A taxonomic framework for typhlopid snakes from the Caribbean and other regions (Reptilia, Squamata)

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Article registration: http://zoobank.org/urn:lsid:zoobank.org:pub:47191405-862B-4FB6-8A28-29AB7E25FBDD
Edited by: Robert W. Henderson. **Date of publication:** 17 January 2014.
Citation: Hedges SB, Marion AB, Lipp KM, Marin J, Vidal N. 2014. A taxonomic framework for typhlopid snakes from the Caribbean and other regions (Reptilia, Squamata). *Caribbean Herpetology* 49:1–61.

Abstract

The evolutionary history and taxonomy of worm-like snakes (scolecophidians) continues to be refined as new molecular data are gathered and analyzed. Here we present additional evidence on the phylogeny of these snakes, from morphological data and 489 new DNA sequences, and propose a new taxonomic framework for the family Typhlopidae. Of 257 named species of typhlopid snakes, 92 are now placed in molecular phylogenies along with 60 additional species yet to be described. Afrotyphlopinae subfam. nov. is distributed almost exclusively in sub-Saharan Africa and contains three genera: *Afrotyphlops, Letheobia,* and *Rhinotyphlops*. Asiatyphlopinae subfam. nov. is distributed in Asia, Australasia, and islands of the western and southern Pacific, and includes ten genera: *Acutotyphlops, Anilios, Asiatyphlops* gen. nov., *Cyclotyphlops, Grypotyphlops, Indotyphlops* gen. nov., *Malayotyphlops* gen. nov., *Ramphotyphlops, Sundatyphlops* gen. nov., and *Xerotyphlops* gen. nov. Madatyphlopinae subfam. nov. occurs only in Madagascar and includes one genus: *Madatyphlops* gen. nov. Typhlopinae occurs in the New World and includes four genera: *Amerotyphlops* gen. nov., *Antillotyphlops* gen. nov., *Cubatyphlops* gen. nov., and *Typhlops*. Scolecophidians are the most ancient (deeply-branching) group of living snakes and their relationships track plate tectonics better than any other vertebrate group. Molecular data reveal large numbers of undescribed species, inferring that the true species diversity of these snakes is greatly underestimated.

Keywords: phylogeny, blindsnakes, Scolecophidia, Typhlopidae, systematics, biogeography, cryptic species.

Introduction

Scolecophidians are distributed on all continents except Antarctica but they are most diverse in tropical regions of continents and tropical islands (McDiarmid *et al.* 1999; Uetz & Hošek 2013). These worm-like snakes have been neglected in nearly all aspects of vertebrate research. Approximately 400 described species are placed in five families: Anomalepididae (anomalepidids, 18 species), Leptotyphlopidae (threadsnakes, 116 species), Typhlopidae (typical blindsnakes, 257 species), Gerrhopilidae (Indo-Malayan blindsnakes, 16 species), and Xenotyphlopidae (round-nosed blindsnake, 1 species) (Adalsteinsson *et al.* 2009; Vidal *et al.* 2010; Uetz & Hošek 2013). The Caribbean islands are unusual in having one of the largest blindsnake faunas in the world, numbering 44 species of typhlopids, with at least 25 additional undescribed species (see below).

This taxonomic update is a continuation of a series of systematic studies of scolecophidian snakes by our group (Hedges 1989; Hedges & Thomas 1991; Hedges *et al.* 1992; Rabosky *et al.* 2004; Thomas & Hedges 2007;

Hedges 2008; Adalsteinsson *et al.* 2009; Vidal *et al.* 2010; Hedges 2011; Marin *et al.* 2013a; Marin *et al.* 2013b; Wegener *et al.* 2013). Until recently (Adalsteinsson *et al.* 2009; Vidal *et al.* 2010), there was no published tree of the evolutionary relationships of scolecophidians, which is remarkable for a major group of vertebrates. One reason for the slow progress in the systematics of these snakes has been the paucity of useful morphological characters, not uncommon in burrowing reptiles with conservative body plans and often an impetus for exploring molecular data (Vidal *et al.* 2008). The use of molecular markers in scolecophidians has proven especially valuable in revealing cryptic species (Hedges & Thomas 1991; Aplin & Donnellan 1993; Rabosky *et al.* 2004; Thomas & Hedges 2007; Hedges 2008; Kornilios *et al.* 2011; Marin *et al.* 2013b) as well as discovering that some species are not valid (Wegener *et al.* 2013).

In recent years, two of us (SBH, NV) have expanded efforts to improve the systematics of scolecophidian snakes, globally, by assembling tissue samples with the help of collaborators working in Africa (W. Branch), Madagascar (M. Vences), and Australia (K. P. Aplin, S. C. Donnellan, P. Doughty, and M. N. Hutchinson) as well as donations of samples from persons working in other regions. This international effort has resulted in the generation of 2,414 DNA sequences from 11 nuclear and mitochondrial genes, all of which have been deposited in GenBank. Our analyses of these data have greatly refined the taxonomy of both of the major groups, the threadsnakes (Adalsteinsson *et al.* 2009) and blindsnakes (Vidal *et al.* 2010), as well as their biogeographic history (Vidal *et al.* 2010; Marin *et al.* 2013a). For example, it has led to the recognition and description of 10 new family group taxa and five new genus group taxa (Adalsteinsson *et al.* 2009; Vidal *et al.* 2010; Hedges 2011). However, these ongoing revisionary efforts have required continued sequence data collection and assembly of useful and relevant morphological characters. We have collected more than 1000 new DNA sequences of scolecophidians, not included in our previous studies, and all of these data, including morphological data, have helped to define supraspecific clades within Typhlopidae unrecognized previously. Although our intent has been to release this revisionary work in a single monograph, we are releasing the pertinent taxonomic information here. Hence, this current work, focused on Typhlopidae, should be viewed more as a preliminary taxonomic synopsis of a larger and more comprehensive work to come later. Here, we present 489 new DNA sequences, and molecular phylogenies that include at least 150 species (described and undescribed) of snakes in this family, along with a revised taxonomic framework and descriptions of new supraspecific taxa.

Materials and Methods

Data collection. Three separate molecular datasets were built for this study. We expanded our worldwide scolecophidian dataset, called here dataset A (Vidal *et al.* 2010), our Australian typhlopid dataset, dataset B (Marin *et al.* 2013a; Marin *et al.* 2013b), and built an expanded West Indian typhlopid dataset, dataset C. Each of the three datasets includes published and new sequences. However, for dataset B, all of the new sequences are from the samples used in Marin *et al.* (2013a, b); to avoid confusion, we list those samples and localities in Appendix 1. GenBank accession numbers for the 182 new sequences used in dataset B are KF992951–KF993132. For the previously published sequences (and museum accession numbers and localities) used in datasets A and C, see Vidal *et al.* (2010). GenBank accession numbers for the 105 new sequences used in dataset A are: KF992846–KF992950. GenBank accession numbers for the 202 new sequences used in dataset C are KF993133–KF993334. See Appendix 1 for details of the new samples used in the molecular analyses.

Laboratory methods. DNA extraction was performed as described in Winnepenninckx *et al.* (1993) or with the DNeasy Tissue Kit from Qiagen. The following genes were used: BDNF, RAG1, BMP2, NT3, and AMEL for dataset A (Vidal *et al.* 2010); cytochrome b, PRLR, BDNF, BMP2, 12S and 16S rRNA for dataset B (Marin *et al.* 2013a; Marin *et al.* 2013b); cytochrome b, ND2, 12S and 16S rRNA, PRLR, BDNF, RAG1, BMP2, NT3, and AMEL for dataset C. Amplification and sequencing was performed using primers from our previous scolecophidian studies (Adalsteinsson *et al.* 2009; Vidal *et al.* 2010; Marin *et al.* 2013a; Marin *et al.* 2013b) with the exception of those for 12S rRNA, 16S

rRNA, and ND2 (always 5′ to 3′): NV-12L2-AAA GCA WRG CAC TGA ARA TGC TWA GAT, NV-12H11-CAC TTT CCA GTA CGC TTA CCA TGT TAC G, JM-12L3-GGG GTG ACG GGC GGT GTG T, JM-12H13-AGT ATA CAT GCA AGW CTC, for the 12S rRNA; L2510-CGC CTG TTT ATC AAA AAC AT (Palumbi *et al.* 1991), H3056-CTC CGG TCT GAA CTC AGA TCA CGT AGG (Hedges 1994), for the 16S rRNA. For ND2, we designed 5 sets of primers: NDF1/NDR1, ND2F1/ND2R3, ND2F4/ND2R4, ND2F5/ND2R5, and ND2F6/ND2R6. Those primers are: ND2F1-CAG CTA AAT AAG CTM TCG GGC CCA TAC C, NDR1-ACT TCT GGT ACT CAR AAR TG, ND2R3-GCT TTG AAG GCY SCT GGT TTA, ND2F4-ACT GGA TTY WTR CCW AAA TGA AT, ND2R4-GAT CCG ATG TCT TTA ATR GTT, ND2F5-CTA AAY CAA ACA CAA CTM CGA, ND2R5-GAT CCG ATG TCT TTA ATR GTT, ND2F6-CCA TTT CAC TTC TGA GTR CCA GAA GT, and ND2R6-TCG KAG TTG TGT TTG RTT TAG. For all genes, DNA amplification was performed in a 21 µL final volume containing 1 µL DMSO, 0.8 µL of dNTP (6.6 mM), 0.12 µL of Taq DNA polymerase (MP Biomedicals or Qiagen), using 2.5 µL of the buffer provided by the manufacturer, 100 $u.ml^{-1}$ and 0.32 µL of each primer at 10 pM, and 1 µL of DNA extract. The PCR conditions were: an initial denaturation for 3 min at 94°C followed by 40 cycles (3 min at 94°C, 40 s at 50°C, 1 min at 72°C) and a final elongation at 72°C for 10 min, using a PCR System 2700 thermocycler (Applied Biosystems).

Both complementary strands of the PCR products were sequenced at Pennsylvania State University and Genoscope (http://www.genoscope.fr). The two strands obtained for each sequence, and multiple sequences, were combined and aligned using the BioEdit Sequence Alignment Editor program (Hall 1999) and alignment tools in MEGA5 (Tamura *et al.* 2011). Any difference between the two strands was coded as undetermined. Amino acid translations were used and alignment was straightforward for all nuclear genes. Alignment was also straightforward for 12S and 16S rRNA as the longest gap had a length of 4 bp. In all analyses, gaps were treated as missing data. Alignments can be obtained from Nicolas Vidal. For dataset A, alignments resulted in 630 BDNF sites, 516 RAG1 sites, 591 BMP2 sites, 639 NT3 sites, and 375 AMEL sites (total: 2751 sites from 5 genes for 127 taxa). For dataset B, alignments resulted in 678 cytochrome b sites, 483 PRLR sites, 669 BDNF sites, 588 BMP2 sites, 717 12S rRNA sites, and 406 16S rRNA sites (total: 3541 sites from 6 genes for 94 taxa). For dataset C, alignments resulted in 1107 cytochrome b sites, 573 16S rRNA sites, 383 12S rRNA sites, 909 ND2 sites, 552 PRLR sites, 630 BDNF sites, 516 RAG1 sites, 588 BMP2 sites, 639 NT3 sites, and 372 AMEL sites (total: 6269 sites from 10 genes for 54 taxa).

Phylogenetic analyses. We built all phylogenies using Maximum Likelihood (ML) and Bayesian methods of inference (BI). ML analyses were performed with RAxML 7.2.7 (Stamatakis 2006; Stamatakis *et al.* 2008), and Bayesian analyses were performed with MrBayes 3.1.2 (Ronquist & Huelsenbeck 2003). For all datasets, we first analyzed each gene separately to check topological congruence before combining them in our final datasets. The partitioning strategy was the same for all three datasets: first codon positions of combined nuclear genes, second codon positions of combined nuclear genes, third codon positions of combined nuclear genes, first codon positions of combined mitochondrial genes, second codon positions of combined mitochondrial genes, third codon positions of combined mitochondrial genes, and combined 12S and 16S rRNA treated as one partition, with a GTR + I + G model applied to each partition for Bayesian analyses and a GTR + G model applied to each partition for RAxML analyses as recommended in Stamatakis (2006).

For Bayesian analyses, four simultaneous Markov chains were run for 5 million generations, sampling every 100 generations, and discarding all samples during a 500,000 generation burnin-in period. Convergence of the Bayesian runs was examined by plots of ln *L* scores and low standard deviation of split frequencies as implemented in MrBayes 3.1.2. Two independent Bayesian runs were performed as an additional check that the chains mixed well and converged. For the ML analyses, we performed 1,000 bootstrap replicates, using the GTRCAT option. The resulting ML and Bayesian trees were visualized with FigTree 1.3.1. (http://tree.bio.ed.ac.uk/software/figtree/).

Morphological data. One of us (SBH) has collected and examined nearly every species of typhlopid snake from Caribbean islands, and has borrowed and examined comparative material from museums (e.g., Hedges & Thomas 1991; Thomas & Hedges 2007). However, most of our morphological data (Tables 1–2), globally, are from the literature, including species descriptions (Table 3), summary articles, and illustrations of head scalation. We report classical characters used in the group, but also with a focus on their diagnostic ability. For example, postnasal

Table 1. Morphological variation in the species of typhlopid snakes. Numbered columns correspond to the 20 numbered characters in the diagnoses. States separated by commas are equally frequent; those in parentheses are uncommon. Abbreviations: (1, eye), d (distinct), i (indistinct); (2, snout), b (beaked), r (rounded), a (acuminate); (3, head scales), c (circular), nc (non circular); (4, frontorostral), p (present), a (absent); (5, nasal division), c (complete), i (incomplete); (6, nasal suture origin), 1 (supralabial 1), 2 (supralabial 2), s1 (suture 1 & 2), s2 (suture 2 & preocular), r (rostral), p (preocular); (7, subocular or subpreocular scales), p (present), a, (absent); (8a, postocular range); (8b, postocular average); (9, preocular-labial contact), 0 (no contact), 0i (intercalary scale), 0s (subpreocular), otherwise single supralabial scales or range of scales contacted are listed; (10a, midbody scale rows, range); (10b, midbody scale rows, average); (11, scale row reduction), p (present), a (absent); (12a, total middorsal scale rows, range); (12b, total middorsal scale rows, average); (13a, caudal scales, range); (13b, caudal scales, average); (14a, total length in mm, range of species maximums); (14b, total length, average of species maximums); (15a, body shape = total length/width, range); (15b, body shape, average); (16a, total length/tail length , range); (16b, total length/tail length, average); (17, dorsal ground color); (18, ventral ground color); (19, dorsal-ventral color difference), 0 (no difference = unicolor), 1 (dorsum darker = bicolor); (20, pattern), bl (blotched or marbled), br (bars), dl (dorsal lines), juv (juveniles), nk (neck band or collar), rt (reticulated), sp (spots or speckling), tr (tail rings), un (unpatterned), v (variable), ven (venter), vl (ventral lines); n/a (not available). Color abbreviations: bk (black), bl (blue), bg (beige), bn (brown), cr (cream), dk (dark), gd (gold), gn (green), gy (gray), lv (lavender), oc (ochre), ol (olive), or (orange), pk (pink or pale red), pl (pale), pu (purple), rd (red), tn (tan), um (umber), un (unpigmented), wt (white), yl (yellow).

	1	2	3	4	5	6	7	8a	9	10a	11
AFROTYPHLOPINAE											
Afrotyphlops angolensis	d	r	nc	a	i	1	a	3	2–3	24–36	p
Afrotyphlops anomalus	d	b	nc	a	i	r	a	4–7?	1–3	29–32	p
Afrotyphlops bibronii	d	r	nc	a	i	1	a	3–4	2	30–34	p
Afrotyphlops blanfordii	d	r	nc	a	i	1	a	4	2–3	28–32	p
Afrotyphlops brevis	d	b	nc	a	i	2	a	3–4	2–3	29–38	p
Afrotyphlops calabresii	d	a	nc	a	i	2	a	2	2–3	20–22	a
Afrotyphlops comorensis	d	r	nc	a	i	2	a	2–4	2–3	20–22	p
Afrotyphlops congestus	d	r	nc	a	i	1	a	3	2–3	24–30	p
Afrotyphlops cuneirostris	d	a	nc	a	i?	2	a	2	2–3	20–24	a(p)
Afrotyphlops decorosus	d	r	nc	a	i?	1	a	4	2–3	24	a
Afrotyphlops elegans	d	r	nc	a	i,c	1	a	3	2–3	18–20	n/a
Afrotyphlops fornasinii	d	r	nc	a	c,i	1	a	4	2	22–26	p,a
Afrotyphlops gierrai	d	r	nc	a	i	1	p	4	0i	26–28	p,a
Afrotyphlops jubanus	d	b	nc	a	i	1	a	4	2–3	24	p
Afrotyphlops kaimosae	d	b	nc	a	i	1	a	5	0	28	a
Afrotyphlops liberiensis	d	r	nc	a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
Afrotyphlops lineolatus	d	r	nc	a	i	1	a	4–5	2–3	26–30	p
Afrotyphlops mucruso	d	b	nc	a	i	1	a	6–7	2–3,2	30–40	p
Afrotyphlops nanus	d	r	nc	a	i	1	a	2–3	2	30	p
Afrotyphlops nigrocandidus	d	r	nc	a	i	1	p(a)	n/a	0i	28–34	p
Afrotyphlops obtusus	d	r	nc	a	i	1	a	>3	2–3	22–26	p
Afrotyphlops platyrhynchus	d	r	nc	a	i	2	a	3	2–3	24	p
Afrotyphlops punctatus	d	r	nc	a	i	1	a	4	2–3	28–32	p(a)
Afrotyphlops rondoensis	d	r	nc	a	i	1	a	3–4	2	22–26	p(a)
Afrotyphlops schlegelii	d	b	nc	a	i	1	a	4–6	2–3	32–45	p
Afrotyphlops schmidti	d	r	nc	a	i	1	a	4	2–3	22–26	p
Afrotyphlops steinhausi	d	r	nc	a	i	1	a	3–4	1–2	26–28	p
Afrotyphlops tanganicanus	d	r	nc	a	i	1	a	3	2–3	21–24	p
Afrotyphlops usambaricus	d	r	nc	a	i	r/1?	a	4	2–3	26–28	p
Letheobia acutirostrata	i	n/a	nc	a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
Letheobia angeli	i	n/a	nc	a	n/a	2	n/a	n/a	n/a	n/a	n/a
Letheobia caeca	i	b	nc	a	c	2(r,1,s1)	p	4	2–3,3	22–26	n/a
Letheobia coecata	i	r	nc	a	c	2	a	2–3?	3	18–20	n/a
Letheobia crossii	i	b	nc	a	c	2	a	3–4	2–3?	22–24	p
Letheobia debilis	i	b	nc	a	i	s1?	p	4	2	18–20	p,a
Letheobia episcopa	i	b	nc	a	c	2	p	4–6?	2–4	20	a
Letheobia erythraea	i	b	nc	a	c	2	p	3–4?	2–3	20–23	p
Letheobia feae	i	b	nc	a	c	2	a	2	2–3	20–22	p,a
Letheobia gracilis	i	b	nc	a	c,i?	s1?	p	4	2–3	22	a

Letheobia graueri	i	b	nc	a	i	1,s1,2	p	2	2–3	24	a
Letheobia kibarae	i	b	nc	a	i	1	p	4	2–3	24	p
Letheobia largeni	i	r	nc	a	c	2	p	4	2–3	22	p
Letheobia leucosticta	i	r	nc	a	c,i?	2	a	3	2–3	22	p
Letheobia lumbriciformis	i	b	nc	a	i	2	p	4	2–3	18	a(p)
Letheobia manni	i	r	nc	a	i	2	p	4	2–3	26	n/a
Letheobia newtoni	i	b	nc	a	c,i?	2	a	3	3	26–28	p
Letheobia pallida	i	r	nc	a	i	2	p	4–7?	2–3	22	p(a)
Letheobia pauwelsi	i	b	nc	a	c	1	p	3–4?	2–3	22	a
Letheobia pembana	i	r	nc	a	n/a	2	p	n/a	n/a	24	p
Letheobia praeocularis	i	b	nc	a	c	2	a	3?	0	24–26	p
Letheobia rufescens	i	b	nc	a	i	2	p	3–5	2	20	p,a
Letheobia simonii	i	b	nc	a	i,c	1	a	2–3	2–3?	20–21	p,a
Letheobia somalica	i	r	nc	a	c	s1?	a	3–6	2–3	24–30	p,a
Letheobia stejnegeri	i	b	nc	a	c	s1?	a	3	2	26	p
Letheobia sudanensis	i	b	nc	a	i	2	p	3	2–3	24	p,a
Letheobia swahilica	i	r	nc	a	c	2	p	4	2–3	22	p(a)
Letheobia toritensis	i	r	nc	a	i	1	p	3	2–3	22–24	p
Letheobia uluguruensis	i	r	nc	a	c	2	p	5	2–3	20–22	p
Letheobia wittei	i	r	nc	a	i	2	p	4	2	20	a
Letheobia zenkeri	i	r	nc	a	c	p	p	2	0s	18	n/a
Rhinotyphlops ataeniatus	d	b	nc	a	c	2	p	4	2–3	24	p(a)
Rhinotyphlops boylei	d	r	nc	a	i	2	a	5	2–3	24–28	p
Rhinotyphlops lalandei	d	b	nc	a	i	1	a	2	2,2–3	26–34	p(a)
Rhinotyphlops leucocephalus	d	b	nc	a	i	2	a	3	2–3	24	n/a
Rhinotyphlops schinzi	d	b	nc	a	i	1	a	4–6	2	22–26	a
Rhinotyphlops scortecci	d	b	nc	a	c	2	p	4–5	2–4	23–25	p(a)
Rhinotyphlops unitaeniatus	d	b	nc	a	c	2	p	6	2–3	24	p
ASIATYPHLOPINAE											
Acutotyphlops banaorum	d	r	nc	p	i	2	a	3–4	3	26	p
Acutotyphlops infralabialis	d	a	nc	p	i?	1	p	3–5	2–3	26–28	p
Acutotyphlops kunuaensis	d	a	nc	p	i	2	p	3–5	2–3	30–36	p
Acutotyphlops solomonis	d	r	nc	p	i	2	p	4–5	0s	29–34	p
Acutotyphlops subocularis	d	a	nc	p	i	2	p	4–5	0s	32–36	p
Anilios affinis	d	r	nc	a	c	2	a	2	2–3	18	n/a
Anilios ammodytes	d	r	nc	a	c,i	p	a	2	2–3	20	n/a
Anilios aspinus	d	r	nc	a	i	2	a	2	2–3	18	n/a
Anilios australis	d	r	nc	a	i	2(s1,s2,p)	a	2–3?	2–3	22	n/a
Anilios batillus	d	a	nc	a	c	2	a	1	2–3	24	p
Anilios bicolor	d	r	nc	a	i	s2?	a	2–3	2–3	22	a
Anilios bituberculatus	d	b	nc	a	i	2	a	2	2–3	20	n/a
Anilios broomi	d	r	nc	a	i,c	2	n/a	n/a	2–3	20	n/a
Anilios centralis	d	b	nc	a	i	2	a	n/a	2–3	20	n/a
Anilios chamodracaena	d	r	nc	a	i	2	a	3	2–3	18	n/a
Anilios diversus	d	r	nc	a	c,i	p	a	2	2–3	20	n/a
Anilios endoterus	d	b	nc	a	i	p	a	2	2–3	22	n/a
Anilios erycinus	d	r	nc	a	c	1	a	2	2–3	20	n/a
Anilios ganei	d	r	nc	a	c	2	a	1	2–3	24	a
Anilios grypus	d	b	nc	a	i,c	2(p,1,s2)	a	3	2–3	18	n/a
Anilios guentheri	d	r	nc	a	i	2	a	2	2–3	18	n/a
Anilios hamatus	d	b	nc	a	i	2(p,1,s1)	a	3	2–3	22	a
Anilios howi	d	r	nc	a	c	2	a	n/a	2–3	18	n/a
Anilios kimberleyensis	d	r	nc	a	i	2	a	n/a	2–3	22	n/a
Anilios leptosomus	d	b	nc	a	c,i	2	a	1–2?	2–3	16–18	a
Anilios leucoproctus	d	r	nc	a	i	2	a	2	2–3	20	n/a
Anilios ligatus	d	r	nc	a	i	1	a	2	2–3	24	n/a
Anilios longissimus	d	r	nc	a	i	2	a	3	2–3	16	a

