverse dorsal scales, and head scale configurations, but differ in color pattern. *Typhlops costaricensis* is uniform brown with little change from dorsal to ventral surfaces while *T. caymanensis* is sharply bicolored, with no pigment ventrally or laterally. Another Central American species, *tenuis*, is more closely related to *costaricensis* than the Biminiensis Group. *Typhlops tenuis* shares with *costaricensis* the numbers of transverse dorsal scales, head scale configurations, but differs from *costaricensis* in having 18 scale rows about the body rather than 20, and a more spotted rather than uniform dorsal pattern. *Typhlops microstomus* shows little relationship to either the Central American species or the Biminiensis Group other than those specific characters mentioned for the groups. The total absence of pigment and the presence of a subocular scale separates *microstomus* from all other western hemisphere species.

Due to the eastwardly open circular arrangement of these species, we have elected to refer to the group as the Caribbean Arc Group. This broader evolutionary unit includes the Biminiensis Group of Thomas (1976), all Central American Species, one northwestern South American species (*T. lehneri*) and the continental island species of northern South America.
Fig. 10. Group comparisons of (A) head width/total length, (B) total length/midbody width, (C) total number of dorsals and (D) total length/tail length ratio of the South American Group and the continental Caribbean Arc Group. Two-letter abbreviations represent the species involved; open rectangle equals one standard deviation; black rectangle two standard errors on either side of the mean; horizontal line, the range of variation; vertical line, the mean (ratios expressed in per cent).
There are four mainland South American species that form a second distinct group. They are easily recognized by the presence of a semidivided nasal shield. All other western hemisphere species have a completely divided nasal. There are several additional features utilized in a univariate analysis that support the recognition of two distinct groups on the mainland of Central and South America. Ratios of total length/anterior body width, total length/midbody width, total length/posterior body width, head width/total length, total length/tail length and total number of dorsal scales from rostral to tail spine (Fig. 10A-D) all separate the two groups. These four species tend to form two species pairs, based on color, color patterns and scale row reductions. Two species described herein are too poorly known to answer questions dealing with geographic variation, but the other two species are relatively well known with over 100 individuals known for each species. *Typhlops reticulatus* and *T. minuisquamus* form one species pair while *T. brongersmianus* and *T. paucisquamus* form the other.

There appear to be three major radiations of *Typhlops* in the tropics of the western hemisphere: 1) the Caribbean Arc Group, representing those species with a completely divided nasal shield and the second and third supralabials in contact with the preocular; 2) the MAR Group of Thomas (1976), representing those species with a completely divided nasal shield and only the third supralabial in contact with the preocular; and 3) the South American Group, representing those species with a semidivided nasal shield and the second and third supralabials in contact with the preocular.

Thomas (1976) suggests that Typhlopidae is a relatively old group and shows a Gondwanaland distribution. In addition, many anatomical features of Typhlopidae and associated scolecophidian families are considered primitive and aren't far removed from a probable lizard-like ancestor. In this regard we concur. He also suggests that the distribution of the Antillean *Typhlops* may be reconcilable with a vicariance zoogeographic model, but failed to confirm this because most of the mainland species were (and in some cases still are) poorly known. All of the characters of the mainland species of the South American Group are also present in the African species of Typhlops (see Roux-Esteve, 1975).

The South American Group (ipso facto) is probably the oldest of the western hemisphere *Typhlops*, based upon its relationship to the African species and the basic premise that this group radiated northward following the Gondwanaland rift. The origin of the MAR Group is unknown because we do not know the time sequence involved in the origin of the Caribbean Plate, nor when the South American Plate coalesced its western border. However, it seems that mainland South American *Typhlops* must have
invaded the Caribbean Plate early in its history and evolved in place as a major Antillean radiation. Many of the MAR species appear to be the result of environmental factors associated with island size, topography and allopatric speciation due to watergap isolation. The initial invasion would have most likely occurred via the Lesser Antillean island chain (if such existed at the time) or via much broader overlap zones between the two plates early in the history of their contact.

The Caribbean Arc Group may have evolved from a second invasion of South American Typhlops considerably later than the MAR one, when there were differential watergaps between the emerging links uniting the North and South American Plates. It would have been possible for individuals to disperse to Cuba, Grand Cayman and the Bahamas via prevailing winds, the Gulf Stream and narrow watergaps. This group likely evolved in isolation within the Central American core and reinvaded South America during the Pleistocene, eventually reaching as far east as the islands of Trinidad, Tobago and Grenada. The group may have reached Grand Cayman, Cuba and the Bahamas via the Cayman Ridge (Thomas, 1976) about the same time.