Anilios margaretae	d	r	nc	a	i	2	a	n/a	2–3	18	n/a
Anilios micrommus	d	r	nc	a	c	2	a	n/a	2–3	18	n/a
Anilios minimus	d	r	nc	a	i	2	a	3	2–3	16	n/a
Anilios nema	d	r	nc	a	i	2	a	2	2–3	16	n/a
Anilios nigrescens	d	r	nc	a	i	1	a	2	2–3	22	n/a
Anilios nigroterminatus	d	b	nc	a	c	2	a	3	2–3	18	n/a
Anilios pilbarensis	d	b	nc	a	i	p	a	1	2–3	22	a
Anilios pinguis	d	b	nc	a	i	2	a	3	2–3	20	n/a
Anilios proximus	d	b	nc	a	i	1	a	2	2–3	20	n/a
Anilios robertsi	d	r	nc	a	i	2	a	2	2–3	22	n/a
Anilios silvia	d	r	nc	a	i	2	a	2–3	2–3	20	n/a
Anilios splendidus	d	b	nc	a	i	2	a	4	2–3	20	n/a
Anilios torresianus	d	r	nc	a	i	2,s1	a	2	2–3	22	n/a
Anilios tovelli	d	r	nc	a	i	p	a	n/a	2–3	20	n/a
Anilios troglodytes	d	r	nc	a	c	2	a	n/a	2–3	22	n/a
Anilios unguirostris	d	b	nc	a	c,i	1	a	2	2–3	24	n/a
Anilios waitii	d	b	nc	a	i	2	a	n/a	2–3	20	n/a
Anilios wiedii	d	r	nc	a	i	2	a	2	2–3	20	n/a
Anilios yampiensis	d	r	nc	a	c,i?	p	a	n/a	2–3	18	n/a
Anilios yirrikalae	d	r	nc	a	i	1	a	2	2–3	24	n/a
Asiatyphlops bothriorhynchus	d	r	nc	a	c	2	a	3	2–3	22–24	n/a
Asiatyphlops diardii	d	r	nc	a	i	2	a	3	2–3	24–28	p
Asiatyphlops fuscus	d	r	nc	a	i	2	a	5	3	24	n/a
Asiatyphlops giadinhensis	d	r	nc	a	i	2	a	2	2–3	22	n/a
Asiatyphlops klemmeri	d	n/a	nc	a	i	2	a	2	n/a	23–24	n/a
Asiatyphlops koshunensis	d	n/a	nc	a	n/a	2	n/a	2	n/a	20–23	n/a
Asiatyphlops leucomelas	d	r	nc	a	c	2	a	2	2–3	22	n/a
Asiatyphlops muelleri	d	r	nc	a	i	2	a	4	2–3	24–30	p
Asiatyphlops oatesii	d	r	nc	a	i	2	a	3	2–3	24	n/a
Asiatyphlops roxaneae	d	r	nc	a	i	2	a	2	2–3	20	p
Asiatyphlops siamensis	d	r	nc	a	i	2	a	2	3	22	n/a
Asiatyphlops tenuicollis	d	r	nc	a	i	2	a	3	2–3	22	n/a
Asiatyphlops trangensis	i	r	nc	a	i	2	n/a	2	2–3	24	a
Cyclotyphlops deharvengi	d	r	c	a	c	s1	p	1	0	22	p
Grypotyphlops acutus	d,i	b	nc	a	i,c	2	p	4(3,5)	2–3	24–34	p
Indotyphlops ahsanai	d	r	nc	a	i	2	a	1	3	18	p
Indotyphlops albiceps	d	r	nc	a	c,i?	2	a	1?	2–3	20	a
Indotyphlops braminus	d	r	nc	a	c	p	a	1	2–3	20	a
Indotyphlops exiguus	d	r	nc	a	c,i?	2	a	1?	3	18	n/a
Indotyphlops filiformis	d	r	nc	a	i	1	a	1?	2–3	20	n/a
Indotyphlops fletcheri	d	r	nc	a	c	2	a	1	2–3	20	n/a
Indotyphlops hypsobothrius	d	r	nc	a	i	2	a	n/a	2–3	20	n/a
Indotyphlops jerdoni	d	r	nc	a	c	2	a	1	3	22	n/a
Indotyphlops khoratensis	i	n/a	nc	a	c	p	n/a	1	n/a	20	n/a
Indotyphlops lankaensis	d	r	nc	a	c	p	a	1	2–3	20	n/a
Indotyphlops lazelli	d	r	nc	a	i	2	a	1	2–3	18	a
Indotyphlops loveridgei	i	r	nc	a	c,i?	s2?	a	1	3	18	n/a
Indotyphlops madgemintonae	d	r	nc	a	c,i?	2	a	1	2–3	18	a
Indotyphlops malcolmi	d	n/a	nc	a	c	2	n/a	1	n/a	20	n/a
Indotyphlops meszoelyi	d	r	nc	a	i	2	a	1	3	18	a
Indotyphlops ozakiae	i	r	nc	a	i	2	n/a	n/a	n/a	20	a
Indotyphlops pammeces	n/a	n/a	nc	a	n/a	p	n/a	n/a	n/a	20	n/a
Indotyphlops porrectus	d	r	nc	a	i,c	2	a	1–2	2–3	18	n/a
Indotyphlops schmutzi	d	r	nc	a	c	2	a	1	2–3	18–20	n/a
Indotyphlops tenebrarum	i	r	nc	a	c	2	a	1	2–3	20	n/a
Indotyphlops veddae	d	r	nc	a	c	2	a	1	2–3	20	n/a
Indotyphlops violaceus	d	r	nc	a	c	p	n/a	n/a	n/a	20	n/a
Malayotyphlops canlaonensis	d	n/a	nc	a	i	2	n/a	2	3	30	n/a

Malayotyphlops castanotus	d	r	nc	a	i	2	a	2	3	26–28	p
Malayotyphlops collaris	d	r	nc	a	i	2	a	3	3	26–28	p
Malayotyphlops hypogius	d	r	nc	a	i	2	a	2	2–3	24	p
Malayotyphlops koekkoeki	i	r	nc	a	i	1	a	n/a	2–3	26	n/a
Malayotyphlops kraali	d	r	nc	a	c	2	a	4	3?	24–28	p
Malayotyphlops luzonensis	d	r	nc	a	c	2	n/a	2	2–3	26	n/a
Malayotyphlops manilae	d	r	nc	a	i	2	p	3	2	28	n/a
Malayotyphlops ruber	d	r	nc	a	i	2	n/a	n/a	3	26	n/a
Malayotyphlops ruficauda	d	r	nc	a	i	2	a	4	3	26–30	n/a
Ramphotyphlops acuticauda	d	r	nc	a	c	2	a	2	2–3	22–24	n/a
Ramphotyphlops adocetus	d	r	nc	a	c	2	a	3	2–3	22	p
Ramphotyphlops angusticeps	d	b	nc	a	c	1	a?	3	2–3	20	n/a
Ramphotyphlops becki	d	r	nc	a	c	2	a	2	2–3	20	n/a
Ramphotyphlops conradi	d	r	nc	a	c	2	a	1	2–3	20	n/a
Ramphotyphlops cumingii	d	b	nc	a	c	2	a	3	3	24–28	n/a
Ramphotyphlops depressus	d	r	nc	a	c	2	a	1–3?	2–3	22–24	p,a
Ramphotyphlops exocoeti	d	r	nc	a	i	2	a	2	2–3	20	n/a
Ramphotyphlops flaviventer	d	r	nc	a	l,c	2	a	2(3)	2–3	22	a(p)
Ramphotyphlops hatmaliyeb	d	r	nc	a	c	2	a	2–3	2–3	22	a
Ramphotyphlops lineatus	d	r	nc	a	i	1	a	2	0	22–24	n/a
Ramphotyphlops lorenzi	d	b	nc	a	i	1	n/a	n/a	2–3	22	n/a
Ramphotyphlops mansuetus	d	b	nc	a	c	2	a	2	2–3	18	n/a
Ramphotyphlops marxi	d	b	nc	a	c	2	a	3	2–3	30	p
Ramphotyphlops melanocephalus	i	b	nc	a	i	2	a	1	0	18	a
Ramphotyphlops multilineatus	d	b	nc	a	i	1	a	2	2–3	20–23	n/a
Ramphotyphlops olivaceus	d	b	nc	a	c,i?	s1	a	3	2–3	20–22	a(p)
Ramphotyphlops similis	d	r	nc	a	i	2	a	1	2–3	20	p
Ramphotyphlops suluensis	d	b	nc	a	c	1	a	2	2–3	22	a
Ramphotyphlops supranasalis	d	r	nc	a	l,c	2	n/a	2–3	2–3	22	p,a
Ramphotyphlops willeyi	d	b	nc	a	c	2	a	2	2–3	22	n/a
Sundatyphlops polygrammicus	d	r	nc	a	l,c	1,s1,2	n/a	n/a	2–3	22	n/a
Xerotyphlops etheridgei	d	r	nc	a	i	2	a	2	2–3	24	p
Xerotyphlops socotranus	d	r	nc	a	i	2	a	2	2–3	24	p
Xerotyphlops vermicularis	d	r	nc	a	i	2	a	2	2–3	20–24	n/a
Xerotyphlops wilsoni	d	r	nc	a	i	2	p	n/a	2–3	24	p
MADATYPHLOPINAE											
Madatyphlops andasibensis	d	r	nc	a	i	2	a	3(2)	2–3	26	p
Madatyphlops arenarius	d	r	nc	a	c,i?	2	a	2–3	2–3	20–24	n/a
Madatyphlops boettgeri	d	r	nc	a	i	2	a	2	2–3	20–22	n/a
Madatyphlops decorsei	d	r	nc	a	i	2	a	2–3	2–3	26–28	n/a
Madatyphlops domerguei	d	r	nc	a	i	2	a	1	2–3	22	n/a
Madatyphlops madagascariensis	d	r	nc	a	i	2	a	2	2–3	24	p
Madatyphlops microcephalus	d	r	nc	a	i	2	a	2–3	n/a	20	n/a
Madatyphlops mucronatus	d	r	nc	a	i	2	a	2–4	2–3	24–28	p,a
Madatyphlops ocularis	d	r	nc	a	c	2	a	2–3	2–3	20	a
Madatyphlops rajeryi	d	r	nc	a	i	2	a	2	2–3	24	p
Madatyphlops reuteri	d	r	nc	a	i	2	a	2	2–3	20	n/a
TYPHLOPINAE											
Amerotyphlops amoipira	d	r	nc	a	i	s1,2	a	2	2–3	18	a
Amerotyphlops brongersmianus	d	r	nc	a	i	2	a	1	2–3	20	p
Amerotyphlops costaricensis	d	r	nc	a	c	2?	a	2	2–3	20	a
Amerotyphlops lehneri	d	r	nc	a	c	2	a	0–1?	2–3	20	a
Amerotyphlops microstomus	i	r	nc	a	c	2	p	2	2–3	18	a
Amerotyphlops minuisquamus	d	r	nc	a	i	2	a	1	2–3	16–18	p
Amerotyphlops paucisquamus	i	r	nc	a	i	2	a	1	2–3	18	a
Amerotyphlops reticulatus	d	r	nc	a	i	2	a	1–4?	2–3	20	p
Amerotyphlops stadelmani	i	r	nc	a	c	2	n/a	n/a	2–3	18	a

Amerotyphlops tasymicris	d	r	nc	a	c	1	a	1	2–3	20	a
Amerotyphlops tenuis	i	r	nc	a	c	2	a	2–3	2–3	17–18	a
Amerotyphlops trinitatus	d	r	nc	a	c	s1	a	1	2–3	20	a
Amerotyphlops tycherus	i	r	nc	a	c	2	a	3–4	2–3	22	a
Amerotyphlops yonenagae	d	r	nc	a	i	2	a	2	2–3	18	a
Antillotyphlops annae	d	r	nc	a	c	n/a	a	2	3–4?	20–22	p
Antillotyphlops catapontus	n/a	n/a	nc	a	c	2	n/a	2	n/a	20	p
Antillotyphlops dominicanus	d	r	nc	a	c	2	a	2	3	22–24	p
Antillotyphlops geotomus	d	r	nc	a	c	2	n/a	2	3	20–22	p
Antillotyphlops granti	d	r	nc	a	c	2	a	2	3	16	p
Antillotyphlops guadeloupensis	d	r	nc	a	c	2	a	2	3	24	p
Antillotyphlops hypomethes	d	r	nc	a	c	2	a	2(1)	3	20	p
Antillotyphlops monastus	d	r	nc	a	c	2	a	2	3	20–22	p
Antillotyphlops monensis	d	a	nc	a	c	2	a	2	3	20	p
Antillotyphlops naugus	n/a	n/a	nc	a	c	2	n/a	2	n/a	18–20	p
Antillotyphlops platycephalus	d	r	nc	a	c	2	a	n/a	3	20–22	p
Antillotyphlops richardi	d	r	nc	a	c	2	a	2	3	20–22	p
Cubatyphlops anchaurus	d	r	nc	a	c	n/a	a	1	2–3	22	p
Cubatyphlops anousius	d	r	nc	a	c	n/a	a	1	2–3	22	p
Cubatyphlops arator	d	r	nc	a	c	2	a	1	2–3	24	p
Cubatyphlops biminiensis	d	r	nc	a	c	2	a	1(2)	2–3	22–24	p,a
Cubatyphlops caymanensis	d	r	nc	a	c	2	a	1(2)	2–3	20	a
Cubatyphlops contorhinus	d	r	nc	a	c	2	a	1	2–3	22	p
Cubatyphlops epactius	d	r	nc	a	c	n/a	a	1	2–3	22	a(p)
Cubatyphlops golyathi	d	r	nc	a	c	2	a	1	2–3	22	p
Cubatyphlops notorachius	d	r	nc	a	c	n/a	a	1	2–3	22	p
Cubatyphlops paradoxus	d	r	nc	a	c	2	a	1	2–3	22	a
Cubatyphlops perimychus	d	r	nc	a	c	n/a	a	1	2–3	22	p,a
Cubatyphlops satelles	d	r	nc	a	c	2	a	1	2–3	22	p
Typhlops agoralionis	d	r	nc	a	c	n/a	a	2	3	20	a
Typhlops capitulatus	d	r	nc	a	c	2	a	2(1)	3	20	a
Typhlops eperopeus	d	r	nc	a	c	2	a	2	3	20	p
Typhlops gonavensis	d	r	nc	a	c	2	a	2	3	20	a
Typhlops hectus	d	r	nc	a	c	2	a	2(3)	3	20–22	p,a
Typhlops jamaicensis	d	r	nc	a	c	2	a	2(1–3)	3	22	a(p)
Typhlops leptolepis	d	r	nc	a	c	2	a	2	3	18–20	p
Typhlops lumbricalis	d	r	nc	a	c	2	a	2(1–3)	3	18–20	p
Typhlops oxyrhinus	d	r	nc	a	c	2	a	2	3	18–20	p
Typhlops pachyrhinus	d	r	nc	a	c	2	a	2	3	18–20	p
Typhlops proancylops	d	r	nc	a	c	2	a	2	3	20	a
Typhlops pusillus	d	r	nc	a	c	2	p	2(1–3)	0s	20–22	p,a
Typhlops rostellatus	d	r	nc	a	c	2	a	2(1)	3	18–20	p
Typhlops schwartzi	d	r	nc	a	c	2	a	1	3	18–20	p
Typhlops silus	d	n/a	nc	a	c,i	2	a	2	3	18–20	p
Typhlops sulcatus	d	r	nc	a	c	2	a	1	3	20	a(p)
Typhlops sylleptor	d	n/a	nc	a	c	2	a	2	3	20	a
Typhlops syntherus	d	r	nc	a	c	2	a	1(2)	3	22	a
Typhlops tetrathyreus	d	r	nc	a	c	2	a	2	3	18–20	p
Typhlops titanops	d	r	nc	a	c	2	a	2	3	20	p

	12a	12b	13a	13b	14a	15a	15b	16a	16b
AFROTYPHLOPINAE									
Afrotyphlops angolensis	350–578	464	n/a	n/a	660	26–60	43.0	58.8	58.8
Afrotyphlops anomalus	365–431	398	n/a	n/a	540	29–37	33.0	47	47.0
Afrotyphlops bibronii	363–453	408	n/a	n/a	484	31–42	36.5	70.5	70.5
Afrotyphlops blanfordii	343–424	384	n/a	n/a	343	29–41	35.0	n/a	n/a

Afrotyphlops brevis	288–557	423	n/a	n/a	765	17–47	32.0	n/a	n/a
Afrotyphlops calabresii	257–302	280	8–12	10	189	18–37	27.5	n/a	n/a
Afrotyphlops comorensis	384–485	435	12–15	13.5	245	42–61	51.5	33.3–50	41.7
Afrotyphlops congestus	310–416	363	10	10	765	19–29	24.0	44.3	44.3
Afrotyphlops cuneirostris	216–257	237	n/a	n/a	158	21–40	30.5	58.4	58.4
Afrotyphlops decorosus	460–542	501	n/a	n/a	510	45–66	55.5	94.3	94.3
Afrotyphlops elegans	315–349	332	n/a	n/a	420	38.2–57.4	47.8	52	52.0
Afrotyphlops fornasinii	232–286	259	n/a	n/a	185	28–45	36.5	37.1	37.1
Afrotyphlops gierrai	372–463	418	n/a	n/a	469	32–58	45.0	n/a	n/a
Afrotyphlops jubanus	391–430	411	n/a	n/a	510	44–57	50.5	n/a	n/a
Afrotyphlops kaimosae	390	390	n/a	n/a	215	43	43.0	53.8	53.8
Afrotyphlops liberiensis	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
Afrotyphlops lineolatus	323–505	414	n/a	n/a	640	21–47	34.0	40	40.0
Afrotyphlops mucruso	307–517	412	n/a	n/a	950	21–58	39.5	49–79	64.0
Afrotyphlops nanus	284–290	287	10–11	10.5	125	23–27	25.0	41.7–47.6	44.7
Afrotyphlops nigrocandidus	464–542	503	n/a	n/a	573	38–51	44.5	62.9	62.9
Afrotyphlops obtusus	406–507	457	4	4	380	46–95	70.5	151.5	151.5
Afrotyphlops platyrhynchus	400–425	413	n/a	n/a	273	50–60	55.0	n/a	n/a
Afrotyphlops punctatus	374–465	420	n/a	n/a	660	26–33	29.5	n/a	n/a
Afrotyphlops rondoensis	312–379	346	n/a	n/a	370	33–45	39.0	57–78	67.5
Afrotyphlops schlegelii	341–620	481	n/a	n/a	804	19–46	32.5	45.5	45.5
Afrotyphlops schmidti	317–374	346	n/a	n/a	605	22–49	35.5	n/a	n/a
Afrotyphlops steinhausi	378–430	404	n/a	n/a	620	41–45	43.0	n/a	n/a
Afrotyphlops tanganicanus	352–425	389	n/a	n/a	390	29–47	38.0	n/a	n/a
Afrotyphlops usambaricus	344–389	367	n/a	n/a	605	27–31	29.0	n/a	n/a
Letheobia acutirostrata	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
Letheobia angeli	n/a	n/a	n/a	n/a	332	n/a	n/a	n/a	n/a
Letheobia caeca	417–561	489	n/a	n/a	425	n/a	n/a	76	76.0
Letheobia coecata	282–334	308	n/a	n/a	165	n/a	n/a	73.5	73.5
Letheobia crossii	459–513	486	8–13	10.5	310	54–85	69.5	55.6–100	77.8
Letheobia debilis	547–668	608	11	11	480	98–129	113.5	125.8–135.7	130.8
Letheobia episcopa	544–581	563	11–15	13	318	74–90	82.0	61.4–111.1	86.3
Letheobia erythraea	443–462	453	11	11	250	68–82	75.0	58.8	58.8
Letheobia feae	407–480	444	8	8	330	51–68	59.5	66.7	66.7
Letheobia gracilis	608–737	673	n/a	n/a	550	70–107	88.5	n/a	n/a
Letheobia graueri	454–622	538	n/a	n/a	450	60–89	74.5	n/a	n/a
Letheobia kibarae	562–623	593	n/a	n/a	525	58–87	72.5	n/a	n/a
Letheobia largeni	432	432	n/a	n/a	274	64–65	64.5	n/a	n/a
Letheobia leucosticta	336	336	n/a	n/a	230	45–47	46.0	n/a	n/a
Letheobia lumbriciformis	465–607	536	n/a	n/a	450	38–83	60.5	n/a	n/a
Letheobia manni	480–508	494	n/a	n/a	360	40	40.0	68.6	68.6
Letheobia newtoni	446–557	502	12	12	400	50–70	60.0	52.6–71.4	62.0
Letheobia pallida	418–429	424	n/a	n/a	265	53–62	57.5	n/a	n/a
Letheobia pauwelsi	483	483	11	11	310	81.6	81.6	62.5	62.5
Letheobia pembana	353	353	n/a	n/a	158	53	53.0	n/a	n/a
Letheobia praeocularis	493–544	519	n/a	n/a	340	67	67.0	n/a	n/a
Letheobia rufescens	585–656	621	n/a	n/a	520	69–90	79.5	n/a	n/a
Letheobia simonii	403–488	446	9–14	11.5	239	49–91	70.0	45.5–100	72.8
Letheobia somalica	555–656	606	11–13	12	670	44–90	67.0	71.4–142.9	107.2
Letheobia stejnegeri	488–548	518	n/a	n/a	465	46–53	49.5	83.6	83.6
Letheobia sudanensis	569–660	615	n/a	n/a	520	57–95	76.0	n/a	n/a
Letheobia swahilica	376–392	384	n/a	n/a	190	49–62	55.5	n/a	n/a
Letheobia toritensis	427–487	457	n/a	n/a	268	62–90	76.0	n/a	n/a
Letheobia uluguruensis	379–416	398	n/a	n/a	245	48–57	52.5	n/a	n/a
Letheobia wittei	501–511	506	n/a	n/a	310	68	68.0	n/a	n/a
Letheobia zenkeri	250–281	266	n/a	n/a	135	35–45	40.0	n/a	n/a
Rhinotyphlops ataeniatus	443–531	487	n/a	n/a	455	34–72	53.0	n/a	n/a

Rhinotyphlops boylei	344–379	362	n/a	n/a	223	33–53	43.0	60.7	60.7
Rhinotyphlops lalandei	334–467	401	n/a	n/a	355	31–63	47.0	n/a	n/a
Rhinotyphlops leucocephalus	369	369	n/a	n/a	220	43	43.0	70.7	70.7
Rhinotyphlops schinzi	413–538	476	14–15	14.5	293	34–64	49.0	50.2	50.2
Rhinotyphlops scortecci	311–405	358	n/a	n/a	280	27–73	50.0	n/a	n/a
Rhinotyphlops unitaeniatus	467–586	527	n/a	n/a	435	38–77	57.5	78.5	78.5
ASIATYPHLOPINAE									
Acutotyphlops banaorum	352–361	357	16–19	17.5	333	32.1–51.2	41.7	25–27.8	26.4
Acutotyphlops infralabialis	418–526	472	14–28	21	372	33.4–57.4	45.4	18.9–100	59.5
Acutotyphlops kunuaensis	360–542	451	11–31	21	373	22.4–57.6	40.0	21.1	21.1
Acutotyphlops solomonis	334–424	379	18–30	24	487	18.2–42.8	30.5	13–34.5	23.8
Acutotyphlops subocularis	363–472	418	14–28	21	394	23.2–43.8	33.5	15.9–33.3	24.6
Anilios affinis	278–357	318	n/a	n/a	220	45–60	52.5	n/a	n/a
Anilios ammodytes	397–432	415	10–16	13	252	57.5	57.5	19.6–62.5	41.1
Anilios aspinus	413–444	429	10–16	13	281	63.6–75.8	69.7	42.8	42.8
Anilios australis	305–401	353	10–18	14	500	24–50	37.0	22–41.7	31.9
Anilios batillus	557	557	n/a	n/a	320	53	53.0	45.7	45.7
Anilios bicolor	300–380	340	12	12	275	34.4	34.4	22–45.8	33.9
Anilios bituberculatus	425–503	464	11–18	14.5	450	40–90	65.0	30.3–66.7	48.5
Anilios broomi	456–460	458	15–16	15.5	250	30–60	45.0	n/a	n/a
Anilios centralis	417–502	460	12–20	16	306	60–69	64.5	32.3–66.7	49.5
Anilios chamodracaena	478–539	509	14–16	15	210	n/a	n/a	33.3–100	66.7
Anilios diversus	397–475	436	8–18	13	352	40–70	55.0	28.6–71.4	50.0
Anilios endoterus	415–454	435	9–16	12.5	400	40–60	50.0	34.5–66.7	50.6
Anilios erycinus	315–335	325	16–23	19.5	350	27.1–44	35.6	35	35.0
Anilios ganei	430–448	439	12–19	15.5	340	36.2–46.9	41.6	33.9–64.2	49.1
Anilios grypus	538–713	626	13–36	24.5	450	63–122	92.5	22.7–90.9	56.8
Anilios guentheri	535–595	565	10–15	12.5	400	40–90	65.0	54.6	54.6
Anilios hamatus	330–396	363	12–18	15	386	28.7–58.7	43.7	24.4–58.8	41.6
Anilios howi	450	450	16	16	210	n/a	n/a	34.5	34.5
Anilios kimberleyensis	500–524	512	12–20	16	296	n/a	n/a	45.5–58.8	52.2
Anilios leptosomus	660–665	663	16–25	20.5	400	70–88	79.0	26.3–66.7	46.5
Anilios leucoproctus	386–426	406	14–17	15.5	250	40–65	52.5	42.2–51.3	46.8
Anilios ligatus	346–452	399	11–17	14	500	20–40	30.0	18.1–37	27.6
Anilios longissimus	750	750	15	15	268	134.2	134.2	111.8	111.8
Anilios margaretae	571–571	571	12	12	306	n/a	n/a	90.9	90.9
Anilios micrommus	493–493	493	15	15	205	n/a	n/a	41.7	41.7
Anilios minimus	457	457	9–17	13	200	51.5–70.4	61.0	n/a	n/a
Anilios nema	529–603	566	9–14	11.5	268	57.1–92.6	74.9	n/a	n/a
Anilios nigrescens	n/a	n/a	n/a	n/a	750	30–60	45.0	45	45.0
Anilios nigroterminatus	n/a	n/a	n/a	n/a	275	55–102	78.5	54	54.0
Anilios pilbarensis	363–425	394	15–22	18.5	371	42.3–57.9	50.1	26.3–42.2	34.3
Anilios pinguis	289–350	320	12–19	15.5	550	20–30	25.0	17.5–38.5	28.0
Anilios proximus	n/a	n/a	n/a	n/a	750	20–40	30.0	50.6	50.6
Anilios robertsi	568	568	12	12	290	67.4	67.4	61.6	61.6
Anilios silvia	286–341	314	17–21	19	175	n/a	n/a	20–50	35.0
Anilios splendidus	377	377	13	13	509	46.3	46.3	46.3	46.3
Anilios torresianus	365	365	19	19	400	34–43	38.5	15–51.5	33.3
Anilios tovelli	n/a	n/a	n/a	n/a	122	36–40	38.0	29.2–34.9	32.1
Anilios troglodytes	655–655	655	14	14	402	n/a	n/a	76.9	76.9
Anilios unguirostris	279–506	393	11–16	13.5	700	38–70	54.0	37–83.3	60.2
Anilios waitii	548–693	621	13–26	19.5	614	57–80	68.5	32.3–100	66.2
Anilios wiedii	n/a	n/a	10	10	300	30–80	55.0	61.3	61.3
Anilios yampiensis	491	491	11	11	128	n/a	n/a	55.6	55.6
Anilios yirrikalae	n/a	n/a	n/a	n/a	200	60–70	65.0	n/a	n/a
Asiatyphlops bothriorhynchus	300–330	315	10	10	180	30	30.0	n/a	n/a
Asiatyphlops diardii	260–303	282	7–8	7.5	430	30.2	30.2	73	73.0

Asiatyphlops fuscus	n/a	n/a	n/a	n/a	214	n/a	n/a	42–42.8	42.4
Asiatyphlops giadinhensis	316–340	328	7–10	8.5	238	26	26.0	43.5–47.6	45.6
Asiatyphlops klemmeri	291–292	292	n/a	n/a	151	28	28.0	60.4	60.4
Asiatyphlops koshunensis	246	246	26	26	290	39–48	43.5	41.7–100	70.9
Asiatyphlops leucomelas	260–325	293	n/a	n/a	130	32	32.0	n/a	n/a
Asiatyphlops muelleri	384–439	412	8–13	10.5	355	32	32.0	88.8	88.8
Asiatyphlops oatesii	n/a	n/a	n/a	n/a	203	31–33	32.0	n/a	n/a
Asiatyphlops roxaneae	329	329	5	5	231	38.5	38.5	76.9	76.9
Asiatyphlops siamensis	368	368	9	9	216	33	33.0	n/a	n/a
Asiatyphlops tenuicollis	480–520	500	12	12	365	64–70	67.0	77.7	77.7
Asiatyphlops trangensis	370	370	11	11	155	30	30.0	55	55.0
Cyclotyphlops deharvengi	294	294	n/a	n/a	146	35.1	35.1	32.3	32.3
Grypotyphlops acutus	448–526	487	7–13	10	630	30–66	48.0	16.9–133.3	75.1
Indotyphlops ahsanai	341	341	7	7	170	68	68.0	68	68.0
Indotyphlops albiceps	317	317	12	12	194	39–64	51.5	n/a	n/a
Indotyphlops braminus	261–368	315	8–15	11.5	203	30–66	48.0	34.5–50	42.3
Indotyphlops exiguus	348	348	12	12	196	60–78	69.0	33.8–66.7	50.3
Indotyphlops filiformis	380–389	385	8	8	135	60	60.0	58.7	58.7
Indotyphlops fletcheri	n/a	n/a	n/a	n/a	149	40–45	42.5	n/a	n/a
Indotyphlops hypsobothrius	n/a	n/a	n/a	n/a	285	52–71	61.5	n/a	n/a
Indotyphlops jerdoni	260–313	287	n/a	n/a	280	35–46	40.5	30	30.0
Indotyphlops khoratensis	315–331	323	n/a	n/a	128	28–43.7	35.9	34.1–53.5	43.8
Indotyphlops lankaensis	229–261	245	11–15	13	130	29.1–33.3	31.2	22.3–39.7	31.0
Indotyphlops lazelli	409–427	418	10	10	158	77–83.2	80.1	55.6	55.6
Indotyphlops loveridgei	430	430	11	11	208	83	83.0	52.6–59.4	56.0
Indotyphlops madgemintonae	336–364	350	8–10	9	200	62–130	96.0	43–76	59.5
Indotyphlops malcolmi	262–282	272	9–11	10	107	31	31.0	23.8–36.8	30.3
Indotyphlops meszoelyi	414–421	418	9–10	9.5	179	53.8–71.4	62.6	45.5–50	47.8
Indotyphlops ozakiae	n/a	n/a	n/a	n/a	n/a	n/a	n/a	34.8	34.8
Indotyphlops pammeces	366–400	383	11	11	140	55–75	65.0	n/a	n/a
Indotyphlops porrectus	388–468	428	7–12	9.5	285	50–90	70.0	43.5–71.4	57.5
Indotyphlops schmutzi	403–413	408	9–12	10.5	140	62.5–93	77.8	n/a	n/a
Indotyphlops tenebrarum	298–326	312	12–14	13	112	43.3–44.8	44.1	36.1–55.5	45.8
Indotyphlops veddae	295–309	302	13–14	13.5	91	60	60.0	32.9	32.9
Indotyphlops violaceus	245–308	277	13	13	111	31	31.0	44.4	44.4
Malayotyphlops canlaonensis	n/a	n/a	n/a	n/a	122	34.1	34.1	48.8	48.8
Malayotyphlops castanotus	300–339	320	10–14	12	253	32	32.0	27.8–50	38.9
Malayotyphlops collaris	412–461	437	9–13	11	255	41	41.0	50–71.4	60.7
Malayotyphlops hypogius	323	323	10	10	176	39.1	39.1	44	44.0
Malayotyphlops koekkoeki	n/a	n/a	n/a	n/a	445	40.4	40.4	62.6	62.6
Malayotyphlops kraali	337–386	362	12	12	295	38.5–42	40.3	n/a	n/a
Malayotyphlops luzonensis	348	348	10	10	260	58	58.0	n/a	n/a
Malayotyphlops manilae	n/a	n/a	12	12	280	56	56.0	56	56.0
Malayotyphlops ruber	360	360	< 15	14	225	36–37	36.5	n/a	n/a
Malayotyphlops ruficauda	420	420	< 15	14	250	31–55	43.0	n/a	n/a
Ramphotyphlops acuticauda	n/a	n/a	n/a	n/a	123	52	52.0	30.8	30.8
Ramphotyphlops adocetus	447–474	461	32	32	390	38.1	38.1	18.3–30.3	24.3
Ramphotyphlops angusticeps	617–653	635	23–27	25	455	65–87.5	76.3	35	35.0
Ramphotyphlops becki	206–241	224	8–15	11.5	117	24.3	24.3	23.4	23.4
Ramphotyphlops conradi	398	398	11	11	175	58.3–59.8	59.1	70	70.0
Ramphotyphlops cumingii	n/a	n/a	n/a	n/a	365	48–52	50.0	n/a	n/a
Ramphotyphlops depressus	289–438	364	13–25	19	315	30.8–76.3	53.6	26.1	26.1
Ramphotyphlops exocoeti	n/a	n/a	n/a	n/a	350	58–66	62.0	38.3–43.8	41.1
Ramphotyphlops flaviventer	264–398	331	13–21	17	383	34.8–60.4	47.6	26.3–27.8	27.1
Ramphotyphlops hatmaliyeb	452–472	462	21	21	416	41.4	41.4	22.6–34.5	28.6
Ramphotyphlops lineatus	438	438	n/a	n/a	480	40–60	50.0	n/a	n/a
Ramphotyphlops lorenzi	n/a	n/a	n/a	n/a	337	56	56.0	n/a	n/a
Ramphotyphlops mansuetus	357	357	16	16	150	50	50.0	30	30.0

Ramphotyphlops marxi	525	525	36	36	180	45	45.0	16.9	16.9
Ramphotyphlops melanocephalus	524	524	20	20	183	91.5	91.5	36.6	36.6
Ramphotyphlops multilineatus	513–586	550	20–22	21	427	46.7–60	53.4	31.1–39	35.1
Ramphotyphlops olivaceus	441–544	493	24–31	27.5	425	42.4–58.3	50.4	n/a	n/a
Ramphotyphlops similis	234–235	235	9–12	10.5	235	18.1–27.4	22.8	25.7–35.6	30.7
Ramphotyphlops suluensis	n/a	n/a	n/a	n/a	340	46	46.0	26	26.0
Ramphotyphlops supranasalis	340–346	343	16–18	17	301	45.4–52.6	49.0	22.9–31.1	27.0
Ramphotyphlops willeyi	369–375	372	11–15	13	195	32–56.7	44.4	n/a	n/a
Sundatyphlops polygrammicus	496	496	16	16	395	33–66	49.5	15–51.5	33.3
Xerotyphlops etheridgei	424	424	10	10	220	55	55.0	87.7	87.7
Xerotyphlops socotranus	435	435	n/a	n/a	255	37–50	43.5	n/a	n/a
Xerotyphlops vermicularis	206	206	16	16	350	40–52	46.0	n/a	n/a
Xerotyphlops wilsoni	n/a	n/a	n/a	n/a	343	38	38.0	n/a	n/a
MADATYPHLOPINAE									
Madatyphlops andasibensis	373–381	377	8–11	9.5	340	27.2–28.1	27.7	34.5–52.6	43.6
Madatyphlops arenarius	375–465	420	7–11	9	220	45–85	65.0	50–111.1	80.6
Madatyphlops boettgeri	349–436	393	7–12	9.5	226	36–58	47.0	62.5–125	93.8
Madatyphlops decorsei	421–600	511	9–13	11	600	28–57	42.5	40–71.4	55.7
Madatyphlops domerguei	252–262	257	6–7	6.5	176	34–39	36.5	43.5–55.6	49.6
Madatyphlops madagascariensis	580	580	15	15	410	46	46.0	46–51.3	48.7
Madatyphlops microcephalus	310–365	338	8–11	9.5	235	34–51	42.5	35.7–62.5	49.1
Madatyphlops mucronatus	488–577	533	13–18	15.5	418	42–64	53.0	33.3–58.8	46.1
Madatyphlops ocularis	523–579	551	16–18	17	404	55–67	61.0	37–43.5	40.3
Madatyphlops rajeryi	412	412	12	12	272	36.8	36.8	36.7	36.7
Madatyphlops reuteri	345–359	352	8–9	8.5	222	38–49	43.5	38–55.6	46.8
TYPHLOPINAE									
Amerotyphlops amoipira	212–242	227	7–12	9.5	208	22.8–27.7	25.3	36.5–70.7	53.6
Amerotyphlops brongersmianus	204	204	12	12	325	24	24.0	30.6	30.6
Amerotyphlops costaricensis	390–413	402	7	7	369	36.4–44.4	40.4	57.8–78.1	68.0
Amerotyphlops lehneri	289–337	313	n/a	n/a	185	31–58	44.5	71.9–125	98.5
Amerotyphlops microstomus	487–556	522	n/a	n/a	366	50–77	63.5	73.5–270.3	171.9
Amerotyphlops minuisquamus	219–253	236	6–11	8.5	361	20.4–33.7	27.1	31.3–52.6	42.0
Amerotyphlops paucisquamus	170–190	180	8–11	9.5	158	16.4–21.8	19.1	26.6	26.6
Amerotyphlops reticulatus	223–301	262	7–15	11	522	22–30	26.0	23.3–62.5	42.9
Amerotyphlops stadelmani	341–369	355	n/a	n/a	310	37–70	53.5	43.9–100	72.0
Amerotyphlops tasymicris	429	429	n/a	n/a	181	48	48.0	70	70.0
Amerotyphlops tenuis	347–441	394	7–11	9	326	34–74	54.0	42.2–91.7	67.0
Amerotyphlops trinitatus	388–389	389	10	10	240	50	50.0	76.9	76.9
Amerotyphlops tycherus	395	395	8	8	371	40.8	40.8	66.2	66.2
Amerotyphlops yonenagae	259–269	264	9–10	9.5	101	25.3–27.4	26.4	48–50.5	49.3
Antillotyphlops annae	400–405	403	14	14	110	57.9	57.9	61.1	61.1
Antillotyphlops catapontus	376–409	393	n/a	n/a	265	n/a	n/a	37.9	37.9
Antillotyphlops dominicanus	434–499	467	n/a	n/a	360	40–50	45.0	n/a	n/a
Antillotyphlops geotomus	329–367	348	n/a	n/a	213	43.6	43.6	39.2	39.2
Antillotyphlops granti	370–386	378	n/a	n/a	154	54–70	62.0	59.2	59.2
Antillotyphlops guadeloupensis	393–430	412	n/a	n/a	162	36.8	36.8	46.3	46.3
Antillotyphlops hypomethes	363–407	385	n/a	n/a	270	41–56	48.5	35–47	41.0
Antillotyphlops monastus	351–394	373	n/a	n/a	258	39.1	39.1	30.7–43	36.9
Antillotyphlops monensis	299–345	322	n/a	n/a	203	40	40.0	60.7	60.7
Antillotyphlops naugus	345–390	368	n/a	n/a	243	n/a	n/a	30.4	30.4
Antillotyphlops platycephalus	350–365	358	11	11	302	45	45.0	39	39.0
Antillotyphlops richardi	300–369	335	12	12	258	50	50.0	35.7–39.7	37.7
Cubatyphlops anchaurus	514	514	n/a	n/a	240	63	63.0	48	48.0
Cubatyphlops anousius	465–513	489	n/a	n/a	197	45–55	50.0	55–56	55.5
Cubatyphlops arator	578–579	579	n/a	n/a	460	51–55	53.0	46–48	47.0
Cubatyphlops biminiensis	454–537	496	n/a	n/a	380	39–58	48.5	42–76	59.0
Cubatyphlops caymanensis	351–408	380	n/a	n/a	260	36–45	40.5	29–35	32

Cubatyphlops contorhinus	502	502	n/a	n/a	316	63	63.0	53	53.0
Cubatyphlops epactius	473–505	489	n/a	n/a	247	53–59	56.0	40.3–47.5	43.9
Cubatyphlops golyathi	629	629	22	22	371	58	58.0	33.7	33.7
Cubatyphlops notorachius	475–529	502	n/a	n/a	301	45–57	51.0	48–75	61.5
Cubatyphlops paradoxus	455–472	464	n/a	n/a	245	n/a	n/a	47–49	48.0
Cubatyphlops perimychus	453–496	475	n/a	n/a	280	41–59	50.0	46–85	65.5
Cubatyphlops satelles	514–527	521	n/a	n/a	350	62–75	68.5	55–61	58.0
Typhlops agoralionis	291–310	301	n/a	n/a	193	31–39	35.0	27–31	29.0
Typhlops capitulatus	358–457	408	n/a	n/a	267	46–57	51.5	29–46	37.5
Typhlops eperopeus	305–329	317	n/a	n/a	281	29–39	34.0	27–31	29.0
Typhlops gonavensis	399–455	427	n/a	n/a	220	46–57	51.5	38–88	63.0
Typhlops hectus	284–328	306	n/a	n/a	230	31–46	38.5	20–44	32.0
Typhlops jamaicensis	373–436	405	n/a	n/a	445	27–44	35.5	n/a	n/a
Typhlops leptolepis	250–308	279	11–15	13	211	29.6–43.7	36.7	18–37	27.5
Typhlops lumbricalis	256–271	264	12–13	12.5	166	28–32.6	30.3	30.8–48	39.4
Typhlops oxyrhinus	265–297	281	10–16	13	257	26.8–46.6	36.7	19.8–37.5	28.7
Typhlops pachyrhinus	243–257	250	11–14	12.5	219	28.4–33	30.7	30.1–31.3	30.7
Typhlops proancylops	283–312	298	n/a	n/a	243	31–46	38.5	20–31	25.5
Typhlops pusillus	245–332	289	15–19	17	226	27–37	32.0	23–39	31.0
Typhlops rostellatus	314–358	336	13	13	222	32–52	42.0	33–66.7	49.9
Typhlops schwartzi	237–282	260	n/a	n/a	326	23–38	30.5	22–41	31.5
Typhlops silus	254–261	258	n/a	n/a	126	30–34	32.0	56.7–63	59.9
Typhlops sulcatus	371–447	409	n/a	n/a	319	37–44	40.5	36–60	48.0
Typhlops sylleptor	305–324	315	n/a	n/a	214	33–34	33.5	27–43	35.0
Typhlops syntherus	299–353	326	8–14	11	209	25–36	30.5	27–51	39.0
Typhlops tetrathyreus	246–294	270	n/a	n/a	273	25–38	31.5	23–47	35.0
Typhlops titanops	231–264	248	n/a	n/a	216	25–30	27.5	21–34	27.5

	17	18	19	20
AFROTYPHLOPINAE				
Afrotyphlops angolensis	gy,dk-gy	yl	1	rt
Afrotyphlops anomalus	bn,ol-bn	yl	1	n/a
Afrotyphlops bibronii	yl-bn,or-bn,dk-bn,bk	oc-yl,bn,dk-bn,bk	0,1	pl-dl
Afrotyphlops blanfordii	ol-gy	pl	1	vl
Afrotyphlops brevis	gn-bn,gy-bn,gd-bn	yl,pl	1	dl(juv)
Afrotyphlops calabresii	rd-bn	wt	1	8–12 dk-dl
Afrotyphlops comorensis	dk-bn,rd-bn	n/a	n/a	n/a
Afrotyphlops congestus	bn-bk,yl	yl	1	bk-bl
Afrotyphlops cuneirostris	rd-bn	wt	1	8 dk-dl
Afrotyphlops decorosus	oc-yl	oc-yl	1	8–10 dk-dl
Afrotyphlops elegans	or-yl	or-yl	1	bk-dl
Afrotyphlops fornasinii	dk-gy,bk	dk-gy,bk	1	yl-bl (ven)
Afrotyphlops gierrai	pl-bn,bl-gy	yl-cr	1	n/a
Afrotyphlops jubanus	bn,dk-bn	pl	1	n/a
Afrotyphlops kaimosae	bk,dk-bn	pl	1	n/a
Afrotyphlops liberiensis	n/a	n/a	n/a	n/a
Afrotyphlops lineolatus	yl,bk	yl,pl	1	bn-dl,bl(ven)
Afrotyphlops mucruso	bk	wt	1	dl,bl
Afrotyphlops nanus	pl-yl,cr-yl	pl-yl,cr-yl	1	dk-dl
Afrotyphlops nigrocandidus	bk,bl-bk,wt,yl	wt,yl	1	bk-bl
Afrotyphlops obtusus	bn,dr-bn,bk	yl,pl-bn,wt	1	wt-dl
Afrotyphlops platyrhynchus	rd-yl	pl-rd-yl	1	n/a
Afrotyphlops punctatus	bn,pu,gy,yl,dk-bn	dk-bn,gy,pl,yl	1	yl-bk-bl-sp
Afrotyphlops rondoensis	bl-gy,bk	wt,yl	1	dl
Afrotyphlops schlegelii	bk	pl	1(0)	bl,dk-vl
Afrotyphlops schmidti	dk-bn,bk	pl	1	dl,sp

Afrotyphlops steinhausi	dk-bn	pl-yl,pl	1	yl-br
Afrotyphlops tanganicanus	yl,bn	yl-bn	0	n/a
Afrotyphlops usambaricus	yl	yl	1	bk-bl
Letheobia acutirostrata	n/a	n/a	n/a	n/a
Letheobia angeli	n/a	n/a	n/a	n/a
Letheobia caeca	pl-bn,pl	pl-bn,pl	0	n/a
Letheobia coecata	bn	pl-bn	1	n/a
Letheobia crossii	pl	pl	0	n/a
Letheobia debilis	pk-tn	pk-tn	0	n/a
Letheobia episcopa	yl-cr	yl-cr	1	n/a
Letheobia erythraea	yl-wt	yl-wt	0	n/a
Letheobia feae	pl	pl	0	n/a
Letheobia gracilis	pl	pl	0	n/a
Letheobia graueri	pl	pl	0	n/a
Letheobia kibarae	pk	pl-pk	0	n/a
Letheobia largeni	wt,cr-wt	cr-wt	0	n/a
Letheobia leucosticta	dk-bn	wt	1	wt-sp
Letheobia lumbriciformis	pl	pl	0	n/a
Letheobia manni	gy	yl-gy	n/a	bk-sp(ven)
Letheobia newtoni	yl-wt	yl-wt	0	n/a
Letheobia pallida	pl	pl	0	n/a
Letheobia pauwelsi	bg	cr,pl	1	n/a
Letheobia pembana	pl	pl	0	n/a
Letheobia praeocularis	bn-gy	pl-bn-gy	1	n/a
Letheobia rufescens	pl-rd,pl	pl-rd,pl	0	n/a
Letheobia simonii	yl-pl,pl	yl-pl,pl	0	dl
Letheobia somalica	ol,pl	pl-ol,pl	0	n/a
Letheobia stejnegeri	yl-wt	yl-wt	0	n/a
Letheobia sudanensis	pl-yl-bn,pl	pl-yl-bn,pl	0	n/a
Letheobia swahilica	pl	pl	0	n/a
Letheobia toritensis	pl	pl	0	n/a
Letheobia uluguruensis	pl	pl	0	n/a
Letheobia wittei	pl	pl	0	n/a
Letheobia zenkeri	pl	pl	0	n/a
Rhinotyphlops ataeniatus	bk,yl-bn,gn-bn	bk,yl-bn,gn-bn	0,1	or-yl-dl(head)
Rhinotyphlops boylei	ol-bn	yl	1	n/a
Rhinotyphlops lalandei	oc-yl,pl-bn,bn,gy,gy-bn	yl,pl,wt	1	n/a
Rhinotyphlops leucocephalus	gy	wt	1	bk-dl
Rhinotyphlops schinzi	yl,rd,pk,bk	pl	1	dk-sp-br
Rhinotyphlops scortecci	dk-bn,bk	dk-bn,bk	1	yl-dl
Rhinotyphlops unitaeniatus	bk,dk-bn	bn-yl	1	yl-dl
ASIATYPHLOPINAE				
Acutotyphlops banaorum	gd-or,pl-or,or-bn,bn	gd,bn-or	1	bk-sp-br
Acutotyphlops infralabialis	bn,dk	yl	1	dk-dl
Acutotyphlops kunuaensis	bn,dk	pl-yl	1	yl-nk
Acutotyphlops solomonis	bn,dk	gd	1	n/a
Acutotyphlops subocularis	bn,dk	yl	1	n/a
Anilios affinis	ol-bn,dk-bn	pl-yl,pl-yl-cr,pk-wt	1	n/a
Anilios ammodytes	pl-gy-bn,pk-pu	pl-gy-bn,pk-pu	1	n/a
Anilios aspinus	pl-pk-tn	pl-pk-tn	0	n/a
Anilios australis	pl,pl-yl,rd-bn,gy-bn	cr,wt	1	n/a
Anilios batillus	or-bn	pl-or-bn	1	dl
Anilios bicolor	bn,pu-bn,dk-bn,gy-bn	gn-wt,yl-wt,cr,wt	1	n/a
Anilios bituberculatus	bn-um,dk-pu-bn	wt	1	n/a
Anilios broomi	pl,pl-bn	wt	1	11 bn-dl
Anilios centralis	pu-bn	pl	1	n/a
Anilios chamodracaena	yl-cr	yl-cr,wt	0	n/a

Anilios diversus	bn,bk-bn,pu-bn	wt,pl-pu-bn	1	n/a
Anilios endoterus	bn,dk-pu-bn,rd-bn	wt,cr	1	n/a
Anilios erycinus	bn-gy,bn	yl	1	dk-dl
Anilios ganei	gy-bn	pl	1	n/a
Anilios grypus	bn,pk-bn,bn-cr	gy-wt	1	n/a
Anilios guentheri	rd-bn,pu-bn	pl-rd-bn,pl-pu-bn	1	n/a
Anilios hamatus	bn-bk,pu-bn	wt,cr	1	n/a
Anilios howi	dk-bn	bn	1	n/a
Anilios kimberleyensis	dk	pl	1	n/a
Anilios leptosomus	pl-gy-bn,pu-bn	gy-wt,pl-pu-bn	0	n/a
Anilios leucoproctus	bn,dk-bn,dk-tn	dk-bn	1	n/a
Anilios ligatus	bn,dk-bn,dk-pu-bn	yl-wt,wt	1	n/a
Anilios longissimus	pl	pl	0	n/a
Anilios margaretae	pk,pu-gy	pl-gy	1	n/a
Anilios micrommus	n/a	n/a	n/a	n/a
Anilios minimus	yl-bn	yl-bn	0	n/a
Anilios nema	pl-yl-bn,gy-bn	pl-yl-bn,pl-gy-bn	1	n/a
Anilios nigrescens	bk,pu-pk-bn	cr,pk	1	n/a
Anilios nigroterminatus	pl-bn	pl-bn,yl	1	n/a
Anilios pilbarensis	pl-pu-bn	cm	1	n/a
Anilios pinguis	bn-yl,dk-bn	pl-bn-yl,wt	1	n/a
Anilios proximus	bn-ol,gy-bn	yl	1	n/a
Anilios robertsi	dk-pu-bn	cr	1	n/a
Anilios silvia	pu-bk,cm	cr,cr-yl	1	11 dk-dl
Anilios splendidus	gy	wt	1	n/a
Anilios torresianus	dk-bn,ol	wt,yl	1	n/a
Anilios tovelli	bn	wt	1	dl
Anilios troglodytes	bn	pl	1	n/a
Anilios unguirostris	ol-bn,dk-ol-bn	yl,wt	1	n/a
Anilios waitii	pl-bn,dk-pu-bn	yl,wt	1	n/a
Anilios wiedii	rd-bn,bk-bn	yl,cr-wt	1	n/a
Anilios yampiensis	bn	pl-bn	1	n/a
Anilios yirrikalae	bn,yl	wt,yl	1	n/a
Asiatyphlops bothriorhynchus	bn-ol,bn	bn-ol,pl-bn	1	n/a
Asiatyphlops diardii	ol-bn,bn,bk	bn,yl,pl-bn	1	n/a
Asiatyphlops fuscus	dk-bn,bn	dk-bn	0	n/a
Asiatyphlops giadinhensis	gd-bn	yl	1	n/a
Asiatyphlops klemmeri	bn	pl-yl-bn	1	vl
Asiatyphlops koshunensis	n/a	n/a	n/a	n/a
Asiatyphlops leucomelas	bk-bn,bk	wt	1	n/a
Asiatyphlops muelleri	bk	cr-wt	1	n/a
Asiatyphlops oatesii	yl,bn	yl-bn	1	dk-dl-sp
Asiatyphlops roxaneae	gd-bn	yl-tn	1	n/a
Asiatyphlops siamensis	gy-ol	yl	1	n/a
Asiatyphlops tenuicollis	ol-bn	yl	1	n/a
Asiatyphlops trangensis	bl	cr-wt	1	n/a
Cyclotyphlops deharvengi	dk-bn	bn	1	n/a
Grypotyphlops acutus	or-gy,bn,gd-bn	gy-wt,yl,pl-bn	1	dl
Indotyphlops ahsanai	dk-bn	n/a	n/a	n/a
Indotyphlops albiceps	bn,pl-bn	cr-wt	1	n/a
Indotyphlops braminus	dk-gy,bn,bk	pl-gy,pl-bn	1	n/a
Indotyphlops exiguus	pl-yl	wt	1	n/a
Indotyphlops filiformis	dk-rd-bn	rd-bn	1	n/a
Indotyphlops fletcheri	dk-pu-bn	pu-bn	1	n/a
Indotyphlops hypsobothrius	pl-bn	wt	1	n/a
Indotyphlops jerdoni	pl-bn,bn,bk	pl-bn	1	n/a
Indotyphlops khoratensis	gy	gy	0	n/a