A second possibility is that Typhlops occupying the contact zone between the Caribbean and South American Plates may have remained in place, only becoming isolated from the MAR Group as watergaps occurred, and later from the South American Group when Miocene orogenies may have isolated sections of northeastern South America by both mountain and water barriers. At this time it would have been plausible for the Caribbean Arc Group to be trapped north and east of the heightening Andean fault zones, and their major dispersal route following emerging Central America.

The Caribbean Arc Group of species is rather unique in that it shares a basic character from each of the other two groups that do not share the same feature. Thus the Caribbean Arc Group appears intermediate in position, suggesting that the second possible explanation for the origin of the three groups may be the more plausible one. However, considering the complex events of plate tectonics, the known age of Typhlops [Eocene-Recent of Europe (Romer, 1966)], it seems unlikely that this problem will be resolved until additional evidence becomes available.

**Specimens examined**

*Typhlops brongersmianus*: ARGENTINA Buenos Aires, no specific locality MNHN 3265; Cordoba, El Tio CNII 2707(2); Corrientes, Manantiales MACN 3368; La Rioja, Patquía, Estancia Breyer USNM 73490 (probably in error); Misiones, no specific locality MACN (no number), Dos de Mayo CNII 3188, 3288-89, Oberá MACN 3554, Santa Ana MACN 4695. BOLIVIA Beni, Amazonian Floodplain ZIM 4367, Barraca Rio Mariui MIZST 1755, BMNH 98.6.9.11, Rio Itenes FMNH 161601; Potosí, Tipesani,

*Typhlops costaricensis*: COSTA RICA Puntarenas, Monteverde, Sierra del Tilarán KU (Laval) 3084, UCR 1960 (= LACM 26767), 2215, 4362, 5229. NICARAGUA Boaco, San José de la Montana AMNH 113546; Matagalpa, Matagalpa MCZ 9528.


*Typhlops microstomus*: GUATEMALA El Peten, El Paso, Rio San Pedro MCZ 38648. MEXICO Campeche, km 143 UWZH 20550; Quintana Roo, X-Can CM 46860, 46816, 47022-23, X-Can Nuevo CM 49016, UCM 40750, 41816-18; Yucatan, no specific locality USNM 61064, Chichen-Itza FMNH 26975-76, MCZ 7114, UMMZ 68244, Dizibil Chaltun FMNH 153526-68, 153590-95, Libre Union FMNH 36346, Merida FMNH 10146, USNM 6590, Piste CM 46903-04, 49555, UCM 41819, Telchaquillo UWZH 20506, Tohil UMMZ 80298.

*Typhlops minusquam*: BRAZIL Amazonas, Manaus MZUSP 5233. COLOMBIA Vaupes, Timbo UTA-R 3987, 6910. GUYANA Kamakusa AMNH 25050, Kartabo AMNH 98189, Tacoba AMNH 25087. PERU Loreto, Iquitos AMNH 52411, 52807, 53776, TCWC 38148, 39130, 42791.

*Typhlops pouciquam*: BRAZIL Pernambuco, no specific locality MCZ 147336, Recife IB 17219.