Indotyphlops lankaensis	pl-bn	pl-bn	1	n/a
Indotyphlops lazelli	pl-bn	wt	1	n/a
Indotyphlops loveridgei	pl-bn	pl-bn	1	n/a
Indotyphlops madgemintonae	dk-bn,yl-bn	pl-bn,yl	1	n/a
Indotyphlops malcolmi	bn	pl	1	dk-nk
Indotyphlops meszoelyi	bn	pl-bn	1	n/a
Indotyphlops ozakiae	n/a	n/a	n/a	n/a
Indotyphlops pammeces	n/a	n/a	n/a	n/a
Indotyphlops porrectus	bn,bk	pl-bn	1	n/a
Indotyphlops schmutzi	pk-bn	pk-bn	1	n/a
Indotyphlops tenebrarum	bn	pk-bn	1	n/a
Indotyphlops veddae	pu-gy	pu-gy	0	n/a
Indotyphlops violaceus	pu	pu	1	n/a
Malayotyphlops canlaonensis	gn-bk	pk-yl	1	n/a
Malayotyphlops castanotus	dk-bn	cr,pl	1	n/a
Malayotyphlops collaris	pl-bn	pl	1	pl-nk
Malayotyphlops hypogius	pl-gy-bn	pl-yl	1	dk-dl
Malayotyphlops koekkoeki	gy-bn	pl-gy-bn	1	n/a
Malayotyphlops kraali	bk,bk-bn	yl	1	yl-sp(ven)
Malayotyphlops luzonensis	rd-ol-bn	yl-bn	1	n/a
Malayotyphlops manilae	rd-bn	yl-wt	1	n/a
Malayotyphlops ruber	rd-bn	rd-bn	1	n/a
Malayotyphlops ruficauda	bk,rd-bn	rd,yl	1	n/a
Ramphotyphlops acuticauda	bn	yl	1	n/a
Ramphotyphlops adocetus	dk-bn	pl	1	n/a
Ramphotyphlops angusticeps	bn	yl	1	n/a
Ramphotyphlops becki	rd-bn,dk-pu-bn	pl-bn	1	n/a
Ramphotyphlops conradi	pl-bn	pl-bn	1	n/a
Ramphotyphlops cumingii	pl-ol,bk-gy,ol-bn	pl,yl	1	n/a
Ramphotyphlops depressus	bn	yl,gd	1	n/a
Ramphotyphlops exocoeti	pl-bn	pl-bn	1	dl
Ramphotyphlops flaviventer	dk-bn,bk,dk-pu	yl	1	n/a
Ramphotyphlops hatmaliyeb	dk-bn	pl	1	n/a
Ramphotyphlops lineatus	yl,pl-bn,bk	yl-wt	1	yl-bn-dl
Ramphotyphlops lorenzi	pl-gy-gn	pl-gy-gn	n/a	n/a
Ramphotyphlops mansuetus	bn	bn	0	n/a
Ramphotyphlops marxi	pl-bn	yl-cr	1	n/a
Ramphotyphlops melanocephalus	bk-bn	pl	1	n/a
Ramphotyphlops multilineatus	bn-gy,gy,bn	br-gy,gy,bn	1	yl-bn-dl
Ramphotyphlops olivaceus	dk-ol,pl-ol-bn	yl,pl-ol-bn	1	dl
Ramphotyphlops similis	bn,dk-bn	yl	1	n/a
Ramphotyphlops suluensis	dk-gy	pl-gy	1	rt
Ramphotyphlops supranasalis	dk-bn,dk-pu,bk	yl	1	n/a
Ramphotyphlops willeyi	ol-bn,bn	yl,pl-bn	1	n/a
Sundatyphlops polygrammicus	dk-bn,ol,ol-gy,pl-yl	wt,wt-pk,pl-yl	1(0)	dl,vl,un
Xerotyphlops etheridgei	pl-bn	pl-yl-wt,bg	1	n/a
Xerotyphlops socotranus	wt	wt	1	pl-bn-dl
Xerotyphlops vermicularis	bn,yl-bn,pk-bn,pu-bn	bn,yl-bn,pk-bn,pu-bn	1	n/a
Xerotyphlops wilsoni	bn	bn	0	n/a
MADATYPHLOPINAE				
Madatyphlops andasibensis	bn	bn	1	yl-nk,yl-sp(ven)
Madatyphlops arenarius	pk-wt,pl	pk-wt,pl	1	n/a
Madatyphlops boettgeri	pl	pl,bg	1	n/a
Madatyphlops decorsei	dk-gy	gy-wt	1	n/a
Madatyphlops domerguei	pl-br	pl-bn	1	n/a
Madatyphlops madagascariensis	bk-bn,bn	bk-bn	1	pl-dl
Madatyphlops microcephalus	bk	bk	1	yl-vl

Madatyphlops mucronatus	gy-bn,ol,bn	gy-bn,ol	1	n/a
Madatyphlops ocularis	pl-bn-gy,bn	pl-bn-gy	1	n/a
Madatyphlops rajeryi	yl,gb	yl,bg	1	n/a
Madatyphlops reuteri	gy,gy-bl,bn	pl-gy,pl-gy-bl	1	n/a
TYPHLOPINAE				
Amerotyphlops amoipira	cr-bn	cr-bn	0	rt
Amerotyphlops brongersmianus	pl-bn	pl-tn	1	rt
Amerotyphlops costaricensis	bn	pl	1	bk-sp,tr
Amerotyphlops lehneri	pl-bn,yl	gy,yl	1	8–10 dk-dl
Amerotyphlops microstomus	pl,pk-wt,yl-ol	pl,pk,wt	0	n/a
Amerotyphlops minuisquamus	bn,bk-bn,yl-bn	pl	1	dl,sp
Amerotyphlops paucisquamus	n/a	pl	1	n/a
Amerotyphlops reticulatus	bn,dk-bn,bk	pl-yl,yl,wt,pl	1	wt-tr
Amerotyphlops stadelmani	pl-yl	pl-yl	1	n/a
Amerotyphlops tasymicris	bn	pl	1	dk-dl
Amerotyphlops tenuis	bn,pl-bn,yl	wt,yl	1	sp
Amerotyphlops trinitatus	yl	yl	1	11 dk-bn-dl
Amerotyphlops tycherus	bn-gy	pl-yl-gy,wt,pl	1	n/a
Amerotyphlops yonenagae	cr	cr	1	dk-bn-dl,bn-bl
Antillotyphlops annae	pk-gy-bg	cr	1	n/a
Antillotyphlops catapontus	gy-bn	pl-pk,pl	1	pl-tr
Antillotyphlops dominicanus	bk-bn	bk-bn	0	n/a
Antillotyphlops geotomus	gy-bn	wt	1	n/a
Antillotyphlops granti	yl,pl-bn	yl-wt,pl	1	n/a
Antillotyphlops guadeloupensis	pl-bn	wt	1	n/a
Antillotyphlops hypomethes	pl-gy-bn	pl	1	n/a
Antillotyphlops monastus	gy-bn	pl	1	n/a
Antillotyphlops monensis	bn,pl-bn	wt	1	dl
Antillotyphlops naugus	dk-bn	gy	1	dl
Antillotyphlops platycephalus	rd-bn,dk-bn	wt,bg	1	n/a
Antillotyphlops richardi	pl-bn	wt,yl-wt	1	n/a
Cubatyphlops anchaurus	pl	pl	1	n/a
Cubatyphlops anousius	pl	pl	0	n/a
Cubatyphlops arator	pl-bn	pl	1	n/a
Cubatyphlops biminiensis	bn,pl-bn	pl,yl-wt	1	n/a
Cubatyphlops caymanensis	bn	pl,yl-wt	1	n/a
Cubatyphlops contorhinus	bn	pl	1	n/a
Cubatyphlops epactius	pl-gy-bn,pl-rd,gy-bn	pl	1	n/a
Cubatyphlops golyathi	dk-bn	pl-bn	1	n/a
Cubatyphlops notorachius	pl-bn	pl	1	n/a
Cubatyphlops paradoxus	dk-bn	pl	1	n/a
Cubatyphlops perimychus	bn,dk-bn	pl	1	n/a
Cubatyphlops satelles	pl-bn	pl	1	n/a
Typhlops agoralionis	pl-bn	pl-bn	1	n/a
Typhlops capitulatus	bn,pl-bn,dk-rd-bn	pl-bn,dk-rd-bn	0,1	n/a
Typhlops eperopeus	bn,pl-tn,dk-bn	pl-tn,pl-bn	1	n/a
Typhlops gonavensis	dk-pu-bn,dk-rd-bn	pu-bn,rd-bn	0	n/a
Typhlops hectus	pl-gy,bn,pl-bn,tn	pl,pl-tn,pl-gy	0,1	dk-nk
Typhlops jamaicensis	bn,dk-bn,pl-bn,gy-bn	pl	1	rt
Typhlops leptolepis	dk-um,dk-bn	dk-um,dk-bn	0	n/a
Typhlops lumbricalis	dk-bn	lt-bn,cr	1	dk-nk
Typhlops oxyrhinus	pl-bn	pl-bn	1	n/a
Typhlops pachyrhinus	dk-bn	pl-bn,cr	1	n/a
Typhlops proancylops	n/a	n/a	1	n/a
Typhlops pusillus	bn,pl-bn,dk-bn	cr,gy-wt,pl	1	n/a
Typhlops rostellatus	dk-bn	dk-bn	1	bk-rt
Typhlops schwartzi	dk-bn	pl	1	n/a

Typhlops silus	pl-cr-bn,bn-gy	pl-cr-bn,pl-bn-gy	1	n/a
Typhlops sulcatus	bn,pl-bn,dk-bn	pl,pl-bn	1	dk-dl
Typhlops sylleptor	bn	pl-bn,pl	1	dk-nk
Typhlops syntherus	bn-tn,bn,pl-bn,pl-tn	wt	1	pl-bl,dl
Typhlops tetrathyreus	tn,bn	pl	1	n/a
Typhlops titanops	gy-bn,tn	pl	1	n/a

Table 2. A summary of morphological variation in the subfamilies and genera of typhlopid snakes. See Table 1 legend for abbreviations.

Taxon	Species	1	2	3	4	5	6	7	8a	8b	9
Afrotyphlopinae	67	d,i	b,r(a)	nc	a	c,i	1,2(r,s1)	a,p	2–6(7)	3.68	2–3(1–2,1–3,2,3,2–4,0)
Afrotyphlops	29	d	r(b,a)	nc	a	i(c)	1(r,2)	a(p)	2–4(5–7)	3.70	2–3(1–2,1–3,2,0)
Letheobia	31	i	b,r	nc	a	c,i	2(r,1,s1,p)	p(a)	3–4(2,5–7)	3.55	2–3(2,3,2–4,0)
Rhinotyphlops	7	d	b(r)	nc	a	c,i	2(1)	a(p)	4–6(2–3)	4.21	2–3(2,2–4)
Asiatyphlopinae	121	d(i)	r(b,a)	nc(c)	a(p)	c,i	2(1,s1,s2,P)	a,p	1–5	2.19	2–3(3,0)
Acutotyphlops	5	d	a,r	nc	p	i	2(1)	p(a)	3–5	4.10	2–3,3,0
Anilios	43	d	b,r(a)	nc	a	c,i	2(1,s1,s2,P)	a	2(1,3–4)	2.21	2–3
Asiatyphlops	13	d(i)	r	nc	a	i(c)	2	a	2–3(4–5)	2.69	2–3(3)
Cyclotyphlops	1	d	r	c	a	c	s1	p	1	1.00	0
Grypotyphlops	1	d,i	b	nc	a	c,i	2	p	4(3,5)	4.00	2–3
Indotyphlops	22	d(i)	r	nc	a	c,i	2(1,p)	a	1(2)	1.03	2–3,3
Malayotyphlops	10	d(i)	r	nc	a	i(c)	2(1)	a(p)	2–4	2.75	3,2–3(2)
Ramphotyphlops	21	d(i)	b,r	nc	a	c,i	2(1,s1)	a(p)	2–3(1)	2.15	2–3(3)
Sundatyphlops	1	d	r	nc	a	c,i	1,s1,2	n/a	n/a	n/a	2–3
Xerotyphlops	4	d	r	nc	a	i	2	a(p)	2	2.00	2–3
Madatyphlopinae	11	d	r	nc	a	i(c)	2	a	2–3(1,4)	2.27	2–3
Madatyphlops	11	d	r	nc	a	i(c)	2	a	2–3(1,4)	2.27	2–3
Typhlopinae	58	d(i)	r(a)	nc	a	c(i)	2(1,s1)	a(p)	1–4	1.66	2–3,3(0,4?)
Amerotyphlops	14	d(i)	r	nc	a	c,i	2(1,s1)	a(p)	1–2(3,4)	1.69	2–3
Antillotyphlops	12	d	r(a)	nc	a	c	2	a	2(1)	2.00	3(4?)
Cubatyphlops	12	d	r	nc	a	c	2	a	1(2)	1.00	2–3
Typhlops	20	d	r	nc	a	c(i)	2	a(p)	2(1,3)	1.85	3(0)

Table 2 (part 2, continued)

Taxon	10a	10b	11	12a	12b	13a	13b	14a	14b	15a	15b	16a	16b
Afrotyphlopinae	18–45	24.8	p,a	216–737	437	4–15	10.8	125–950	403	17–129	52.4	33–152	68.2
Afrotyphlops	18–45	27.2	p(a)	216–620	391	4–15	9.6	125–950	481	17–95	39.5	33–152	60.8
Letheobia	18–30	22.3	p,a	250–737	484	8–15	11.1	135–670	350	35–129	66.6	46–143	79.0
Rhinotyphlops	22–34	25.0	p,a	311–586	425	14–15	14.5	220–455	323	27–77	48.9	50–79	65.0
Asiatyphlopinae	16–36	21.8	p,a	206–750	408	5–36	14.6	91–750	293	18–134	49.8	13–133	47.1
Acutotyphlops	26–36	30.4	p	334–542	415	11–31	20.9	333–487	392	18–58	38.2	13–100	31.1
Anilios	16–24	20.1	a(p)	278–750	466	8–36	15.0	122–750	353	20–134	55.8	15–112	49.7
Asiatyphlops	20–30	23.2	p,a	246–520	339	5–26	11.1	130–430	243	26–70	35.2	42–100	65.6
Cyclotyphlops	22	22.0	p	294	294	n/a	n/a	146	146	35	35.1	32.3	32.3
Grypotyphlops	24–34	29.0	p	448–526	487	7–13	10.0	630	630	30–66	48	17–133	75.1
Indotyphlops	18–22	19.4	a(p)	229–468	345	7–15	10.8	91–285	175	28–130	57.6	22–76	46.4
Malayotyphlops	24–30	26.8	p	300–461	367	9–14	11.9	122–445	256	31–58	42.0	28–71	51.8
Ramphotyphlops	18–30	21.7	p,a	206–653	419	8–36	19.8	117–480	302	18–88	48.8	17–70	31.8
Sundatyphlops	22	22.0	n/a	496	496	16	16.0	395	395	33–58	45.5	15–52	33.3
Xerotyphlops	20–24	23.5	p	206–435	355	10–16	13.0	220–350	292	37–55	45.6	87.7	87.7
Madatyphlopinae	20–28	22.9	p,a	252–600	429	6–18	11.2	176–600	320	27–85	45.6	33–125	53.7
Madatyphlops	20–28	22.9	p,a	252–600	429	6–18	11.2	176–600	320	27–85	45.6	33–125	53.7
Typhlopinae	16–24	20.3	p,a	170–629	369	6–22	11.7	101–522	264	16–77	42.7	18–270	48.7
Amerotyphlops	16–22	19.1	a(p)	170–556	327	6–15	9.4	101–522	287	16–77	38.7	23–270	66.8
Antillotyphlops	16–24	20.5	p	299–499	378	11–14	12.3	110–360	233	37–70	46.8	30–61	44.5
Cubatyphlops	20–24	22.1	p,a	351–629	503	22	22.0	197–460	304	36–75	54.7	29–85	50.4
Typhlops	18–22	20.0	p,a	231–457	312	8–19	13.1	126–445	243	23–57	35.9	18–88	36.8

Table 2 (part 3, continued)

Taxon	17	18	19	20
Afrotyphlopinae	v(wt,cr,bn,yl,bl,pl-gn,pk)	wt,cr,yl(bn,bk)	1,0	un(dl)
Afrotyphlops	dk-bn (yl,pl-bl,pk,pl-gn)	yl,yl-wt,cr,wt	1(0)	un(dl)
Letheobia	pl(pk,cr,wt,un)	pl(pk,cr,wt,un)	0(1)	un
Rhinotyphlops	bn(pl-yl,pl-gn,pk)	wt,yl-wt(bn,bk)	1	un(dl)
Asiatyphlopinae	bn,dk-bn,pl-bn(v)	wt,cr,yl-wt	1(0)	un(dl)
Acutotyphlops	dk-bn(gd-or)	yl-wt,gd	1	un(br,dl)
Anilios	bn(cr,tn,pk,gy,pl-yl)	wt,cr,yl-wt	1(0)	un(dl)
Asiatyphlops	bn(gd-bn,ol-dn,bk-bn,yl-bn,rd-bn,lv-gy,bk)	yl,yl-wt(wt,cr,yl-tn,yl-bn,pl-bn)	1(0)	un(dl)
Cyclotyphlops	dk-bn	bn	1	un
Grypotyphlops	gy,bn,gd-bn	gy-wt,yl,pl-bn	1	un(dl)
Indotyphlops	bn(cr,gy,yl-bn,rd-bn,lv-gy,bk)	v(wt,cr,pl-bn,lv-gy)	1(0)	un(dl)
Malayotyphlops	v(bn,gy-bn,rd-bn,gn-bk,bk)	v(cr,yl-wt,rd,pk,pk-yl)	1	un(dl,sp,nk)
Ramphotyphlops	dk-bn(bn,tn,gy,lv)	cr,yl-wt(gy-gn,pk-wt,tn,bn)	1(0)	un(dl)
Sundatyphlops	dk-bn,ol,ol-gy,pl-yl	wt,wt-pk,pl-yl	1(0)	dl,vl,un
Xerotyphlops	wt,bn	wt,cr,bn	1(0)	un(dl)
Madatyphlopinae	bn(wt,pk,cr,yl,gy)	v(wt,pk,cr,yl,gy,bn)	1	un(dl,nk)
Madatyphlops	bn(wt,pk,cr,yl,gy)	v(wt,pk,cr,yl,gy,bn)	1	un(dl,nk)
Typhlopinae	bn(cr,tn,yl-wt,un)	un(wt,cr,bn)	1(0)	un(sp,dl,rt)
Amerotyphlops	bn,yl	wt,cr,yl	1(0)	sp,dl,rt
Antillotyphlops	bn,gy-bn,yl	wt,cr(bn)	1(0)	un(dl)
Cubatyphlops	bn(un,pk)	un(cr)	1(0)	un
Typhlops	bn,tn	un,wt,cr	1(0)	un(dl)

Table 3. Classification of snakes of the Family Typhlopidae.

This study	Previous classification
Afrotyphlopinae	
Afrotyphlops angolensis (Bocage 1866)	*Afrotyphlops angolensis*
Afrotyphlops anomalus (Bocage 1873)	*Megatyphlops anomalus*
Afrotyphlops bibronii (Smith 1846)	*Afrotyphlops bibronii*
Afrotyphlops blanfordii (Boulenger 1889)	*Afrotyphlops blanfordii*
Afrotyphlops brevis (Scortecci 1929a)	*Megatyphlops brevis*
Afrotyphlops calabresii (Gans & Laurent 1965)	*Typhlops calabresii*
Afrotyphlops comorensis (Boulenger 1889)	*Typhlops comorensis*
Afrotyphlops congestus (Duméril & Bibron 1844)	*Afrotyphlops congestus*
Afrotyphlops cuneirostris (Peters 1879)	*Typhlops cuneirostris*
Afrotyphlops decorosus (Peters 1875)	*Letheobia decorosa*
Afrotyphlops elegans (Peters 1868)	*Typhlops elegans*
Afrotyphlops fornasinii (Bianconi 1847)	*Afrotyphlops fornasinii*
Afrotyphlops gierrai (Mocquard 1897)	*Afrotyphlops gierrai*
Afrotyphlops jubanus (Broadley & Wallach 2007)	*Letheobia jubanus*
Afrotyphlops kaimosae (Loveridge 1935)	*Afrotyphlops kaimosae*
Afrotyphlops liberiensis (Hallowell 1848)	*Typhlops liberiensis*
Afrotyphlops lineolatus (Jan 1863)	*Afrotyphlops lineolatus*
Afrotyphlops mucruso (Peters 1854)	*Megatyphlops mucruso*
Afrotyphlops nanus Broadley & Wallach, 2009	*Afrotyphlops nanus*
Afrotyphlops nigrocandidus (Broadley & Wallach 2000)	*Afrotyphlops nigrocandidus*
Afrotyphlops obtusus (Peters 1865)	*Letheobia obtusa*
Afrotyphlops platyrhynchus (Sternfeld 1910)	*Typhlops platyrhynchus*
Afrotyphlops punctatus (Leach 1819)	*Afrotyphlops punctatus*
Afrotyphlops rondoensis (Loveridge 1942)	*Afrotyphlops rondoensis*
Afrotyphlops schlegelii (Bianconi 1847)	*Megatyphlops schlegelii*
Afrotyphlops schmidti (Laurent 1956)	*Afrotyphlops schmidti*
Afrotyphlops steinhausi (Werner 1909b)	*Afrotyphlops steinhausi*
Afrotyphlops tanganicanus (Laurent 1964)	*Afrotyphlops tanganicanus*
Afrotyphlops usambaricus (Laurent 1964)	*Afrotyphlops usambaricus*
Letheobia acutirostrata (Andersson 1916)	*Letheobia acutirostrata*
Letheobia angeli (Guibé 1952)	*Letheobia angeli*
Letheobia caeca (Duméril 1856)	*Letheobia caeca*
Letheobia coecata (Jan 1863)	*Typhlops coecata*
Letheobia crossii (Boulenger 1893)	*Letheobia crossii*
Letheobia debilis (Joger 1990)	*Letheobia debilis*
Letheobia episcopa Franzen & Wallach, 2002	*Letheobia episcopa*
Letheobia erythraea (Scortecci 1929b)	*Letheobia erythraea*
Letheobia feae (Boulenger 1906)	*Letheobia feae*
Letheobia gracilis (Sternfeld 1910)	*Letheobia gracilis*
Letheobia graueri (Sternfeld 1912)	*Letheobia graueri*

Letheobia kibarae (Witte 1953)	*Letheobia kibarae*
Letheobia largeni Broadley & Wallach, 2007	*Letheobia largeni*
Letheobia leucosticta (Boulenger 1898a)	*Letheobia leucosticta*
Letheobia lumbriciformis (Peters 1874)	*Letheobia lumbriciformis*
Letheobia manni (Loveridge 1941)	*Typhlops manni*
Letheobia newtoni (Bocage 1890)	*Letheobia newtoni*
Letheobia pallida Cope, 1868	*Letheobia pallida*
Letheobia pauwelsi Wallach, 2005	*Letheobia pauwelsi*
Letheobia pembana Broadley & Wallach, 2007	*Letheobia pembana*
Letheobia praeocularis (Stejneger 1894)	*Letheobia praeocularis*
Letheobia rufescens (Chabanaud 1916)	*Letheobia rufescens*
Letheobia simonii (Böttger 1879)	*Letheobia simonii*
Letheobia somalica (Boulenger 1895a)	*Letheobia somalica*
Letheobia stejnegeri (Loveridge 1931)	*Letheobia stejnegeri*
Letheobia sudanensis (Schmidt 1923)	*Letheobia sudanensis*
Letheobia swahilica (Broadley & Wallach 2007)	*Letheobia swahilica*
Letheobia toritensis (Broadley & Wallach 2007)	*Letheobia toritensis*
Letheobia uluguruensis (Barbour & Loveridge 1928)	*Letheobia uluguruensis*
Letheobia wittei (Roux-Estève 1974)	*Letheobia wittei*
Letheobia zenkeri (Sternfeld 1908)	*Typhlops zenkeri*
Rhinotyphlops ataeniatus (Boulenger 1912)	*Letheobia ataeniatus*
Rhinotyphlops boylei (FitzSimons 1932)	*Rhinotyphlops boylei*
Rhinotyphlops lalandei (Schlegel 1839)	*Rhinotyphlops lalandei*
Rhinotyphlops leucocephalus (Parker 1930)	*Rhinotyphlops leucocephalus*
Rhinotyphlops schinzi (Böttger 1887)	*Rhinotyphlops schinzi*
Rhinotyphlops scortecci (Gans & Laurent 1965)	*Letheobia scortecci*
Rhinotyphlops unitaeniatus (Peters 1878)	*Letheobia unitaeniata*
Asiatyphlopinae	
Acutotyphlops banaorum Wallach *et al.* 2007	*Acutotyphlops banaorum*
Acutotyphlops infralabialis (Waite 1918a)	*Acutotyphlops infralabialis*
Acutotyphlops kunuaensis Wallach, 1995	*Acutotyphlops kunuaensis*
Acutotyphlops solomonis (Parker 1939)	*Acutotyphlops solomonis*
Acutotyphlops subocularis (Waite 1897a)	*Acutotyphlops subocularis*
Anilios affinis (Boulenger 1889)	*Ramphotyphlops affinis*
Anilios ammodytes (Montague *et al.* 1914)	*Ramphotyphlops ammodytes*
Anilios aspinus (Couper *et al.* 1998)	*Ramphotyphlops aspinus*
Anilios australis (Gray 1845)	*Ramphotyphlops australis*
Anilios batillus (Waite 1894)	*Ramphotyphlops batillus*
Anilios bicolor (Peters 1858)	*Ramphotyphlops bicolor*
Anilios bituberculatus (Peters 1863)	*Ramphotyphlops bituberculatus*
Anilios broomi (Boulenger 1898b)	*Ramphotyphlops broomi*
Anilios centralis (Storr 1984)	*Ramphotyphlops centralis*

Anilios chamodracaena (Ingram & Covacevich 1993)	*Ramphotyphlops chamodracaena*
Anilios diversus (Waite 1894)	*Ramphotyphlops diversus*
Anilios endoterus (Waite 1918b)	*Ramphotyphlops endoterus*
Anilios erycinus (Werner 1901)	*Ramphotyphlops erycinus*
Anilios ganei (Aplin 1998)	*Ramphotyphlops ganei*
Anilios grypus (Waite 1918b)	*Ramphotyphlops grypus*
Anilios guentheri (Peters 1865)	*Ramphotyphlops guentheri*
Anilios hamatus (Storr 1981)	*Ramphotyphlops hamatus*
Anilios howi (Storr 1983)	*Ramphotyphlops howi*
Anilios kimberleyensis (Storr 1981)	*Ramphotyphlops kimberleyensis*
Anilios leptosomus (Robb 1972)	*Ramphotyphlops leptosomus*
Anilios leucoproctus (Boulenger 1889)	*Ramphotyphlops leucoproctus*
Anilios ligatus (Peters 1879)	*Ramphotyphlops ligatus*
Anilios longissimus (Aplin 1998)	*Ramphotyphlops longissimus*
Anilios margaretae (Storr 1981)	*Ramphotyphlops margaretae*
Anilios micrommus (Storr 1981)	*Ramphotyphlops micrommus*
Anilios minimus (Kinghorn 1929)	*Ramphotyphlops minimus*
Anilios nema (Shea & Horner 1997)	*Ramphotyphlops nema*
Anilios nigrescens Gray, 1845	*Ramphotyphlops nigrescens*
Anilios nigroterminatus (Parker 1931)	*Ramphotyphlops nigroterminatus*
Anilios pilbarensis (Aplin & Donnellan 1993)	*Ramphotyphlops pilbarensis*
Anilios pinguis (Waite 1897b)	*Ramphotyphlops pinguis*
Anilios proximus (Waite 1893)	*Ramphotyphlops proximus*
Anilios robertsi (Couper *et al.* 1998)	*Ramphotyphlops robertsi*
Anilios silvia (Ingram & Covacevich 1993)	*Ramphotyphlops silvia*
Anilios splendidus (Aplin 1998)	*Ramphotyphlops splendidus*
Anilios torresianus (Schlegel 1839)	*Ramphotyphlops polygrammicus*
Anilios tovelli (Loveridge 1945)	*Ramphotyphlops tovelli*
Anilios troglodytes (Storr 1981)	*Ramphotyphlops troglodytes*
Anilios unguirostris (Peters 1867b)	*Ramphotyphlops unguirostris*
Anilios waitii (Boulenger 1895b)	*Ramphotyphlops waitii*
Anilios wiedii (Peters 1867a)	*Ramphotyphlops wiedii*
Anilios yampiensis (Storr 1981)	*Ramphotyphlops yampiensis*
Anilios yirrikalae (Kinghorn 1942)	*Ramphotyphlops yirrikalae*
Asiatyphlops bothriorhynchus (Günther 1864)	*Typhlops bothriorhynchus*
Asiatyphlops diardii (Schlegel 1839)	*Typhlops diardii*
Asiatyphlops fuscus (Duméril & Duméril 1851)	*Typhlops fuscus*
Asiatyphlops giadinhensis (Bourret 1937)	*Typhlops giadinhensis*
Asiatyphlops klemmeri (Taylor 1962)	*Typhlops klemmeri*
Asiatyphlops koshunensis (Ôshima 1916)	*Typhlops koshunensis*
Asiatyphlops leucomelas (Boulenger 1890)	*Typhlops leucomelas*
Asiatyphlops muelleri (Schlegel 1839)	*Typhlops muelleri*
Asiatyphlops oatesii (Boulenger 1890)	*Typhlops oatesii*

Asiatyphlops roxaneae (Wallach 2001)	*Typhlops roxaneae*
Asiatyphlops siamensis (Günther 1864)	*Typhlops siamensis*
Asiatyphlops tenuicollis (Peters 1864)	*Typhlops tenuicollis*
Asiatyphlops trangensis (Taylor 1962)	*Typhlops trangensis*
Cyclotyphlops deharvengi in den Bosch & Ineich 1994	*Cyclotyphlops deharvengi*
Grypotyphlops acutus (Duméril & Bibron 1844)	*Letheobia acutus*
Indotyphlops ahsanai (Khan 1999)	*Typhlops ahsanai*
Indotyphlops albiceps (Boulenger 1898a)	*Ramphotyphlops albiceps*
Indotyphlops braminus (Daudin 1803)	*Ramphotyphlops braminus*
Indotyphlops exiguus (Jan 1864)	*Typhlops exiguus*
Indotyphlops filiformis (Duméril & Bibron 1844)	*Typhlops filiformis*
Indotyphlops fletcheri (Wall 1919)	*Typhlops fletcheri*
Indotyphlops hypsobothrius (Werner 1917)	*Typhlops hypsobothrius*
Indotyphlops jerdoni (Boulenger 1890)	*Typhlops jerdoni*
Indotyphlops khoratensis (Taylor 1962)	*Typhlops khoratensis*
Indotyphlops lankaensis (Taylor 1947)	*Typhlops lankaensis*
Indotyphlops lazelli (Wallach & Pauwels 2004)	*Typhlops lazelli*
Indotyphlops loveridgei (Constable 1949)	*Typhlops loveridgei*
Indotyphlops madgemintonae (Khan 1999)	*Typhlops madgemintonae*
Indotyphlops malcolmi (Taylor 1947)	*Typhlops malcolmi*
Indotyphlops meszoelyi (Wallach 1999)	*Typhlops meszoelyi*
Indotyphlops ozakiae (Niyomwan *et al.* 2001)	*Ramphotyphlops ozakiae*
Indotyphlops pammeces (Günther 1864)	*Typhlops pammeces*
Indotyphlops porrectus (Stoliczka 1871)	*Typhlops porrectus*
Indotyphlops schmutzi (Auffenberg 1980)	*Typhlops schmutzi*
Indotyphlops tenebrarum (Taylor 1947)	*Typhlops tenebrarum*
Indotyphlops veddae (Taylor 1947)	*Typhlops veddae*
Indotyphlops violaceus (Taylor 1947)	*Typhlops violaceus*
Malayotyphlops canlaonensis (Taylor 1917)	*Typhlops canlaonensis*
Malayotyphlops castanotus (Wynn & Leviton 1993)	*Typhlops castanotus*
Malayotyphlops collaris (Wynn & Leviton 1993)	*Typhlops collaris*
Malayotyphlops hypogius (Savage 1950)	*Typhlops hypogius*
Malayotyphlops koekkoeki (Brongersma 1934)	*Typhlops koekkoeki*
Malayotyphlops kraali (Doria 1874)	*Typhlops kraali*
Malayotyphlops luzonensis (Taylor 1919)	*Typhlops luzonensis*
Malayotyphlops manilae (Taylor 1919)	*Typhlops manilae*
Malayotyphlops ruber (Böttger 1897)	*Typhlops ruber*
Malayotyphlops ruficauda (Gray 1845)	*Typhlops ruficaudus*
Ramphotyphlops acuticauda (Peters 1877)	*Ramphotyphlops acuticauda*
Ramphotyphlops adocetus Wynn *et al.* 2012	*Ramphotyphlops adocetus*
Ramphotyphlops angusticeps (Peters 1877)	*Ramphotyphlops angusticeps*
Ramphotyphlops becki Tanner, 1948	*Ramphotyphlops becki*
Ramphotyphlops conradi (Peters 1875)	*Typhlops conradi*

Ramphotyphlops cumingii (Gray 1845)	*Ramphotyphlops cumingii*
Ramphotyphlops depressus Peters, 1880	*Ramphotyphlops depressus*
Ramphotyphlops exocoeti (Boulenger 1887)	*Ramphotyphlops exocoeti*
Ramphotyphlops flaviventer (Peters 1864)	*Ramphotyphlops flaviventer*
Ramphotyphlops hatmaliyeb Wynn *et al.* 2012	*Ramphotyphlops hatmaliyeb*
Ramphotyphlops lineatus (Schlegel 1839)	*Ramphotyphlops lineatus*
Ramphotyphlops lorenzi (Werner 1909b)	*Ramphotyphlops lorenzi*
Ramphotyphlops mansuetus (Barbour 1921)	*Ramphotyphlops mansuetus*
Ramphotyphlops marxi (Wallach 1993)	*Ramphotyphlops marxi*
Ramphotyphlops melanocephalus (Duméril & Bibron 1844)	*Ramphotyphlops melanocephalus*
Ramphotyphlops multilineatus (Schlegel 1839)	*Ramphotyphlops multilineatus*
Ramphotyphlops olivaceus (Gray 1845)	*Ramphotyphlops olivaceus*
Ramphotyphlops similis (Brongersma 1934)	*Ramphotyphlops similis*
Ramphotyphlops suluensis (Taylor 1918)	*Ramphotyphlops suluensis*
Ramphotyphlops supranasalis (Brongersma 1934)	*Ramphotyphlops supranasalis*
Ramphotyphlops willeyi (Boulenger 1900)	*Ramphotyphlops willeyi*
Sundatyphlops polygrammicus (Schlegel 1839)	*Ramphotyphlops polygrammicus*
Xerotyphlops etheridgei (Wallach 2002)	*Typhlops etheridgei*
Xerotyphlops socotranus (Boulenger 1889)	*Typhlops socotranus*
Xerotyphlops vermicularis (Merrem 1820)	*Typhlops vermicularis*
Xerotyphlops wilsoni (Wall 1908)	*Typhlops wilsoni*
Madatyphlopinae	
Madatyphlops andasibensis (Wallach & Glaw 2009)	*Typhlops andasibensis*
Madatyphlops arenarius (Grandidier 1872)	*Typhlops arenarius*
Madatyphlops boettgeri (Boulenger 1893)	*Typhlops boettgeri*
Madatyphlops decorsei (Mocquard 1901)	*Typhlops decorsei*
Madatyphlops domerguei (Roux-Estève 1980)	*Typhlops domerguei*
Madatyphlops madagascariensis (Böttger 1877)	*Typhlops madagascariensis*
Madatyphlops microcephalus (Werner 1909a)	*Typhlops microcephalus*
Madatyphlops mucronatus (Böttger 1880)	*Typhlops mucronatus*
Madatyphlops ocularis (Parker 1927)	*Typhlops ocularis*
Madatyphlops rajeryi (Renoult & Raselimanana 2009)	*Typhlops rajeryi*
Madatyphlops reuteri (Böttger 1881)	*Typhlops reuteri*
Typhlopinae	
Amerotyphlops amoipira (Rodrigues & Juncá 2002)	*Typhlops amoipira*
Amerotyphlops brongersmianus (Vanzolini 1976)	*Typhlops brongersmianus*
Amerotyphlops costaricensis (Jiménez & Savage 1963)	*Typhlops costaricensis*
Amerotyphlops lehneri (Roux 1926)	*Typhlops lehneri*
Amerotyphlops microstomus (Cope 1866)	*Typhlops microstomus*
Amerotyphlops minuisquamus (Dixon & Hendricks 1979)	*Typhlops minuisquamus*
Amerotyphlops paucisquamus (Dixon & Hendricks 1979)	*Typhlops paucisquamus*
Amerotyphlops reticulatus (Linnaeus 1758)	*Typhlops reticulatus*

Amerotyphlops stadelmani (Schmidt 1936)	*Typhlops stadelmani*
Amerotyphlops tasymicris (Thomas 1974a)	*Typhlops tasymicris*
Amerotyphlops tenuis (Salvin 1860)	*Typhlops tenuis*
Amerotyphlops trinitatus (Richmond 1965)	*Typhlops trinitatus*
Amerotyphlops tycherus (Townsend *et al.* 2008)	*Typhlops tycherus*
Amerotyphlops yonenagae (Rodrigues 1991)	*Typhlops yonenagae*
Antillotyphlops annae (Breuil 1999)	*Typhlops annae*
Antillotyphlops catapontus (Thomas 1966)	*Typhlops catapontus*
Antillotyphlops dominicanus (Stejneger 1904)	*Typhlops dominicanus*
Antillotyphlops geotomus (Thomas 1966)	*Typhlops geotomus*
Antillotyphlops granti (Ruthven & Gaige 1935)	*Typhlops granti*
Antillotyphlops guadeloupensis (Richmond 1966)	*Typhlops guadeloupensis*
Antillotyphlops hypomethes (Hedges & Thomas 1991)	*Typhlops hypomethes*
Antillotyphlops monastus (Thomas 1966)	*Typhlops monastus*
Antillotyphlops monensis (Schmidt 1926)	*Typhlops monensis*
Antillotyphlops naugus (Thomas 1966)	*Typhlops naugus*
Antillotyphlops platycephalus (Duméril & Bibron 1844)	*Typhlops platycephalus*
Antillotyphlops richardi (Duméril & Bibron 1844)	*Typhlops richardi*
Cubatyphlops anchaurus (Thomas & Hedges 2007)	*Typhlops anchaurus*
Cubatyphlops anousius (Thomas & Hedges 2007)	*Typhlops anousius*
Cubatyphlops arator (Thomas & Hedges 2007)	*Typhlops arator*
Cubatyphlops biminiensis (Richmond 1955)	*Typhlops biminiensis*
Cubatyphlops caymanensis (Sackett 1940)	*Typhlops caymanensis*
Cubatyphlops contorhinus (Thomas & Hedges 2007)	*Typhlops contorhinus*
Cubatyphlops epactius (Thomas 1968)	*Typhlops epactius*
Cubatyphlops golyathi (Dominguez & Moreno 2009)	*Typhlops golyathi*
Cubatyphlops notorachius (Thomas & Hedges 2007)	*Typhlops notorachius*
Cubatyphlops paradoxus (Günther 1875)	*Typhlops paradoxus*
Cubatyphlops perimychus (Thomas & Hedges 2007)	*Typhlops perimychus*
Cubatyphlops satelles (Thomas & Hedges 2007)	*Typhlops satelles*
Typhlops agoralionis Thomas & Hedges 2007	*Typhlops agoralionis*
Typhlops capitulatus Richmond 1964	*Typhlops capitulatus*
Typhlops eperopeus Thomas & Hedges 2007	*Typhlops eperopeus*
Typhlops gonavensis Richmond 1964	*Typhlops gonavensis*
Typhlops hectus Thomas 1974b	*Typhlops hectus*
Typhlops jamaicensis (Shaw 1802)	*Typhlops jamaicensis*
Typhlops leptolepis Dominguez *et al.* 2013	*Typhlops leptolepis*
Typhlops lumbricalis (Linnaeus 1758)	*Typhlops lumbricalis*
Typhlops oxyrhinus Dominguez & Diaz Jr. 2011	*Typhlops oxyrhinus*
Typhlops pachyrhinus Dominguez & Diaz Jr. 2011	*Typhlops pachyrhinus*
Typhlops proancylops Thomas & Hedges 2007	*Typhlops proancylops*
Typhlops pusillus Barbour 1914	*Typhlops pusillus*
Typhlops rostellatus Stejneger 1904	*Typhlops rostellatus*

Typhlops schwartzi Thomas 1989a	*Typhlops schwartzi*
Typhlops silus Legler 1959	*Typhlops lumbricalis*
Typhlops sulcatus Cope 1868a	*Typhlops sulcatus*
Typhlops sylleptor Thomas & Hedges 2007	*Typhlops sylleptor*
Typhlops syntherus Thomas 1965	*Typhlops syntherus*
Typhlops tetrathyreus Thomas 1989	*Typhlops tetrathyreus*
Typhlops titanops Thomas 1989	*Typhlops titanops*

separation (narrow, moderate, and wide) is often reported but it has little diagnostic value with regard to clades identified here in the molecular phylogenies. Likewise, while we found retrocloacal sacs and a protrusible hemipenis (Robb 1966) to be useful in diagnosing some clades, we did not find that traits derived from viscera (Broadley & Wallach 2007; 2009) show strong correlations with the molecular clades and therefore do not include them here. This lack of correlation between molecular phylogeny and visceral traits was also encountered in leptotyphlopids (Adalsteinsson *et al.* 2009). As discussed elsewhere (Hedges 2008), body shape and organ size in animals, especially snakes, is negatively allometric (i.e., disproportionate with body size) and this might explain why variation in position, shape, and gain and loss of organs does not appear to be strongly tied to phylogeny.

We identified 20 characters that we considered useful in the diagnoses. We list them by individual species (Table 1) and by subfamilies and genera (Table 2). (1) Eye (distinct, indistinct). The eye was scored as distinct if it was visible at all, and indistinct if it was indistinguishable (sometimes scored from illustrations). (2) Snout (rounded, acuminate, or beaked). Head shape in blindsnakes varies depending on the observation angle (dorsal or lateral), and whether the snout protrudes beyond the lower jaw. Our interest here was in scoring three conditions used to diagnose clades previously: a beaked condition (hooked or keeled rostral), acute condition (pointed, viewed dorsally), or the common "rounded" condition (including most other conditions such as blunt and trilobed). (3) Head scales (circular, non-circular). A circular arrangement is found in *Cyclotyphlops* but not in other genera. (4) Frontorostral (present, absent). This scale is present in *Acutotyphlops* but absent in other genera. (5) Nasal division (complete, incomplete). The nasal suture is either in contact with the rostral (complete) or not in contact (incomplete). (6) Nasal suture origin. Typically the nasal suture is in contact with a supralabial scale, or sometimes the rostral scale or the preocular scale or the seam between two supralabials or between a supralabial and the preocular. (7) Suboculars or subpreoculars (present, absent). Here we score whether there are unusual lateral head scales (suboculars, subpreoculars) besides the typical ones, which are the nasal, preocular, ocular, and labials. (8) Postoculars. The number of these scales varies among genera and is diagnostic. (9) Preocular-labial contact. The lower edge of the preocular scale typically contacts one or several supralabial scales. (10) Midbody scale rows. We summarize the ranges by taxon, and averages of species averages (or, if not available, range midpoints). (11) Scale row reduction (present, absent). If present, then the posterior scale row count is lower than the midbody (or anterior) count. This character remains unreported in many species. (12). Total scale rows (between frontal and caudal spine). We summarize the ranges by taxon, and averages (or, if not available, range midpoints). (13). Caudals. We summarize the ranges by taxon, and averages (or, if not available, range midpoints). (14) Total length (mm). Because snakes have indeterminate growth and most measured specimens have not been sexed to determine if they are adults, we only used maximum known length within a species. For genera and subfamilies we report ranges of species maximums, and taxon averages. Historically, total length rather than snout-vent length is used for body size in the scolecophidian literature because tails are typically only 1–3% of body length. (15) Total length divided by midbody diameter. This is a commonly used ratio in scolecophidians to indicate body shape. (16) Total length divided by tail length. This is a commonly used ratio in scolecophidians to indicate relative tail length. (17) Dorsal color and (18) ventral color. For these two characters we emphasize ground color. A snake can also be unpigmented, in which case it may appear pale pink or gray. (19) Bicolor condition (present, absent). Most typhlopids are darker dorsally, which is called bicolor, although one genus (*Letheobia*) and occasional species

of other genera are unicolor. We did not consider anterior-posterior color differences in this character. (20) Pattern. Most blindsnakes lack a distinct pattern, but if a pattern is present at all it is often in the form of dark lines that are 1-scale wide. Some species have pale collars, and others have blotches, but these patterns are rare and were not diagnostic of molecular clades or correlated with scalation. If the pattern has a distinctive color, we so indicate.

Here we treat the 257 described species of snakes in the Family Typhlopidae. Previously, Vidal *et al.* (2010) defined two related families occurring in the Old World: Gerrhopilidae (15 species) and Xenotyphlopidae (2 species). Since then, *Xenotyphlops mocquardi* (Wallach *et al.* 2007b) has been placed in the synonymy of *X. grandidieri* by Wegener *et al.* (2013). Members of Gerrhopilidae (and the genus *Gerrhopilus*) have gland-like structures peppered over the scales of the head, 1 subpreocular or subocular scale (absent in 6 species), low midbody scale rows (18–24, but usually 18; average 18.6), small body size (average, 167 mm TL), and typically are thin-bodied with long tails. We tentatively assign one additional species, *Gerrhopilus thurstoni,* to Gerrhopilidae. It is small, has low midbody scale rows (20), and has an unusual yellow dorsum similar to another Indian species of the genus, *G. tindalli.*

Systematic accounts

Family Typhlopidae Merrem, 1820

Subfamily Afrotyphlopinae subfam. nov.

African Blindsnakes

Type genus. *Afrotyphlops* Broadley & Wallach 2009.

Diagnosis. Members of this subfamily have (1) eye, distinct or indistinct, (2) snout, rounded or beaked (rarely acuminate), (3) head scale arrangement, non-circular, (4) frontorostral, absent, (5) nasal, completely or incompletely divided, (6) nasal suture origin, 1st or 2nd supralabial (rarely rostral or 1st/2nd suture), (7) subocular, absent or present, (8) postoculars, 2–6 (rarely 7; average, 3.68), (9) preocular-labial contact, supralabials 2 & 3 (rarely none, 1st, or 4th), (10) midbody scale rows, 18–45 (average, 24.8), (11) scale row reduction, present or absent, (12) total scale rows, 216–737 (average, 437), (13) caudals, 4–15 (average, 10.8), (14) maximum total length, 125–950 (average, 403) mm, (15) total length/midbody diameter, 17–129 (average, 52.4), (16) total length/tail length, 33–152 (average, 68.2), (17) dorsal color, variable (white, cream, pink, brown, yellow, pale blue, pale green, or pale red), (18) ventral color, usually white, cream, or yellow (rarely brown or black), (19) dorsum darker than, or similar to, venter, (20) overall, usually no distinctive pattern, although sometimes with longitudinal lines (Tables 1–2); molecular phylogenetic support (Fig. 1).

The subfamily Afrotyphlopinae is distinguished from the other three subfamilies by more postocular scales (3.68 versus 2.19 in Asiatyphlopinae, 2.27 in Madatyphlopinae, and 1.66 in Typhlopinae; average of species mean values), more midbody scales (24.8 versus 21.8 in Asiatyphlopinae, 22.9 in Madatyphlopinae, and 20.3 in Typhlopinae), larger maximum body size (403 mm TL versus 294 mm in Asiatyphlopinae, 320 mm in Madatyphlopinae, and 264 mm in Typhlopinae), and shorter tails (TL/TA 68.2 versus 47.1 in Asiatyphlopinae, 53.7 in Madatyphlopinae, and 48.7 in Typhlopinae).

Content. Three genera: *Afrotyphlops* Broadley & Wallach 2009*, Letheobia* Cope 1868*,* and *Rhinotyphlops* Fitzinger 1843 (Table 3).

Distribution. Afrotyphlopinae is distributed almost exclusively in sub-Saharan Africa (including satellite islands and islets), with two species occurring in the Middle East.

Etymology. As for the type-genus.

Remarks. The subfamily Afrotyphlopinae is well-defined in the molecular phylogeny of Vidal *et al.* (2010), and in the tree here (Fig. 1). Within this African clade of blindsnakes, Vidal *et al.* (2010) found that the arrangement of species did not agree in some respects with the taxonomic proposal of Broadley and Wallach (2009), who

Figure 1. Phylogenetic ML tree of typhlopid snakes based on an analysis of DNA sequences of five nuclear protein-coding genes (data set A). Nodes with asterisks are supported by posterior probability > 95% and ML bootstrap probability > 70%. The tree is rooted with 22 outgroup species (not shown) including a monitor lizard, and species of alethinophidian, leptotyphlopid, gerrhopilid, and xenotyphlopid snakes (Vidal *et al.* 2010).

had erected two new genera: *Afrotyphlops* and *Megatyphlops*. For example, species assigned by those authors to *Megatyphlops* appeared nested among species assigned by them to *Afrotyphlops*. As has been noted (Broadley & Wallach 2009), there has been a great diversity of different generic assignments for African species of typhlopid snakes. Here, we have added new sequences to the molecular phylogeny and have interpreted these new results in light of our compilation of morphological data (Tables 1–2). In so doing, we have corrected the errors in the current taxonomy of this group (subfamily), reassigning some species of *Letheobia*, *Rhinotyphlops*, and *Typhlops* to other genera. We believe that this new taxonomy retains the status quo as best as possible and recognizes major clades of species sharing suites of morphological traits.

Genus *Afrotyphlops* Broadley & Wallach, 2009

African Giant Blindsnakes

Type species. *Acontias punctatus* Leach *in* Bowdich 1819:493, by original designation.

Diagnosis. Species of *Afrotyphlops* have (1) eye, distinct, (2) snout, rounded (sometimes beaked or acuminate), (3) head scale arrangement, non-circular, (4) frontorostral, absent, (5) nasal, incompletely divided (rarely complete), (6) nasal suture origin, 1st supralabial (sometimes 2nd supralabial or rarely rostral), (7) suboculars or subpreoculars, absent (rarely a subpreocular/intercalary present), (8) postoculars, 2–4 (rarely 5–7; average 3.70), (9) preocular-labial contact, supralabials 2 & 3 (rarely none, 1–2, 1–3, or 2), (10) midbody scale rows, 18–45 (average, 27.2), (11) scale row reduction, present (rarely absent), (12) total scale rows, 216–620 (average, 391), (13) caudals, 4–15 (average, 9.6), (14) maximum total length, 125–950 (average, 481) mm, (15) total length/midbody diameter, 17–95 (average, 39.5), (16) total length/tail length, 33–152 (average, 60.8), (17) dorsal color, dark brown (sometimes yellow, bluish, reddish, or greenish), (18) ventral color, yellow, yellowish, cream, or white, (19) dorsum darker than venter, (20) overall, usually patternless, but sometimes with longitudinal lines (Tables 1–2); molecular phylogenetic support (Fig. 1).

From *Letheobia*, *Afrotyphlops* is distinguished by having a distinct eye (versus indistinct), lacking subocular scales (versus present), and having a dark (versus pale) dorsum. Species of *Afrotyphlops* also average larger in size and have more robust bodies, although there is variation in those traits. From *Rhinotyphlops*, *Afrotyphlops* is distinguished by its more rounded snout in lateral profile (versus beaked), except several species formerly in the genus *Megatyphlops*, fewer caudals (9.6 versus 14.5), and larger size (481 versus 323 mm average TL).

Content. Twenty-nine species: *Afrotyphlops angolensis, A. anomalus, A. bibronii, A. blanfordii, A. brevis, A. calabresii, A. comorensis, A. congestus, A. cuneirostris, A. decorosus, A. elegans, A. fornasinii, A. gierrai, A. jubanus, A. kaimosae, A. liberiensis, A. lineolatus, A. mucruso, A. nanus, A. nigrocandidus, A. obtusus, A. platyrhynchus, A. punctatus, A. rondoensis, A. schlegelii, A. schmidti, A. steinhausi, A. tanganicanus,* and *A. usambaricus* (Table 3).

Distribution. *Afrotyphlops* is distributed entirely in sub-Saharan Africa (including satellite islands and islets).

Etymology. The generic name is a masculine noun formed from the adjective *africanus* (*a, um*; i.e., 'from Africa') and the Greek noun *typhlops* (the blind).

Remarks. The molecular phylogeny of Vidal et al. (2010), and the updated phylogeny here (Fig. 1), formed a group of 10 African species that includes the type species of *Afrotyphlops, A. punctatus*. That species and the other nine species all lack subocular scales and their nasal suture origin is at the 1st supralabial, in contrast to most species of *Letheobia* that have one or more suboculars and a nasal suture origin at the 2nd supralabial. Other characters (see diagnosis above) also were consistent with the division of the two genera. We include in this genus most species of *Afrotyphlops* listed by Broadley and Wallach (2009), but not all. They included *A. angeli* and *A. manni*, but we place them here in *Letheobia* based on the diagnostic characters (e.g., indistinct eye, presence of subocular, and nasal suture origin at the 2nd supralabial). Also, of the 10 species of *Afrotyphlops* with molecular data, two (*A. mucroso* and *A. schlegelii*) were placed in a separate genus, *Megatyphlops*, by Broadley and Wallach (2009). However, their position in the tree, nested within the clade of *Afrotyphlops* species (Vidal et al. 2010), indicated that either *Megatyphlops* is a synonym of *Afrotyphlops*, or that additional genera should be recognized to

correct the paraphyly of *Afrotyphlops*. Because it is not obvious to us how character data would justify subdividing *Afrotyphlops* into many genera, we instead place *Megatyphlops* in the synonymy of *Afrotyphlops*. In addition, the molecular phylogenies show that a species placed in the genus *Letheobia* (*L. obtusa*) by Broadley and Wallach clustered with the *Afrotyphlops* clade. Therefore, we have transferred that species and its close relatives (*L. decorosa* and *L. jubana*) to *Afrotyphlops* and note that their external characters agree with our diagnosis of *Afrotyphlops*: all 3 species lack a subocular scale and 2 of those species have the nasal suture origin at the 1st supralabial (1st or 2nd in *A. jubanus*). Finally, we place four species of *Typhlops* in *Afrotyphlops*: *T. calabresii*, *T. cuneirostris*, *T. comorensis*, and *T. platyrhynchus*. These species have flattened snouts and are reddish dorsally, suggesting that they are related, and they share diagnostic characters of *Afrotyphlops*: distinct eye, nasal incompletely divided, subocular absent, robust body, and a dark dorsum.