*Typhlops reticulatus*: BOLIVIA Beni, confluence of Rio Sena with Rio Madre de Dios UMMZ 59771, Villa Bella CM 3345; La Paz, Charobamba BMNH 95.11.21.10. BRAZIL Acre, Guajara-Mirim IB 17115; Amapá, Ciudad de Oiapoque IB 13768, Macapa IB 25475, Serra do Navio Macapa IB 24782; Amazonas, Canabuca, Parana de Jacare BMNH 1926.4.30.10, Costa do Marrecacu, Rio Solimoes MCZ 3718, Tapurucuara, Rio Negro IB 22152; Ceará, Limeiro do Norte IB 20335; Mato Grosso, 12°51′5 S 51°46′6 W BMNH 1922.402, Rio Teles Pires MZUSP 3133; Para, no specific locality IB 14762, 14750, 14752, MCZ 2878, 5504, Arrai, I. Marajo IB 14761, Belem MZUSP 3733, IB 16245, KU 124590, Caninde, Rio Gurupi MZUSP 4262, Maracanaelha IB 25429, Marajo Island BMNH 1023.11.9.101, Xirigui, Rio Xingu MZUSP 18313, Rondonia, Porto Velho, Rio Madeira USNM 48932. COLOMBIA Amazonas, left shore of Rio Aquarico, tributary of Rio Napo (Ecuador) FMNH 165551, Leticia MCZ 48962, 48963; Meta,
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Carimagua MCZ 141088, Peralonzo, Cano Pachaquiariito USNM 195000, Villavicencio IB 7207, 10163, MZUSP 5993, USNM 195890, 195901-02. CAYENNE no specific locality BMNH 51.7.17.87, MNHN 1974.850, 3215, 5219, 5505, 8620, USNM 5597. ECUADOR Esmeraldas, Playa, east of Sua KU 147998; Napo, Lagarto Cocha USNM 106649, Limoncocha LACM 73343, 74424, 75181. GUYANA Kalacoon AMNH 8110, Kartabo AMNH 21820, 21332, 67882, northern Acraybas Mountains KU 42360, Maraburua USNM 164216-17, Orenouque River, Courantyne Basin MCZ 42360, Macasseema, Pomne River BMNH 87.1.22.15, Santa Rosa Island, Moruca River UMMZ 55835. PERU Loreto, no specific locality ANSP 13054-55, FMNH 11174, Iquitos AMNH 52435-36, 53678, TCWC 38146, 42053, Mishana TCWC 39128-20, 40520, 42790; Moropon TCWC 40530, 44720, Orellana AMNH 52912, Pampa Hermosa AMNH 16060; Rio Itaya AMNH 52060, 52433-34, 52608, 52806, 56067-70; Rio Maniti TCWC 38147; Rio Nanay AMNH 56071; Royaboya, Subirana Valley MCZ 38701. MEXICO Tabasco, Teapa BMNH 90.4.24.5; Veracruz, no specific locality FMNH 105181, 105184, USNM 6602; Cuautlapan LACM 121901-02, UMMZ 19215, 19220; Fornt de las Flores UIMNH 4674-75; La Victoria UTA-R 3710; Orizaba USNM 6344(2); Potrero Viejo FMNH 10182, USNM 110304; Xico FMNH 70687.

*Typhlops tenensis*: GUATEMALA no specific locality BMNH 84.1.3.11; Alta Verapaz, Finca Volcan UMMZ 28084; Verapaz, Coban BMNH 1946.1.11.71, UMMZ 80855. HONDURAS Yoro, Subirana Valley MCZ 38701. MEXICO Tabasco, Teapa BMNH 90.4.24.5; Veracruz, no specific locality FMNH 105181, 105184, USNM 6602; Cuautlapan LACM 121901-02, UMMZ 19215, 19220; Fortin de las Flores UIMNH 4674-75; La Victoria UTA-R 3710; Orizaba USNM 6344(2); Potrero Viejo FMNH 10182, USNM 110304; Xico FMNH 70687.

*Typhlops trinitatis*: TRINIDAD Arima Road, 3 mi above Simla AMNH 80820.

*Rampophytophils* (*Typhlina*) *braminus*: GUATEMALA Guatemala City UTA-R 3841. MEXICO Guerrero, Acahuizotla TCWC 8582; 1 mi W Acahuizotla TCWC 7407-09; Acapulco AMNH 63970, 62939, LACM 2172, SDMNH 46303-04; Agua del Obispo FMNH 108012, 108016, KU 67635-35, UIMNH 19215, USNM 110510; 2 mi S Agua del Obispo FMNH 108007; Chilpancingo FMNH 38285, near Chilpancingo MVZ 45028-29, 50872; 3 mi N Chilpancingo AMNH 165386; 4 mi S Chilpancingo UIMNH 19214; 5 mi N Coyuca SDNH 46303-04; El Limoncocha FMNH 108006, 108009, 108014-15, 108017, UIMNH 19216-18; km 212, So of Iguana FSM 40758; Pie de la Cuesta MVZ 66221; Rio Balsas CAS 137700, MVZ 76738; Tepecan de Galeana CAS 13043-45, 135004-05, 134986; 1 mi S Tierra Colorada KU 67637; Morelos, Cuernavaca FMNH 154709; Queretaro, Queretaro TCWC 47049-51; Sinaloa, Mazatlan KU 63416-18, 73487, 82980, LACM 74070, 105204-95, USNM 152455; 5 mi N Matatlan AMNH 85777; Rosario AMNH 91604. UNITED STATES Hawaii, UIMNH 5510-11, 41344, TCWC 35353.

**Holotype material of Typhlops examined**

basimaculatus USNM 6602, 61064 (syntypes), brongersmius MZUSP 5218, costaricensis UCR 1960 (= LACM 26767), crassum MNHN 208, longissimus MNHN 1061, melanocephalus MNHN 138, microstomus USNM 6344(2), 6590 (syntypes), minuisquamus TCWC 39130, nasutus BMNH 1946.10.45, paucisquamus MCZ 147336, psittacus MRNH 2017, stadelmani MCZ 38701, troscheli MNHN 3222, unilineatus MNHN 1064.
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