Genus *Letheobia* Cope, 1868

African Gracile Blindsnakes

Type species. *Onychocephalus caecus* Duméril, 1856:462, by subsequent designation of Peters, 1881:70.

Diagnosis. Species of *Letheobia* have (1) eye, indistinct, (2) snout, beaked or rounded, (3) head scale arrangement, non-circular, (4) frontorostral, absent, (5) nasal, completely or incompletely divided, (6) nasal suture origin, 2nd supralabial (rarely, 1st supralabial, suture (1/2), rostral, or preocular), (7) suboculars or subpreoculars, present (rarely absent), (8) postoculars, 3–4 (rarely 2, 5–7; average, 3.55), (9) preocular-labial contact, supralabials 2 & 3 (sometimes 2nd, 3rd, 2–4, or none), (10) midbody scale rows, 18–30 (average 22.3), (11) scale row reduction, present or absent, (12) total scale rows, 250–737 (average, 484), (13) caudals, 8–15 (average, 11.1), (14) maximum total length, 135–670 (average, 350) mm, (15) total length/midbody diameter, 35–129 (average, 66.6), (16) total length/tail length, 45.5–143 (average, 79.0), (17) dorsal color, usually pale (pink, cream, white, colorless), (18) ventral color, usually pale (pink, cream, white, unpigmented), (19) dorsum same color as venter, and (20) overall, a patternless, unicolor snake (Tables 1–2); molecular phylogenetic support (Fig. 1).

From *Afrotyphlops* and *Rhinotyphlops*, *Letheobia* is distinguished by having an indistinct eye (versus distinct), having subocular scales present (versus absent), and having a pale (versus dark) dorsum.

Content. Thirty-one species: *Letheobia angeli, L. acutirostrata, L. caeca, L. coecata, L. crossii, L. debilis, L. episcopa, L. erythraea, L. feae, L. gracilis, L. graueri, L. kibarae, L. largeni, L. leucosticta, L. lumbriciformis, L. manni, L. newtoni, L. pallida, L. pauwelsi, L. pembana, L. praeocularis, L. rufescens, L. simonii, L. somalica, L. stejnegeri, L. sudanensis, L. swahilica, L. toritensis, L. uluguruensis, L. wittei,* and *L. zenkeri* (Table 3).

Distribution. *Letheobia* is distributed throughout sub-Saharan Africa, including West Africa, Central Africa, and Eastern Africa, as far south as the Democratic Republic of the Congo and Tanzania.

Etymology. Although not stated in the original description, the generic name is a feminine noun formed from the Greek *lethe* (forgotten) and *bios* (life), meaning forgotten life, an appropriate reference to blindsnakes.

Remarks. The molecular phylogeny of Vidal *et al.* (2010), and the updated phylogeny here (Fig. 1), formed a group of four African species, placed in *Letheobia* by Broadley & Wallach (2007): *L. episcopa, L. feae, L. newtoni*, and *L. simonii*. Broadley & Wallach (2009) removed two species (*L. angeli* and *L. manni*) and placed them in *Afrotyphlops*, but we place them back in *Letheobia* here because they have the diagnostic external characters of that genus. We also tentatively place *Typhlops coecatus* and *T. zenkeri* in *Letheobia* based on their external morphology: *L. coecata* has an origin of the nasal suture at the 2nd supralabial as in most species and usually has a pallid coloration, traits more often associated with *Letheobia*. *Letheobia zenkeri* has a subocular scale and pale, unicolor pattern, as in most *Letheobia*. In addition, our molecular phylogenies show that a species placed in the genus *Letheobia* (*L. obtusa*) by Broadley & Wallach (2007) clustered with the *Afrotyphlops* clade. Therefore, we have transferred that species and its close relatives (*L. decorosa* and *L. jubanus*) to *Afrotyphlops* and note that their external characters agree with our diagnosis of *Afrotyphlops*: all three species lack a subocular scale and two of those species have the nasal suture origin at the 1st supralabial (1st or 2nd in *A. jubanus*). Broadley & Wallach (2007) clarified the type species desig-

nation of this genus.

Genus *Rhinotyphlops* Fitzinger, 1843
African Beaked Blindsnakes

Type species. *Typhlops lalandei* Schlegel, 1839:38, by original designation.

Diagnosis. Species of *Rhinotyphlops* have (1) eye, distinct, (2) snout, beaked (rarely rounded), (3) head scale arrangement, non-circular, (4) frontorostral, absent, (5) nasal, completely or incompletely divided, (6) nasal suture origin, 2nd supralabial (sometimes 1st supralabial), (7) suboculars or subpreoculars, absent (sometimes present), (8) postoculars, 4–6 (rarely 2–3; average 4.21), (9) preocular-labial contact, supralabials 2 & 3 (sometimes 2nd or 2–4), (10) midbody scale rows, 22–34 (average, 25.0), (11) scale row reduction, present (sometimes absent), (12) total scale rows, 311–586 (average, 425), (13) caudals, 14–15 (average, 14.5), (14) maximum total length, 220–455 (average, 323) mm, (15) total length/midbody diameter, 27–77 (average, 48.9), (16) total length/tail length, 50.2–78.5 (average, 65.0), (17) dorsal color, brown (sometimes yellowish, greenish, or reddish), (18) ventral color, white or yellowish (sometimes brownish or black), (19) dorsum darker than venter, (20) overall, either patternless or with longitudinal lines (Tables 1–2); molecular phylogenetic support (Fig. 1).

From *Letheobia*, *Rhinotyphlops* is distinguished by having a distinct eye (versus indistinct), lacking subocular scales (versus present), having a higher average number of midbody scale rows (25.0 versus 22.3), having a higher average number of caudals (14.5 versus 11.1), and having a dark (versus pale) dorsum. From *Afrotyphlops*, *Rhinotyphlops* is distinguished by having more caudals (14.5 versus 9.6) and smaller size (323 versus 481 mm average TL).

Content. Seven species: *Rhinotyphlops ataeniatus, R. scortecci, R. unitaeniatus, R. boylei, R. lalandei, R. leucocephalus,* and *R. schinzi* (Table 3).

Distribution. *Rhinotyphlops* is distributed in eastern and southern Africa to South Africa. Four of the species occur in Somalia.

Etymology. The generic name is a masculine noun formed from the Greek adjective *rhinos* (beaked) and Greek noun *typhlops* (the blind), in reference to the beak-shaped snout of these blindsnakes.

Remarks. The molecular phylogeny of Vidal *et al.* (2010), and the updated phylogeny here (Fig. 1), place the type species of *Rhinotyphlops*, *R. lalandei*, in a group with another beaked species, *R. unitaeniatus*. The latter species was placed in the genus *Letheobia* by Broadley & Wallach (2007). Therefore, we have transferred that species and its close relatives in the *L. unitaeniata* complex (*L. ataeniata* and *L. scorteccii*) to *Rhinotyphlops* and note that their external characters agree with our diagnosis of *Rhinotyphlops*.

Subfamily Asiatyphlopinae subfam. nov.
Asian Blindsnakes

Type genus. *Asiatyphlops* **gen. nov.**

Diagnosis. Members of this subfamily have (1) eye, distinct (rarely indistinct), (2) snout, rounded (sometimes beaked or acuminate), (3) head scale arrangement, non-circular (circular in *Cyclotyphlops*), (4) frontorostral, absent (present in *Acutotyphlops*), (5) nasal, completely or incompletely divided, (6) nasal suture origin, 2nd supralabial (rarely 1st, 1/2 suture, 2/preocular suture, or preocular), (7) suboculars or subpreoculars, absent or present, (8) postoculars, 1–5 (average, 2.19), (9) preocular-labial contact, supralabials 2 & 3 (rarely none, 3rd, or preocular absent), (10) midbody scale rows, 16–36 (average, 21.8), (11) scale row reduction, present or absent, (12) total scale rows, 206–750 (average, 408), (13) caudals, 5–36 (average, 14.6), (14) maximum total length, 91–750 (average, 293) mm, (15) total length/midbody diameter, 18–134 (average, 49.8), (16) total length/tail length, 13–133 (average, 47.1), (17) dorsal color, variable but usually shades of brown, (18) ventral color, variable but usually white, cream, or yellowish, (19) dorsum darker than venter, (20) overall, usually no distinctive pattern (sometimes with longitudinal

lines) (Tables 1–2); molecular phylogenetic support (Fig. 1).

The subfamily Asiatyphlopinae is distinguished from Afrotyphlopinae in having fewer postocular scales (2.19 versus 3.68; average of species mean values), fewer midbody scales (21.8 versus 24.8), smaller body size (293 versus 403 mm TL), and longer tails (TL/TA 47.1 versus 68.2). It is distinguished from Typhlopinae in having more postocular scales (2.19 versus 1.66; average of species averages), more midbody scales (21.8 versus 20.3), and slightly larger body size (294 versus 264 mm TL). Individual genera of Asiatyphlopinae differ from Madatyphlopinae in the following ways: *Acutotyphlops* has a frontorostral and complete nasal division (versus absent, and suture incomplete), *Cyclotyphlops* has a circular arrangement of head scales (versus non-circular), *Grypotyphlops* has suboculars present (versus absent), *Indotyphlops* has 1 postocular (versus 2–3), *Asiatyphlops, Malayotyphlops,* and *Xerotyphlops* have fewer average total scale rows (339, 367, and 355 versus 429), *Ramphotyphlops* and *Sundatyphlops* have longer tails (TL/TA = 31.8 and 33.3 versus 53.7, averages), and *Anilios* has a solid, awn-like protrusible hemipenis and retrocloacal sacs (versus non-protrusible hemipenis and retrocloacal sacs absent).

Content. Ten genera: *Acutotyphlops* Wallach 1995*, Anilios* Gray 1845*, Asiatyphlops* gen. nov.*, Cyclotyphlops* in den Bosch & Ineich 1994*, Grypotyphlops* Peters 1881*, Indotyphlops* gen. nov.*, Malayotyphlops* gen. nov., *Ramphotyphlops* Fitzinger 1843, *Sundatyphlops* gen. nov., and *Xerotyphlops* gen. nov.

Distribution. Asiatyphlopinae is distributed widely in southern and eastern Asia, the Malay Archipelago, Australasia, and islands of the western and southern Pacific.

Etymology. As for the type-genus.

Remarks. The subfamily Asiatyphlopinae was initially defined as a clade in the molecular phylogeny of Vidal *et al.* (2010), but the additional species added in subsequent studies (Marin *et al.* 2013a; Marin *et al.* 2013b), and this study (Figs. 1–2), have clarified the relationships further. This is the largest subfamily of typhlopids, with 10 genera and 121 species. The large morphological data set (Tables 1–2) has helped to allocate species that are not in the molecular phylogeny, and this has led to many generic changes, including description of five new genera here. The formerly pan-tropical genus *Typhlops* is now restricted to Caribbean islands.

Genus *Acutotyphlops* Wallach, 1995

Sharp-nosed Blindsnakes

Type species. *Acutotyphlops kunuaensis* Wallach, 1995:141, by original designation.

Diagnosis. Species of *Acutotyphlops* have (1) eye, distinct, (2) snout, acuminate or rounded, (3) head scale arrangement, non-circular, (4) frontorostral, present, (5) nasal, incompletely divided, (6) nasal suture origin, 2nd supralabial (sometimes 1st), (7) suboculars or subpreoculars, present (rarely absent), (8) postoculars, 3–5 (average, 4.10), (9) preocular-labial contact, supralabials 2 & 3, 3rd, or none, (10) midbody scale rows, 26–36 (average, 30.4), (11) scale row reduction, present, (12) total scale rows, 334–542 (average, 415), (13) caudals, 11–31 (average, 20.9), (14) maximum total length, 333–487 (average, 392) mm, (15) total length/midbody diameter, 18–58 (average, 38.2), (16) total length/tail length, 13–100 (average, 31.1), (17) dorsal color, dark brown (rarely golden orange), (18) ventral color, yellowish or gold, (19) dorsum darker than venter, (20) overall, either patternless or with bars or longitudinal lines (Tables 1–2); molecular phylogenetic support (Fig. 1).

Acutotyphlops differs from other typhlopids in having a frontorostral scale (Wallach 1995; Wallach *et al.* 2007a).

Content. Five species: *Acutotyphlops banaorum, A. infralabialis, A. kunuaensis, A. solomonis,* and *A. subocularis* (Table 3).

Distribution. *Acutotyphlops* is distributed in the Philippines, Indonesia, Papua New Guinea, and the Solomon Islands.

Etymology. The generic name is a masculine noun formed from the Latin adjective *acutus* (pointed) and Greek noun *typhlops* (the blind), in reference to the acuminate (pointed) snouts of these blindsnakes.

Remarks. The molecular phylogeny (Fig. 1) places the type species of *Acutotyphlops* in a group with two

other species (one undescribed).

Genus *Anilios* Gray, 1845
Australian Blindsnakes

Type species. *Anilios australis* Gray, 1845:145, by subsequent designation of Stejneger, 1904:683.

Diagnosis. Species of *Anilios* have (1) eye, distinct, (2) snout, rounded or beaked (rarely acuminate), (3) head scale arrangement, non-circular, (4) frontorostral, absent, (5) nasal, completely or incompletely divided, (6) nasal suture origin, 2nd supralabial (sometimes 1st, 1/2 suture, 2/preocular suture, or preocular), (7) suboculars or subpreoculars, absent, (8) postoculars, 2 (rarely 1, 3, or 4; average, 2.21), (9) preocular-labial contact, supralabials 2 & 3, (10) midbody scale rows, 16–24 (average, 20.1), (11) scale row reduction, absent (rarely present), (12) total scale rows, 278–750 (average, 466), (13) caudals, 8–36 (average, 15.0), (14) maximum total length, 122–750 (average, 353) mm, (15) total length/midbody diameter, 20–134 (average, 55.8), (16) total length/tail length, 15–112 (average, 49.7), (17) dorsal color, usually brown (sometimes cream, tan, pinkish, grey, or yellowish), (18) ventral color, usually white, cream, or yellowish, (19) dorsum darker than venter, (20) overall, usually patternless or sometimes with longitudinal lines (Tables 1–2); molecular phylogenetic support (Figs. 1–2).

From other genera of Asiatyphlopinae, *Anilios* differs from *Acutotyphlops* in lacking a frontorostral and from *Cyclotyphlops* in having non-circular head scales (versus circular arrangement). It differs from *Grypotyphlops* in lacking subocular scales. It differs from *Asiatyphlops*, *Cyclotyphlops*, *Malayotyphlops*, *Indotyphlops*, and *Xerotyphlops* in having more total scale rows (466 versus 294–367, averages). It differs from other genera except *Indotyphlops* in having a thin body (TL/MBD = 55.8 versus 35.1–46.6 in those other genera; averages). It differs from *Sundatyphlops* and *Ramphotyphlops* in having relatively short tails (TL/TA = 49.7 versus 31.8–33.3).

Content. Forty-three species: *Anilios affinis, A. ammodytes, A. aspinus, A. australis, A. batillus, A. bicolor, A. bituberculatus, A. broomi, A. centralis, A. chamodracaena, A. diversus, A. endoterus, A. erycinus, A. ganei, A. grypus, A. guentheri, A. hamatus, A. howi, A. kimberleyensis, A. leptosomus, A. leucoproctus, A. ligatus, A. longissimus, A. margaretae, A. micrommus, A. minimus, A. nema, A. nigrescens, A. nigroterminatus, A. pilbarensis, A. pinguis, A. proximus, A. robertsi, A. silvia, A. splendidus, A. torresianus, A. tovelli, A. troglodytes, A. unguirostris, A. waitii, A. wiedii, A. yampiensis,* and *A. yirrikalae* (Table 3). Broad molecular sampling of populations within Australia has shown that the true species diversity is even greater, likely exceeding 100 species (Marin *et al.* 2013b) (Fig. 2).

Distribution. *Anilios* is distributed almost entirely in Australia, with two species occurring additionally in New Guinea (*A. leucoproctus* and *A. torresianus*) and a third species occurring only in New Guinea (*A. erycinus*).

Etymology. The generic name is a masculine noun formed from the Greek *an-* (not) and noun *helios* (sun), in reference to the below-ground lifestyle of these snakes.

Remarks. Wallach (2006) named *Austrotyphlops* for this Australian clade, but *Anilios* is an earlier, available name. To diagnose the clade, Wallach (2006) used two reproductive traits that had been discussed in the literature previously (Robb 1966; McDowell 1974), for the more inclusive clade of *Ramphotyphlops* s.l.: a solid, awn-like protrusible hemipenis and retrocloacal sacs. Therefore, those characters are not diagnostic of the Australian clade (here, *Anilios*), as pointed out recently (Savage & Boundy 2012). Also, Savage & Boundy (2012) clarified the type species of *Anilios*. The current molecular phylogenies (Figs. 1–2) contain 27 of the 44 described species, which is a relatively large percentage of the genus, and those 27 species may actually represent 56–92 species based on molecular data (Marin *et al.* 2013a; Marin *et al.* 2013b). Our molecular phylogenies (Figs. 1–2) indicate that *Anilios polygrammicus* is a polyphyletic species, with the Australian populations (Queensland) belonging to *Anilios* and the Lesser Sunda Islands populations (including the type locality on Timor) belonging to another genus, *Sundatyphlops* (see below). With *S. polygrammicus* removed from *Anilios*, the only available name for the populations from northeastern Australia is *Anilios torresianus* (type locality, Murray Island, Queensland). We also assign populations from nearby southern New Guinea to this species. We suspect that further study will reveal that both *Sundatyphlops polygrammicus* and *Anilios torresianus* are complexes of species, based on their distribution on multiple

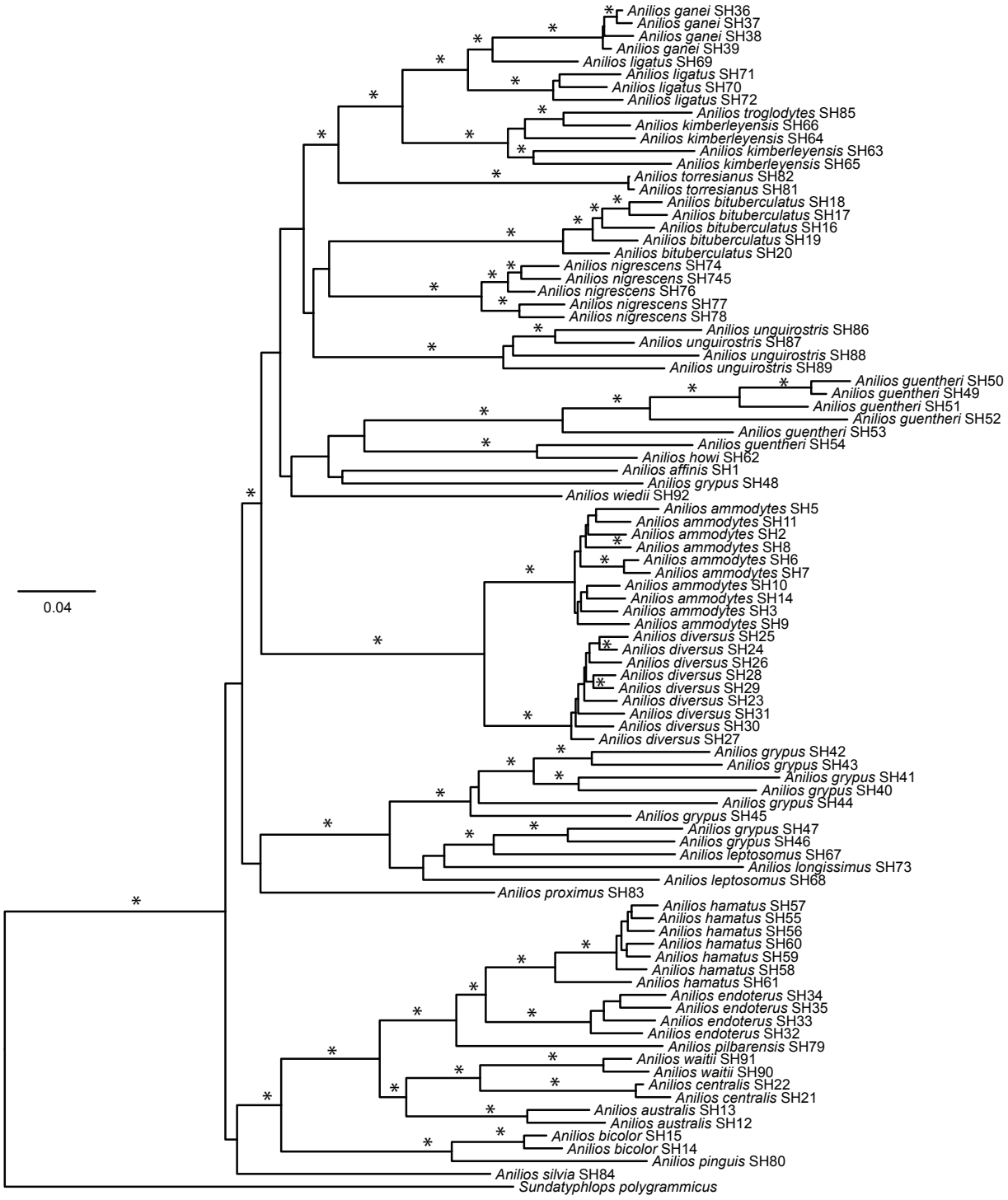

Figure 2. Phylogenetic ML tree of typhlopid snakes from Australia and nearby areas based on an analysis of DNA sequences of 3 nuclear protein-coding genes and 3 mitochondrial genes (data set B). Nodes with asterisks are supported by posterior probability > 95% and ML bootstrap probability > 70%. The tree is rooted with *Acutotyphlops subocularis* (not shown).

land masses.

Genus *Asiatyphlops* gen. nov.
Southeast Asian Blindsnakes

Type species. *Typhlops mülleri* Schlegel, 1839:39.

Diagnosis. Species of *Asiatyphlops* have (1) eye, distinct (rarely indistinct), (2) snout, rounded, (3) head scale arrangement, non-circular, (4) frontorostral, absent, (5) nasal, incompletely divided (sometimes completely divided), (6) nasal suture origin, 2nd supralabial, (7) suboculars or subpreoculars, absent, (8) postoculars, 2–3 (rarely, 4–5; average, 2.69), (9) preocular-labial contact, supralabials 2 & 3 (sometimes 3rd only), (10) midbody scale rows, 20–30 (average, 23.2), (11) scale row reduction, present (sometimes absent), (12) total scale rows, 246–520 (average, 339), (13) caudals, 5–26 (average, 11.1), (14) maximum total length, 130–430 (average, 243) mm, (15) total length/midbody diameter, 26–70 (average, 35.2), (16) total length/tail length, 42–100 (average, 65.6), (17) dorsal color, shades of brown (golden-brown, olive-brown, blackish-brown, yellowish-brown, grayish-olive, or blue), (18) ventral color, nearly always yellow or yellowish (white, cream, yellow, yellowish-tan, yellowish-brown, bright yellow, or pale brown), (19) dorsum darker than venter, (20) overall, uniform, but sometimes with a dark lineate pattern (Tables 1–2); molecular phylogenetic support (Fig. 1).

From other genera of Asiatyphlopinae, *Asiatyphlops* differs from *Acutotyphlops* in lacking a frontorostral and from *Cyclotyphlops* in having non-circular head scales (versus circular arrangement). It differs from *Grypotyphlops* in lacking subocular scales. It differs from *Acutotyphlops, Malayotyphlops,* and *Grypotyphlops* in having fewer average midbody scale rows (23.2 versus 26.8–30.4). It differs from *Anilios*, *Grypotyphlops*, and *Sundatyphlops* in having fewer total scale rows (339 versus 466–496, averages). It differs from *Anilios*, *Grypotyphlops*, *Indotyphlops*, *Ramphotyphlops*, *Sundatyphlops*, and *Xerotyphlops* in having a robust body (TL/MBD = 35.2 versus 45.5–57.6 in those other genera; averages). It differs from most genera except *Grypotyphlops* and *Xerotyphlops* in having a relatively short tail (TL/TA = 65.6 versus 31.5–51.0; averages). Compared with *Indotyphlops*, species of *Asiatyphlops* are larger (average of maximum TLs among species, 243 versus 175 mm), thicker-bodied (TL/MBD = 35.2 versus 57.6, averages), shorter-tailed (TL/TA = 65.6 versus 46.4, averages), always have >1 postocular scale (versus usually 1), and have more midbody scale rows (average, 23.2 versus 19.4). Also, they nearly always have yellow on the venter (versus lacking a yellowish venter in *Indotyphlops*, except one species).

Content. Thirteen species: *Asiatyphlops bothriorhynchus, A. diardii, A. fuscus, A. giadinhensis, A. klemmeri, A. koshunensis, A. leucomelas, A. muelleri, A. oatesii, A. roxaneae, A. siamensis, A. tenuicollis,* and *A. trangensis* (Table 3).

Distribution. *Asiatyphlops* is broadly distributed in southern and southeastern Asia, including Bangladesh, Cambodia, southern China, India, Indonesia, Laos, Malaysia, Myanmar, Nepal, Singapore, Taiwan, Thailand, and Vietnam. Unlike *Indotyphlops*, it does not have a major presence in peninsular India or Sri Lanka.

Etymology. The generic name is a masculine noun formed from the adjective *asianus* (*a, um*; i.e., 'from Asia') and the Greek noun *typhlops* (the blind).

Remarks. Blindsnakes from southern and southeast Asia have been difficult to classify in the past using morphology (Taylor 1965; McDowell 1974; Khan 1999; Wallach 1999; 2000; Wallach & Pauwels 2004). The molecular phylogenetic evidence (Vidal *et al.* 2010; Marin *et al.* 2013a; Marin *et al.* 2013b) (Figs 1, 2) has assisted greatly, even though species sampling is still sparse. Those molecular data show that three major groups are present on the mainland of southern and southeast Asia: Gerrhopilidae (Vidal *et al.* 2010), *Asiatyphlops*, and *Indotyphlops.* Snakes of the genus *Asiatyphlops* are stout-bodied with 1 postocular scale, high midbody scale rows (usually >20), short tails, and yellow venters. *Indotyphlops* are thin-bodied blindsnakes with >1 postocular scale, low midbody scale rows (usually 18–20), longer tails, and venters that are pale but not yellow. Geographically, members of *Asiatyphlops* are primarily distributed in Southeast Asia as far west as northeastern India (Assam) and with one species (*A. leucomelas*) occurring in Sri Lanka. Other species in Sri Lanka and peninsular India are allocated to *Indotyphlops*, and therefore we have some reservation in the generic assignment of *A. leucomelas*. However, the species is con-

sistent with the diagnostic characters of *Asiatyphlops*. We chose *Typhlops mülleri* Schlegel as type species because it is in our molecular phylogeny and has a precise type locality (Padang, Sumatra).

Genus *Cyclotyphlops* in den Bosch & Ineich, 1994
Sulawesi Blindsnakes

Type species. *Cyclotyphlops deharvengi* in den Bosch & Ineich, 1994: 208, by monotypy.

Diagnosis. The single species of *Cyclotyphlops* has (1) eye, distinct, (2) snout, rounded, (3) head scale arrangement, circular, (4) frontorostral, absent, (5) nasal, completely divided, (6) nasal suture origin, junction of 1st and 2nd supralabial, (7) suboculars or subpreoculars, present, (8) postoculars, 1, (9) preocular-labial contact, absent, (10) midbody scale rows, 22, (11) scale row reduction, present, (12) total scale rows, 294, (13) caudals, unreported, (14) maximum total length, 146 mm, (15) total length/midbody diameter, 35.1, (16) total length/tail length, 32.3, (17) dorsal color, dark brown, (18) ventral color, brown, (19) dorsum darker than venter, (20) overall, patternless (Tables 1–2); no molecular phylogenetic information is available.

Cyclotyphlops differs from all other genera in the Asiatyphlopinae in having a circular arrangement of head scales (in den Bosch & Ineich 1994).

Content. One species: *Cyclotyphlops deharvengi* (Table 3).

Distribution. *Cyclotyphlops* is distributed on the Indonesian island of Sulawesi.

Etymology. The generic name is a masculine noun formed from the Greek nouns *kyklos* (circle) and *typhlops* (the blind), in reference to the circular arrangement of head scales in this species.

Remarks. Although this genus stands out in terms of head scalation, the same can be said of *Acutotyphlops*, yet the latter genus is nested deeply within Asiatyphlopinae. For that reason, there is no justification yet to recognize *Cyclotyphlops* as a separate family. However, until more material becomes available, including DNA sequence data, its assignment to the Asiatyphlopinae remains tentative.

Genus *Grypotyphlops* Peters, 1881
Indian Beaked Blindsnakes

Type species. *Onychocephalus acutus* Duméril & Bibron, 1844:333, by original designation.

Diagnosis. Species of *Grypotyphlops* have (1) eye, distinct or indistinct, (2) snout, beaked, (3) head scale arrangement, non-circular, (4) frontorostral, absent, (5) nasal, completely or incompletely divided, (6) nasal suture origin, 2nd supralabial, (7) suboculars or subpreoculars, present, (8) postoculars, 4 (rarely 3 or 5; average, 4.0), (9) preocular-labial contact, supralabials 2 & 3, (10) midbody scale rows, 24–30, (11) scale row reduction, present, (12) total scale rows, 448–526 (average, 487), (13) caudals, 7–13 (average, 10.0), (14) maximum total length, 630 mm, (15) total length/midbody diameter, 30–66 (average, 48.0), (16) total length/tail length, 17–133 (average, 75.1), (17) dorsal color, gray, brown, or golden brown, (18) ventral color, grayish-white, yellow, or pale brown, (19) dorsum darker than venter, (20) overall, coloration is uniform, although pale scale centers may appear as weakly-defined lines (Tables 1–2); no molecular phylogenetic information is available.

From other genera of Asiatyphlopinae except *Acutotyphlops* and *Cyclotyphlops*, *Grypotyphlops* differs in having subocular scales (versus absent). *Grypotyphlops* differs from *Acutotyphlops* in lacking a frontorostral and from *Cyclotyphlops* in having non-circular head scales (versus circular arrangement). Although one species of *Xerotyphlops* has a subocular scale, *Grypotyphlops* differs from that genus in having more postoculars (3–5 versus 2), more midbody scale rows (29 versus 23.5, averages), and more total scale rows (448–526 versus 206–435). At 630 mm TL, *Grypotyphlops* also stands out in its large size.

Content. One species: *Grypotyphlops acutus* (Table 3).

Distribution. *Grypotyphlops* is distributed in peninsular India south of the Ganges and Rajputana river basins.

Etymology. The generic name is a masculine noun formed from the Greek adjective *grypos* (hook-nosed) and Greek noun *typhlops* (the blind), in reference to the beaked snouts of these blindsnakes.

Remarks. We agree with Dixon & Hendricks (1979) that the type locality of another beaked blindsnake, *Onychocephalus unilineatus* Duméril & Bibron, is in error and unlikely from French Guiana. We also agree with Wallach (2003) that *O. unilineatus* is a synonym of *Grypotyphlops acutus*, and that recognition of *Grypotyphlops* is warranted based on morphology.

Genus *Indotyphlops* gen. nov.
South Asian Blindsnakes

Type species. *Typhlops pammeces* Günther, 1864:444.

Diagnosis. Species of *Indotyphlops* have (1) eye, distinct (sometimes indistinct), (2) snout, rounded, (3) head scale arrangement, non-circular, (4) frontorostral, absent, (5) nasal, completely or incompletely divided, (6) nasal suture origin, 2nd supralabial (sometimes preocular, or rarely 1st supralabial), (7) suboculars or subpreoculars, absent, (8) postoculars, 1 in all 18 species recorded, but variable (1–2) in 1 of those species, (9) preocular-labial contact, supralabials 2 & 3 (sometimes 3rd only), (10) midbody scale rows, 18–20 (22 in 1 species; average, 19.4), (11) scale row reduction, absent (sometimes present), (12) total scale rows, 229–468 (average, 345), (13) caudals, 7–15 (average, 10.8), (14) maximum total length, 91–285 (average, 175) mm, (15) total length/midbody diameter, 28–130 (average, 57.6), (16) total length/tail length, 22.3–76 (average, 46.4), (17) dorsal color, shades of brown (sometimes cream, gray, yellowish-brown, reddish brown, lavender-gray, or black), (18) ventral color, variable (white, cream, pale brown, lavender-gray), (19) dorsum darker than venter, (20) overall, uniform, but often with a darker median row of scales giving a slight lineate appearance (Tables 1–2); molecular phylogenetic support (Fig. 1).

From other genera of Asiatyphlopinae, *Indotyphlops* differs in having a single postocular (versus 2 or more). Exceptions are *Cyclotyphlops*, 3 species of *Anilios*, and 3 species of *Ramphotyphlops*. It also has the lowest number of midbody scales (19.4 versus 20.1–30.4 in others; averages), and no scale reduction (6 of 7 species recorded; versus reduction present in *Acutotyphlops*, *Cyclotyphlops*, *Malayotyphlops*, *Grypotyphlops*, and *Xerotyphlops*). In total length, *Indotyphlops* is one of the smallest genera (TL = 175 mm versus > 243 mm in all others except *Cyclotyphlops*). It is also the thinnest genus in the subfamily (TL/MBD = 57.6 versus < 56 in other genera). *Indotyphlops* lacks yellow on the venter (except one species) whereas *Asiatyphlops*, with which it is broadly sympatric, has yellow on the venter.

Content. Twenty-two species: *Indotyphlops ahsanai, I. albiceps, I. braminus, I. exiguus, I. filiformis, I. fletcheri, I. hypsobothrius, I. jerdoni, I. khoratensis, I. lankaensis, I. lazelli, I. loveridgei, I. madgemintonae, I. malcolmi, I. meszoelyi, I. ozakiae, I. pammeces, I. porrectus, I. schmutzi, I. tenebrarum, I. veddae,* and *I. violaceus* (Table 3).

Distribution. *Indotyphlops* is broadly distributed in southern and southeastern Asia, including Bhutan, Cambodia, southern China, India and Sri Lanka, Indonesia, Laos, Malaysia, Myanmar, Nepal, and Thailand. Most species occur in South Asia, especially India and Sri Lanka. One invasive species, *I. braminus*, now has a nearly global distribution.

Etymology. The generic name is a masculine noun formed from the adjective *indianus* (*a, um*; i.e., 'from India') and the Greek noun *typhlops* (the blind).

Remarks. Blindsnakes from southern and southeastern Asia have proven especially difficult to classify in the past using morphology, such that there has been little agreement (McDowell 1974; Khan 1999; Wallach 1999; 2000; Wallach & Pauwels 2004). Species have generally been placed in two genera, *Ramphotyphlops* and *Typhlops*. However, with molecular phylogenetic evidence, Vidal *et al.* (2010) showed that the "*Typhlops ater* Group" represents a well-defined and deeply-divergent lineage that they named as a separate family, Gerrhopilidae. That study and subsequent molecular studies (Marin *et al.* 2013a; Marin *et al.* 2013b) (Figs. 1, 2) have allowed us to further clarify the taxonomy, while recognizing that molecular sampling is still sparse. In addition to allocating species to *Anilios*, *Malayotyphlops*, *Ramphotyphlops* s.s., and *Sundatyphlops*, we have erected *Asiatyphlops* and

Indotyphlops for the remaining species, most of which occur on the mainland of southern and southeast Asia. The relationships of species within *Indotyphlops* are not yet established, but the close relationship of the globally invasive species *I. braminus* to an Indian species (*I. pammeces*) suggests an origin in India. See also Remarks for *Asiatyphlops* concerning allocation of *A. leucomelas*.

Genus *Malayotyphlops* gen. nov.

Malay Archipelago Blindsnakes

Type species. *Typhlops luzonensis* Taylor, 1919:105.

Diagnosis. Species of *Malayotyphlops* have (1) eye, distinct (rarely indistinct), (2) snout, rounded, (3) head scale arrangement, non-circular, (4) frontorostral, absent, (5) nasal, incompletely divided (sometimes completely divided), (6) nasal suture origin, 2nd supralabial (rarely, 1st supralabial), (7) suboculars or subpreoculars, absent (rarely present), (8) postoculars, 2–4 (average, 2.75), (9) preocular-labial contact, supralabials 2 & 3 or 3rd only (rarely 2nd only), (10) midbody scale rows, 24–30 (average, 26.8), (11) scale row reduction, present, (12) total scale rows, 300–461 (average, 367), (13) caudals, 9–14 (average, 11.9), (14) maximum total length, 122–445 (average, 256) mm, (15) total length/midbody diameter, 31–58 (average, 42.0), (16) total length/tail length, 28–71 (average, 51.8), (17) dorsal color, variable (brown, gray-brown, reddish brown, greenish-black, black), (18) ventral color, variable (cream, yellowish, red, pink, pinkish-yellow), (19) dorsum darker than venter, (20) overall, patternless or with longitudinal lines, series of spots, or collar (Tables 1–2); only one species is included in the molecular phylogeny (Fig. 1).

In lacking a protrusible hemipenis and retrocloacal sacs (McDowell 1974), *Malayotyphlops* is separated from most other blindsnakes occurring in Southeast Asia, Indonesia, Australasia, and the western Pacific: *Acutotyphlops*, *Anilios*, *Cyclotyphlops*, *Ramphotyphlops*, and *Sundatyphlops*. From other genera of Asiatyphlopinae, *Malayotyphlops* differs from *Acutotyphlops* in lacking a frontorostral and from *Cyclotyphlops* in having non-circular head scales (versus circular arrangement). It differs from *Grypotyphlops* in lacking subocular scales. It differs from *Cyclotyphlops* and *Indotyphlops* in having more postoculars (2.75 versus 1.0–1.03; averages). It differs from *Anilios, Cyclotyphlops, Indotyphlops, Ramphotyphlops, Sundatyphlops,* and *Xerotyphlops* in having higher average midbody scale rows (26.8 versus 19.4–23.5). It differs from *Anilios*, *Grypotyphlops*, and *Sundatyphlops* in having fewer total scale rows (367 versus 466–496, averages) and smaller body size (TL = 256 versus 353–630; averages). See also comments below regarding other potential diagnostic characters.

Content. Ten species: *Malayotyphlops canlaonensis, M. castanotus, M. collaris, M. hypogius, M. koekkoeki, M. kraali, M. luzonensis, M. manilae, M. ruber,* and *M. ruficauda* (Table 3).

Distribution. *Malayotyphlops* is distributed widely in the Malay Archipelago, including the Philippines (7 species), Bunyu Island off of northern Borneo (1 species), and Seram and Kai in the Maluku Islands (1 species).

Etymology. The generic name is a masculine compound noun formed from the adjective *malayanus* (*a, um*; i.e., 'from the Malay Archipelago') and the Greek noun *typhlops* (the blind).

Remarks. This genus corresponds to the "*Typhlops ruficauda* Group" of McDowell (1974), who pointed out the reduction in the second supralabial in these species as a potential diagnostic character. This is also reflected in our scoring of preocular-labial contact with supralabial 3 (only) in 5 of the 8 species, instead of the usual contact with supralabials 2–3. Other potential diagnostic characters include the absence of a rectal caecum and fusion of glandular lines underlying the postnasal and preocular (McDowell 1974; Wynn & Leviton 1993), although more taxa will need to be surveyed to assess the usefulness of these characters. In the past, several authors incorrectly amended, as *ruficaudus*, the species name (a noun) of *Malayotyphlops ruficauda* to match the gender of the genus. Although Taylor (1919) placed "*Typhlops manilae*" in the "*ater* Group," now Gerrhopilidae (Vidal *et al.* 2010), we place it in *Malayotyphlops*. Taylor's only reason for that placement was presence of a subocular scale. Subocular scales are common (not constant) in Gerrhopilidae but they are also common in several other genera and rare in yet other genera. Otherwise, the characters of *M. manilae* are more consistent with traits of *Malayotyphlops*, especially

in high midbody scale rows (28, versus 18 in Gerrhopilidae) and short tail (TL/TA = 56 versus ~20–30).

Genus *Ramphotyphlops* Fitzinger, 1843
Western Pacific Blindsnakes

Type species. *Typhlops multilineatus* Schlegel, 1839:40, by original designation.

Diagnosis. Species of *Ramphotyphlops* have (1) eye, distinct (rarely indistinct), (2) snout, rounded or beaked, (3) head scale arrangement, non-circular, (4) frontorostral, absent, (5) nasal, completely or incompletely divided, (6) nasal suture origin, supralabial 2 (sometimes 1 or 1/2 suture), (7) suboculars or subpreoculars, absent (rarely present), (8) postoculars, 2–3 (rarely 1; average, 2.15), (9) preocular-labial contact, supralabials 2–3 (rarely 3 only or fused with ocular or nasal), (10) midbody scale rows, 18–30 (average, 21.7), (11) scale row reduction, present or absent, (12) total scale rows, 206–653 (average, 419), (13) caudals, 8–36 (average, 19.8), (14) maximum total length, 117–480 (average, 302) mm, (15) total length/midbody diameter, 18–91.5 (average, 48.8), (16) total length/tail length, 16.7–70 (average, 31.8), (17) dorsal color, usually dark brown (sometimes medium brown, tan, gray, or purplish), (18) ventral color, usually cream or yellowish-white (sometimes gray-green, pinkish, tan, or brown), (19) dorsum darker than venter, (20) overall, usually either patternless or with longitudinal lines (Tables 1–2); molecular phylogenetic support (Fig. 1).

Ramphotyphlops is part of a larger, more inclusive clade (*Ramphotyphlops* s.l.) that shares a solid, awn-like protrusible hemipenis and retrocloacal sacs (Robb 1966; McDowell 1974), although not all species have been examined for those traits. Presumably these characters distinguish it from other genera in the Asiatyphlopinae, except those three genera formerly in *Ramphotyphlops* s.l. and thus the closest relatives of *Ramphotyphlops* s.s.: *Acutotyphlops*, *Anilios*, and *Sundatyphlops*. From *Acutotyphlops*, *Ramphotyphlops* can be distinguished by lacking a frontorostral scale. From *Anilios*, it can be distinguished by its smaller maximum size (mean among species, 302 versus 354 mm TL), higher mean number of midbody scales (21.7 versus 20.1), and longer tails (TL/TA = 31.8 versus 49.7; averages). From *Sundatyphlops*, it can be distinguished by its smaller maximum size (302 versus 395 mm TL; only *R. angusticeps*, 455 mm TL, has a greater maximum size).

Content. Twenty-one species: *Ramphotyphlops acuticauda, R. adocetus, R. angusticeps, R. becki, R. conradi, R. cumingii, R. depressus, R. exocoeti, R. flaviventer, R. hatmaliyeb, R. lineatus, R. lorenzi, R. melanocephalus, R. mansuetus, R. marxi, R. multilineatus, R. olivaceus, R. similis, R. suluensis, R. supranasalis*, and *R. willeyi* (Table 3).

Distribution. *Ramphotyphlops* is distributed broadly on many islands in the western Pacific Ocean, north and south of the Equator (especially in Indonesia, New Guinea, Philippines, and the Solomon Islands, but on many other islands as well) and with one species occurring in Southeast Asia.

Etymology. The generic name is a masculine noun formed from the Greek adjective *ramphos* (curved beak or bill) and Greek noun *typhlops* (the blind), in reference to the pointed or beak-like snout in most species of this genus.

Remarks. We include *Ramphotyphlops conradi* (Sulawesi), usually assigned to *Typhlops*, because it shares more characters with this genus than with others, and because of its distribution. We also place *Cathetorhinus melanocephalus* in this genus, contra Wallach & Pauwels (2008). Those authors argued that it was excluded from *Ramphotyphlops* because it has a different supralabial imbrication pattern, broad rostral, lack of superior nasal suture, and black head. Those scalation characters are unusual, although they are likely inter-related in an evolutionary sense, and thus not trenchant. Otherwise most of the characters of this species are consistent with the genus *Ramphotyphlops*, including beaked head, low midbody scales, no scale reduction, high total scale rows, high caudals, and long tail.

Genus *Sundatyphlops* gen. nov.
Lesser Sunda Blindsnakes

Type species. *Typhlops polygrammicus* Schlegel, 1839:40.

Diagnosis. Species of *Sundatyphlops* have (1) eye, distinct, (2) snout, rounded, (3) head scale arrangement, non-circular, (4) frontorostral, absent, (5) nasal, incompletely or completely divided, (6) nasal suture origin, supralabial 1, 2, or 1/2 suture, (7) suboculars or subpreoculars, unreported, (8) postoculars, unreported, (9) preocular-labial contact, supralabials 2–3, (10) midbody scale rows, 22, (11) scale row reduction, unreported, (12) total scale rows, 496, (13) caudals, 16, (14) maximum total length, 395 mm, (15) total length/midbody diameter, 33–58 (average, 45.5), (16) total length/tail length, 15–52 (average, 33.3), (17) dorsal color, usually dark brown, olive, olive gray, or pale yellow, (18) ventral color, whitish, whitish-pink, or pale yellow, (19) dorsum darker than (rarely similar to) venter, (20) pattern of longitudinal dark lines on yellow ground color, sometimes with same lineate pattern (but paler) on venter (Tables 1–2); only one species is included in the molecular phylogeny (Fig. 1).

As noted in the previous account, *Sundatyphlops* shares with *Acutotyphlops*, *Anilios*, and *Ramphotyphlops* a solid, awn-like protrusible hemipenis and retrocloacal sacs (Robb 1966; McDowell 1974), although not all species have been examined for those traits. From *Acutotyphlops*, *Sundatyphlops* can be distinguished by lacking a frontorostral scale. From *Anilios*, it can be distinguished by its larger maximum size (mean among species, 395 versus 353 mm TL), higher mean number of midbody scales (22 versus 20.1), and longer tails (TL/TA = 33.3 versus 49.7; averages). From *Ramphotyphlops*, it can be distinguished by its higher total scale rows (496 versus 419; averages) and larger maximum size (395 versus 302 mm TL; only *R. angusticeps*, 455 mm TL, has a greater maximum size).

Content. A single species, *Sundatyphlops polygrammicus* (Table 3).

Distribution. *Sundatyphlops* is distributed in the Lesser Sunda Islands, including Flores, Komodo, Lombok, Moyo (near Sumbawa), Sumba, Sumbawa, and Timor-Leste, and West Timor (De Lang 2011).

Etymology. The generic name is a masculine noun formed from the adjective *sundanus* (*a, um*; i.e., 'from Sunda') and the Greek noun *typhlops* (the blind).

Remarks. See Remarks for *Anilios* regarding our distinction of the Lesser Sunda populations of *Anilios polygrammicus* s.l. as a species distinct from populations inhabiting northeastern Australia (Queensland) and southern New Guinea which we assign to *Anilios torresianus* (comb. nov.). Not only are they different species, but we place them in different genera. Remarkably, the species *A. torresianus* is more closely related to all other Australian species (potentially 90+ species; Fig. 2) than it is to populations once considered conspecific, here called *Sundatyphlops polygrammicus*. Two potentially diagnostic characters identified by us are total middorsal scales (496 in *S. polygrammicus* versus 365 in *A. torresianus*) and the pattern of 11 black lines on a yellow ground color that gave *S. polygrammicus* its name (versus a braided pattern of pale-edged scales in *A. torresianus*). However, both species are in need of more systematic work, as it is quite likely that each is complex of species, given their distributions on multiple land masses. Several synonyms exist for *S. polygrammicus* (type locality, "Timor"), which we consider as subspecies following De Lang (2011): *S. p. elberti* (Roux 1911) from Lombok, *S. p. florensis* (Boulenger 1897) from Flores, *S. p. brongersmai* (Mertens 1929) from Sumba, *S. p. undecimlineatus* (Mertens 1927) from Sumbawa; *S. soensis* (De Jong 1930) from Timor apparently is a synonym of *S. p. polygrammicus*. See also accounts by Mertens (1929) and Focart (1953), and allocation of subspecies to islands by De Lang (2011). As McDowell (1974) pointed out, most authors who have reviewed specimens of *A. polygrammicus* s.l. in the past have confused characters of different populations (here, different genera). Hence a careful review of the museum material is needed. Here, we use only character data noted from specimens of known locality. The lineate pattern was described for snakes from Flores (*S. p. florensis*), Sumbawa (*S. p. undecimlineatus*), and Lombok (*S. p. elberti*), with apparently only faint lines in Sumba snakes (*S. p. brongersmai*). The brief description of the type material by Schlegel (1839), from Timor, does not mention lines specifically, although his name (*polygrammicus*) infers that it was also lineate. However, he mentioned that the dark brown scales have a "yellow edge," and by that it must be inferred that the lines are one scale wide and formed by parallel yellow edges that do not include the scale tip. This is an important distinction, because populations in Australia previously confused with *S. polygrammicus* have a braided pattern (Cogger 2000), whereby the entire scale edge is pale, instead of just the parallel edges. Considering all of this, and that the lineate

pattern has been associated with snakes from widely scattered localities in the Lesser Sunda Islands, we assume, tentatively, that it is diagnostic of this species and genus, even if it was not explicitly mentioned in all accounts. Our DNA sample comes from Moyo, an islet off of Sumbawa, and presumably *S. p. undecimlineatus* (De Lang 2011).

Genus *Xerotyphlops* gen. nov.
Desert Blindsnakes

Type species. *Typhlops vermicularis* Merrem, 1820:158.

Diagnosis. Species of *Xerotyphlops* have (1) eye, distinct, (2) snout, rounded, (3) head scale arrangement, non-circular, (4) frontorostral, absent, (5) nasal, incompletely divided, (6) nasal suture origin, supralabial 2, (7) suboculars or subpreoculars, absent (rarely present), (8) postoculars, 2 (average, 2.0), (9) preocular-labial contact, supralabials 2 & 3, (10) midbody scale rows, 20–24 (average, 23.5), (11) scale row reduction, present, (12) total scale rows, 206–435 (average, 355), (13) caudals, 10–16 (average, 13.0), (14) maximum total length, 220–350 (average, 292) mm, (15) total length/midbody diameter, 37–55 (average, 45.6), (16) total length/tail length, 88, (17) dorsal color, whitish or brown, (18) ventral color, whitish, cream, or brown, (19) dorsum darker than (or same as) venter, (20) overall, either patternless or darker longitudinal lines, (Tables 1–2); molecular phylogenetic support (Fig. 1).

From other genera of Asiatyphlopinae, *Xerotyphlops* has the shortest tail (TL/TA = 87.7 versus 31.1–75.1; averages). It differs from *Acutotyphlops* in lacking a frontorostral and from *Cyclotyphlops* in having non-circular head scales (versus circular arrangement). It differs from *Grypotyphlops* in lacking subocular scales (rarely present). It differs from *Cyclotyphlops* and *Indotyphlops* in having more postoculars (2.00 versus 1.0–1.03; averages). It differs from *Anilios, Indotyphlops,* and *Ramphotyphlops* in having higher average midbody scale rows (23.5 versus 19.4–21.7; averages). It differs from *Anilios, Grypotyphlops,* and *Sundatyphlops* in having fewer total scale rows (355 versus 466–496; averages) and smaller body size (TL = 292 versus 353–630; averages). It differs from *Malayotyphlops* in having lower average midbody scales (23.5 versus 26.8; averages). It differs from *Asiatyphlops* and *Cyclotyphlops* in having a thinner body (TL/MBD = 45.6 versus 35.1–35.2; averages).

Content. Four species: *Xerotyphlops etheridgei, X. socotranus, X. vermicularis,* and *X. wilsoni* (Table 3).

Distribution. *Xerotyphlops* is distributed in xeric regions of three continents, including the Sahara Desert and Socotra Island (Africa), southwestern Asia, and southeastern Europe. Although the genus occurs in xeric regions, at least one species (*X. vermicularis*) apparently prefers more humid microhabitats (Kornilios *et al.* 2011), which is not uncommon for organisms occurring in desert regions. Another species, *X. socotranus*, often inhabits areas with little moisture and vegetation (Rösler & Wranik 2004; Razzetti *et al.* 2011).

Etymology. The generic name is a masculine noun formed from the Greek adjective *xeros* (desert) and Greek noun *typhlops* (the blind), in reference to the desert region where these species occur. As an alternate meaning, the rarity of species in this large region could be described as a 'blindsnake desert.'

Remarks. The molecular phylogeny of Vidal *et al.* (2010), and the updated phylogeny here (Fig. 1), show that *Xerotyphlops* is an early offshoot of typhlopid snakes. We include *Xerotyphlops etheridgei* from Mauritania, which is a geographic outlier (Wallach 2002), and *X. wilsoni*, known only from the lost holotype (McDiarmid *et al.* 1999). A photograph in life of *X. socotranus* shows the lineate pattern (Razzetti *et al.* 2011). There are likely additional species confused within *X. vermicularis* (Kornilios *et al.* 2011; Kornilios *et al.* 2013).

Subfamily Madatyphlopinae subfam. nov.
Malagasy Blindsnakes

Type genus. *Madatyphlops* gen. nov.

Diagnosis. As for the genus.

Content. One genus: *Madatyphlops* gen. nov. (Table 3).

Distribution. Madatyphlopinae is only known from Madagascar.

Etymology. As for the genus.

Genus *Madatyphlops* gen. nov.
Malagasy Blindsnakes

Type species. *Onychocephalus arenarius* Grandidier, 1872:9.

Diagnosis. Species of *Madatyphlops* have (1) eye, distinct, (2) snout, rounded, (3) head scale arrangement, non-circular, (4) frontorostral, absent, (5) nasal, incompletely (sometimes completely) divided, (6) nasal suture origin, supralabial 2, (7) suboculars or subpreoculars, absent, (8) postoculars, 2–3 (rarely 1 or 4; average, 2.27), (9) preocular-labial contact, supralabials 2 & 3, (10) midbody scale rows, 20–28 (average, 22.9), (11) scale row reduction, present or absent, (12) total scale rows, 252–600 (average, 429), (13) caudals, 6–18 (average, 11.2), (14) maximum total length, 176–600 (average, 320) mm, (15) total length/midbody diameter, 27–85 (average, 45.6), (16) total length/tail length, 33–125 (average, 53.7), (17) dorsal color, usually brown but variable (sometimes white, pink, cream, yellow, gray), (18) ventral color, variable (white, pink, cream, yellow, gray, brown), (19) dorsum darker than venter, (20) overall, usually patternless (rarely with line or yellow nuchal collar) (Tables 1–2); molecular phylogenetic support (Fig. 1).

Madatyphlops is distinguished from all genera of Afrotyphlopinae in having fewer postocular scales (2.27 versus 3.68), fewer midbody scales (22.9 versus 24.8), smaller body size (320 versus 403 mm TL), and longer tails (TL/TA = 53.7 versus 68.2; averages). It is distinguished from all genera of Typhlopinae in having more postocular scales (2.27 versus 1.66), more midbody scales (22.9 versus 20.3), more total scale rows (429 versus 369; averages), and larger body size (320 versus 264 mm TL). *Madatyphlops* is distinguished from individual genera of Asiatyphlopinae in the following ways: *Acutotyphlops* has a frontorostral and complete nasal division (versus absent, and suture incomplete), *Cyclotyphlops* has a circular arrangement of head scales (versus non-circular), *Grypotyphlops* has suboculars present (versus absent), *Indotyphlops* has 1 postocular (versus 2–3), *Asiatyphlops, Malayotyphlops,* and *Xerotyphlops* have fewer average total scale rows (339, 367, and 355 versus 429), *Ramphotyphlops* and *Sundatyphlops* have longer tails (TL/TA = 31.8 and 33.3 versus 53.7; averages), and *Anilios* has a solid, awn-like protrusible hemipenis and retrocloacal sacs (versus non-protrusible hemipenis and retrocloacal sacs absent). Xenotyphlopidae (*Xenotyphlops*) also occurs on Madagascar, but it differs from *Madatyphlops* in having a circular rostral scale and single enlarged anal shield (Vidal *et al.* 2010).

Content. Eleven species: *Madatyphlops andasibensis, M. arenarius, M. boettgeri, M. decorsei, M. domerguei, M. madagascariensis, M. microcephalus, M. mucronatus, M. ocularis*, *M. rajeryi*, and *M. reuteri* (Table 3).

Distribution. *Madatyphlops* is known only from Madagascar.

Etymology. The generic name is a masculine noun formed from the adjective *madagascarianus* (*a, um*; 'from Madagascar') and the Greek noun *typhlops* (the blind).

Remarks. *Madatyphlops* is represented in the molecular phylogeny of Vidal *et al.* (2010), and in the tree here (Fig. 1), by two described species: *M. andasibensis* and *M. arenarius*. These two species are consistent with other typhlopid species in Madagascar, previously assigned to the genus *Typhlops* (McDiarmid *et al.* 1999; Glaw & Vences 2007; Vidal *et al.* 2010), in having a distinct eye, rounded snout, lacking suboculars, having the nasal suture origin at the 2nd supralabial, and in having the nasal incompletely divided (completely divided in *M. ocularis*). Although variable in color, they tend to lack a pattern (Glaw & Vences 2007).

Subfamily Typhlopinae Merrem, 1820
New World Blindsnakes

Type genus. *Typhlops* Oppel, 1811.

Diagnosis. Members of this subfamily have (1) eye, distinct (sometimes indistinct), (2) snout, rounded (rarely acuminate), (3) head scale arrangement, non-circular, (4) frontorostral, absent, (5) nasal, completely divided

(sometimes incompletely divided), (6) nasal suture origin, supralabial 2 (rarely 1 or 1/2 suture), (7) suboculars or subpreoculars, absent (rarely present), (8) postoculars 1–4 (average, 1.66), (9) preocular-labial contact, supralabials 2 & 3 or 3rd only (rarely none), (10) midbody scale rows, 16–24 (average, 20.3), (11) scale row reduction, present or absent, (12) total scale rows, 170–629 (average, 369), (13) caudals, 6–22 (average, 11.7), (14) maximum total length, 101–522 (average, 264) mm, (15) total length/midbody diameter, 16–77 (average, 42.7), (16) total length/tail length, 18–270 (average, 48.7), (17) dorsal color, brown (sometimes cream, tan, yellowish, or unpigmented), (18) ventral color, unpigmented (sometimes white, cream, or rarely brown), (19) dorsum darker than venter, (20) overall, usually patternless snakes, but rarely with indistinct spots, lines, and reticulations (Tables 1–2); molecular phylogenetic support (Figs. 1, 3).

The subfamily Typhlopinae is distinguished from Afrotyphlopinae in having fewer postocular scales (1.66 versus 3.69; averages), fewer midbody scales (20.3 versus 24.8), fewer total scale rows (369 versus 437), smaller body size (264 versus 403 mm TL), stouter body (TL/MBD 42.7 versus 52.4), and longer tails (TL/TA 48.7 versus 68.2). It is distinguished from Asiatyphlopinae in having fewer postocular scales (1.66 versus 2.19), fewer midbody scales (20.3 versus 21.8), and fewer total scale rows (369 versus 408). It is distinguished from the Madatyphlopinae in having fewer postocular scales (1.66 versus 2.27), fewer midbody scales (20.3 versus 22.9), fewer total scale rows (369 versus 429), and smaller body size (264 versus 320 mm TL).

Content. Four genera: *Amerotyphlops* gen. nov.*, Antillotyphlops* gen. nov. *, Cubatyphlops* gen. nov.*,* and *Typhlops* Oppel 811 (Table 3).

Distribution. The subfamily Typhlopinae is distributed in the New World tropics, from eastern Mexico (Veracruz) to southern South America (Bolivia and Argentina), with a large radiation on Caribbean islands.

Etymology. The subfamily name derives from the genus *Typhlops*, which is a Greek noun (the blind).

Remarks. This is the best known subfamily of blindsnakes, because it is the most densely sampled group with molecular data. However, no molecular data have been collected for any species of the genus *Amerotyphlops* in Middle America.

Genus *Amerotyphlops* gen. nov.

American Blindsnakes

Type species. *Typhlops brongersmianus* Vanzolini, 1976:247.

Diagnosis. Species of *Amerotyphlops* have (1) eye, distinct or indistinct, (2) snout, rounded, (3) head scale arrangement, non–circular, (4) frontorostral, absent, (5) nasal, completely or incompletely divided, (6) nasal suture origin, supralabial 2 (sometimes 1 or 1/2 suture), (7) suboculars or subpreoculars, absent (rarely present), (8) postoculars, 1–2 (rarely 3–4, average, 1.69), (9) preocular–labial contact, supralabials 2 & 3, (10) midbody scale rows, 16–22 (average, 19.1), (11) scale row reduction, absent (rarely present), (12) total scale rows, 170–556 (average, 327), (13) caudals, 6–15 (average, 9.4), (14) maximum total length, 101–522 (average, 287) mm, (15) total length/midbody diameter, 16–77 (average, 38.7), (16) total length/tail length, 23–270 (average, 66.8), (17) dorsal color, brown or yellow, (18) ventral color, white, cream, or yellow, (19) dorsum darker than venter, (20) overall color pattern often consists of spots, lines, reticulations, and/or a band over region of eyes (Tables 1–2); molecular phylogenetic support (Figs. 1, 3).

This genus is distinguished from two other genera of the subfamily Typhlopinae, *Antillotyphlops* and *Typhlops*, in that the preocular contacts supralabials 2 and 3 (versus preocular contact with supralabial 3 only) (Thomas 1968; 1976; Dixon & Hendricks 1979; Thomas & Hedges 2007). Although *Amerotyphlops* can be distinguished from those genera, it is more difficult to separate it from the primarily Cuban genus *Cubatyphlops*. It shares with that genus the preocular contact with supralabials 2 and 3, and presence of a single postocular in some species. However, it can be nearly completely distinguished from *Cubatyphlops* in total scale rows: there are minimally 453 in 11 of the 12 species of that genus (*C. caymanensis*, 351–408) whereas in *Amerotyphlops*, the maximum number of total scale rows is 441, except in one species, *A. microstomus* (487–556). Concerning the two overlap species, *C.*

caymanensis is separated from *Amerotyphlops* in the molecular phylogeny, and *A. microstomus* is separated from *Cubatyphlops* in having 2 postoculars instead of 1 postocular. Also, 8 of the 14 species of *Amerotyphlops* can be distinguished from *Cubatyphlops* in having either an incompletely divided nasal scale (*A. minuisquamus*, *A. paucisquamus*, *A. reticulatus*, and *A. yonenagae*) or a patterned (lines or spots) dorsum and/or head (*A. brongersmianus*, *A. minuisquamus*, *A. paucisquamus*, *A. reticulatus*, *A. tasymicris*, *A. tenuis, A. trinitatus*, and *A. yonenagae*) or both. In *Cubatyphlops*, the nasal is completely divided and there is no distinct pattern.

Content. Fourteen species: *Amerotyphlops amoipira, A. brongersmianus, A. costaricensis, A. lehneri, A. microstomus, A. minuisquamus, A. paucisquamus, A. reticulatus, A. stadelmani, A. tasymicris, A. tenuis, A. trinitatus, A. tycherus,* and *A. yonenagae* (Table 3).

Distribution. *Amerotyphlops* is distributed in the New World, primarily on the mainland, ranging from eastern Mexico (Veracruz) to southern South America (Bolivia and Argentina), and includes a West Indian species, *A. tasymicris* in Grenada and the Grenadines.

Etymology. The generic name is a masculine noun formed from the adjective *americanus* (*a, um*; 'from America') and Greek noun *typhlops* (the blind).

Remarks. Molecular data are available for only 3 of 14 species in this genus, which remains a gap in knowledge. Nonetheless, the suite of characters shared by the species, noted above, indicates that it is a monophyletic group with a geographic cohesiveness.

Genus *Antillotyphlops* gen. nov.

Antillean Blindsnakes

Type species. *Typhlops hypomethes* Hedges & Thomas, 1991:452.

Diagnosis. Species of *Antillotyphlops* have (1) eye, distinct, (2) snout, rounded (rarely acuminate), (3) head scale arrangement, non-circular, (4) frontorostral, absent, (5) nasal, completely divided, (6) nasal suture origin, supralabial 2, (7) suboculars or subpreoculars, absent, (8) postoculars, 2 (rarely 1; average 2.0), (9) preocular-labial contact, supralabial 3, (10) midbody scale rows, 16–24 (average, 20.5), (11) scale row reduction, present, (12) total scale rows, 299–499 (average, 378), (13) caudals, 11–14 (average, 12.3), (14) maximum total length, 110–360 (average, 233) mm, (15) total length/midbody diameter, 37–70 (average, 46.8), (16) total length/tail length, 30–61 (average, 44.5), (17) dorsal color, brown, grayish-brown, or yellow, (18) ventral color, white or cream (rarely brown), (19) dorsum darker than venter, and (20) overall, lacking any distinctive pattern (spots, lines, or stripes), although rarely faint trace of lines (Tables 1–2); molecular phylogenetic support (Figs. 1, 3).

Antillotyphlops is distinguished from *Cubatyphlops* by the presence of 2 postoculars (versus 1) and preocular contact with supralabial 3 only (versus contact with supralabials 2 and 3 in *Cubatyphlops*). The same distinction holds for *Antillotyphlops* versus the more distantly related *Amerotyphlops*, although 4 species of that genus have more than 1 postocular (Thomas 1968; 1976; Dixon & Hendricks 1979; Thomas & Hedges 2007). A closer comparison is needed between *Antillotyphlops* and *Typhlops*. With a cladistic analysis of morphological characters, Thomas (1989) found that species placed here in the genus *Antillotyphlops* (*A. dominicana*, *A. granti, A. monensis*, and *A. richardi*) formed a group based on the sharing of attenuate hemipenes, although he included *Typhlops sulcatus* in that group and placed *A. monastus* in a separate group with *T. jamaicensis* (hemipene data are not available for some species). Also, *Antillotyphlops* have more total scale rows than *Typhlops* (378 versus 312; averages) and are thinner-bodied (TL/MBD = 46.8 versus 35.9; averages).

Content. Twelve species: *Antillotyphlops annae*, *A. catapontus*, *A. dominicanus, A. geotomus, A. granti, A. guadeloupensis, A. hypomethes, A. monastus, A. monensis*, *A. naugus*, *A. platycephalus*, and *A. richardi* (Table 3).

Distribution. *Antillotyphlops* is distributed on islands in the eastern Caribbean, including Puerto Rico (and its satellite islets), the U.S. and British Virgin Islands, the Turks and Caicos Islands, and the Lesser Antilles (south to Dominica).

Etymology. The generic name is a masculine noun formed from the adjective *antilleus* (*a, um*; 'from the

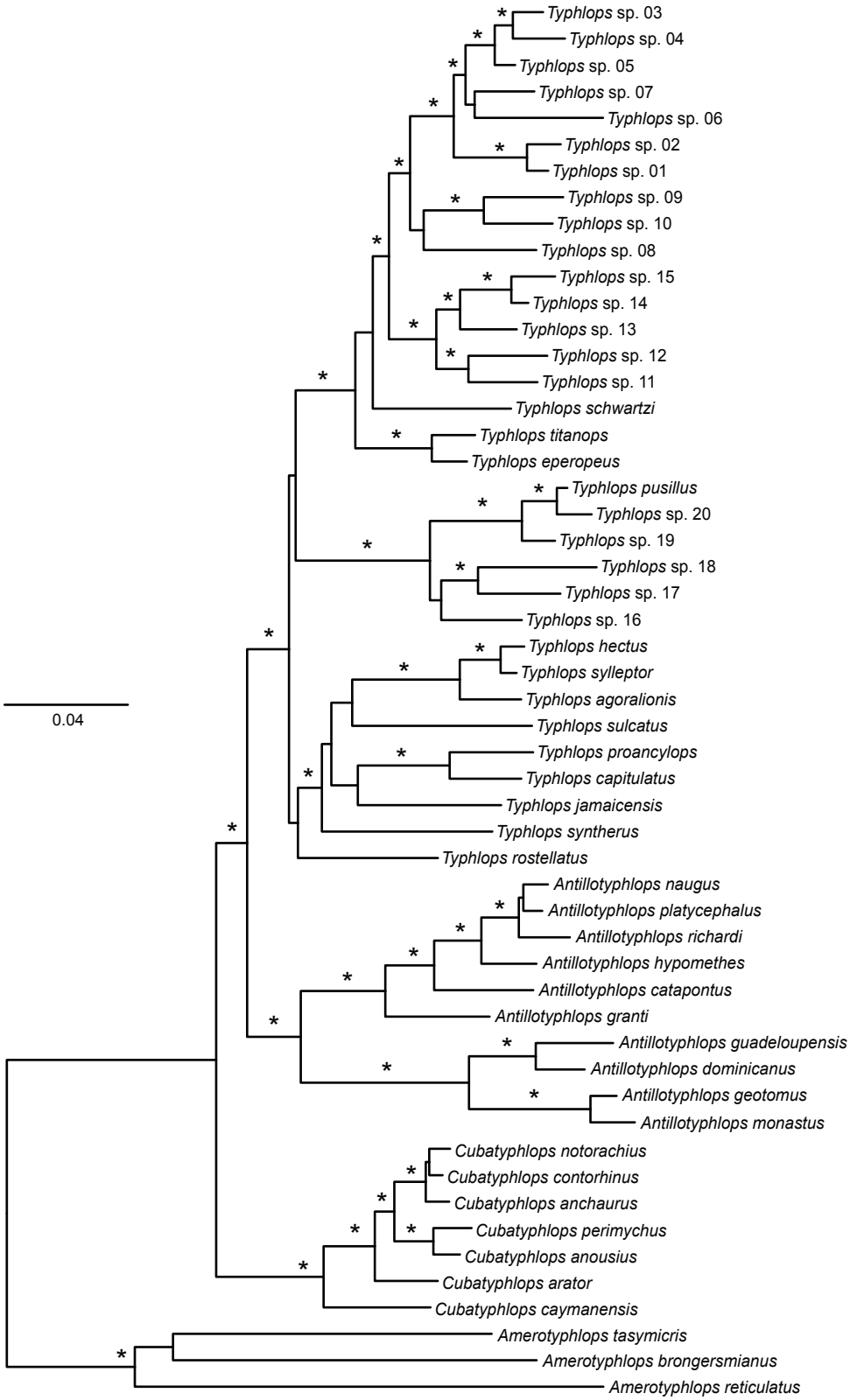

Figure 3. Phylogenetic ML tree of typhlopid snakes from Caribbean islands based on an analysis of DNA sequences of 6 nuclear protein-coding genes and 4 mitochondrial genes (dataset C). Nodes with asterisks are supported by posterior probability > 95% and ML bootstrap probability > 70%. The tree is rooted with *Indotyphlops braminus* (not shown).

Antilles') and Greek noun *typhlops* (the blind).

Remarks. Molecular data are available for nearly all known species in this genus and its monophyly is well supported. It is also a geographically cohesive group.

Genus *Cubatyphlops* gen. nov.

Cuban blindsnakes

Type species. *Typhlops biminiensis* Richmond, 1955:2.

Diagnosis. Species of *Cubatyphlops* have (1) eye, distinct, (2) snout, rounded, (3) head scale arrangement, non-circular, (4) frontorostral, absent, (5) nasal, completely divided (rarely incomplete), (6) nasal suture origin, supralabial 2, (7) suboculars or subpreoculars, absent, (8) postoculars, 1 (rarely 2; average 1.0), (9) preocular-labial contact, supralabials 2 & 3 (rarely none), (10) midbody scale rows, 20–24 (average, 22.1), (11) scale row reduction, present or absent, (12) total scale rows, 351–629 (average, 503), (13) caudals, 22, (14) maximum total length, 197–460 (average, 304) mm, (15) total length/midbody diameter, 36–75 (average, 54.7), (16) total length/tail length, 29–85 (average, 50.4), (17) dorsal color, brown (sometimes unpigmented, pinkish), (18) ventral color, unpigmented (pinkish) or rarely cream, (19) dorsum darker than venter, (20) overall, lacking any distinctive pattern (spots, lines, or stripes) (Tables 1–2); molecular phylogenetic support (Figs. 1, 3).

This genus is distinguished from the other two major genera inhabiting the Caribbean islands, *Antillotyphlops* and *Typhlops*, in that the preocular contacts supralabials 2 and 3, and one postocular is present (versus preocular contact with supralabial 3 only, and the presence of two postoculars) (Thomas 1968; 1976; Dixon & Hendricks 1979; Thomas & Hedges 2007). Species in this genus also stand out among closely related genera in being unusually thin, with individuals of all species except one having TL/MBD ratios above 50, being unusually long (up to 460 mm TL), and in having an unusually high number of total scale rows (to 629). Although *Cubatyphlops* can be distinguished from its closely related genera, it is more difficult to separate it from the primarily mainland New World genus *Amerotyphlops*. It shares with that genus the preocular contact with supralabials 2 and 3, and, in some species of *Amerotyphlops,* the presence of a single postocular. However, it can be nearly completely distinguished from the mainland genus in having a high number of total scale rows, minimally 453 in 11 of the 12 species (*C. caymanensis*, 351–408); in *Amerotyphlops*, the maximum number of total scale rows is 441, except in one species, *A. microstomus* (487–556). Concerning the two overlap species, *C. caymanensis* is separated from *Amerotyphlops* in the molecular phylogeny, and *A. microstomus* is separated from *Cubatyphlops* in having 2 postoculars instead of one postocular. Also, 8 of the 14 species of *Amerotyphlops* can be distinguished from *Cubatyphlops* in having either an incompletely divided nasal scale (*A. minuisquamus*, *A. paucisquamus*, and *A. reticulatus*, and *A. yonenagae*) or a patterned (lines or spots) dorsum and/or head (*A. brongersmianus*, *A. minuisquamus*, *A. paucisquamus*, *A. reticulatus*, *A. tasymicris*, *A. tenuis, A. trinitatus*, and *A. yonenagae*) or both. In *Cubatyphlops*, the nasal is completely divided and they have no distinct pattern.

Content. Twelve species: *Cubatyphlops anchaurus*, *C. anousius*, *C. arator, C. biminiensis, C. caymanensis, C. contorhinus, C. epactius, C. golyathi, C. notorachius, C. paradoxus, C. perimychus*, and *C. satelles* (Table 3).

Distribution. *Cubatyphlops* is distributed primarily in Cuba, but with species in the Cayman Islands and the Bahamas.

Etymology. The generic name is a masculine noun formed from the adjective *cubanus* (*a, um*; 'from Cuba') and Greek noun *typhlops* (the blind).

Remarks. Given the high total scale rows and lack of any distinctive color pattern in this genus, compared with the mainland genus *Amerotyphlops*, it is likely that both genera are monophyletic.

Genus *Typhlops* Oppel (1811)
Antillean Blindsnakes

Type species. [*Anguis*] *lumbricalis* Linnaeus, 1758:228, by subsequent designation of Fitzinger, 1843:24.

Diagnosis. Species of *Typhlops* have (1) eye, distinct, (2) snout, rounded, (3) head scale arrangement, non-circular, (4) frontorostral, absent, (5) nasal, completely divided (rarely incomplete), (6) nasal suture origin, supralabial 2, (7) suboculars or subpreoculars, absent (rarely present), (8) postoculars, 2 (rarely 1 or 3; average, 1.85), (9) preocular-labial contact, supralabial 3 (rarely none), (10) midbody scale rows, 18 or 22 (average, 20.0), (11) scale row reduction, present or absent, (12) total scale rows, 231–457 (average, 312), (13) caudals, 8–19 (average, 13.1), (14) maximum total length, 126–445 (average, 243) mm, (15) total length/midbody diameter, 23–57 (average, 35.9), (16) total length/tail length, 18–88 (36.8), (17) dorsal color, always pigmented, brown or tan, (18) ventral color, unpigmented (pinkish), white, or cream, (19) dorsum darker than venter, and (20) overall, lacking any distinctive pattern (spots, lines, or stripes), although rarely a faint trace of a dorsal line (Tables 1–2); molecular phylogenetic support (Figs. 1, 3).

Among its closest relatives (Figs. 1, 3), *Typhlops* is distinguished from *Cubatyphlops* by the presence of 2 postoculars (versus 1; except in 3 species of *Typhlops* with 1 postocular) and preocular contact with supralabial 3 only (versus contact with supralabials 2 and 3 in *Cubatyphlops*) (Table 2). The same distinction holds for *Typhlops* versus the more distantly related *Amerotyphlops*, although 4 species of that latter genus have more than 1 postocular (Thomas 1968; 1976; Dixon & Hendricks 1979; Thomas & Hedges 2007). *Typhlops* and *Antillotyphlops* require closest comparison. Thomas (1989) found that species placed here in the genus *Typhlops* formed a group separate from species placed here in *Antillotyphlops* based on reduction of the basihyal and a lower number of total middorsal scale rows. He excluded *T. jamaicensis* and *T. sulcatus* from that definition, but the molecular data place those two species together with others in *Typhlops* sensu stricto.

Content. Twenty species: *Typhlops agoralionis, T. capitulatus, T. eperopeus, T. gonavensis, T. hectus, T. jamaicensis, T. leptolepis, T. lumbricalis, T. oxyrhinus, T. pachyrhinus, T. proancylops, T. pusillus, T. rostellatus, T. schwartzi, T. silus, T. sulcatus, T. sylleptor, T. syntherus, T. tetrathyreus,* and *T. titanops* (Table 3).

Distribution. *Typhlops* is distributed primarily on islands in the western Caribbean, including Cuba (and its satellite islets), Hispaniola, and The Bahamas.

Etymology. The generic name, a masculine noun, is a Greek noun meaning 'the blind.'

Remarks. Molecular data are available for nearly all known species in this genus and its monophyly is well-supported. It is also a geographically cohesive group that includes a large number of undescribed species (Fig. 3) (Hedges *et al.*, in preparation).

Discussion

Although much has been learned about scolecophidians in recent years, mainly through molecular phylogenetic studies, these snakes remain poorly known. There will undoubtedly be many new species discovered in the future, and additional large clades resolved. Scolecophidians are the most ancient group of living snakes and have had a long history on the southern continents (Vidal *et al.* 2010). The single most common theme that we have encountered in studying the evolution of these snakes is their close association with geography, borne out in this new classification. Their occurrence on islands never connected to continents (Hedges *et al.* 1992; Hedges 1996a; b; 2008; Vidal *et al.* 2010) proves that they are capable of dispersing (rafting) over deep water, yet their relationships track plate tectonics perhaps better than any other vertebrate group (Vidal *et al.* 2010). They have unusually small distributions, with many species known from a single locality, and sympatric species sometimes have no distinguishing scale counts (Hedges & Thomas 1991; Thomas & Hedges 2007). This explains why so many undescribed species have been discovered using molecular data (Hedges & Thomas 1991; Marin *et al.* 2013b). These features make them an intriguing group to study, for understanding biogeography, ecology, behavior, and speciation.

Acknowledgments

This work was funded primarily by a grant from the U.S. National Science Foundation to SBH (DEB-0818798, 'Systematics and biogeography of scolecophidian snakes'), and partly by DEB-1136590 and DEB-0918891. NV and JM were supported by 'Consortium National de Recherche en Génomique' and the 'Service de Systématique Moléculaire' of the Muséum National d'Histoire Naturelle (UMS 2700; OMSI). It is part of agreement number 2005/67 between Genoscope and the Muséum National d'Histoire Naturelle for the project 'Macrophylogeny of life,' directed by Guillaume Lecointre. We thank Lana Brahmakulam, Haley Chutz, Natalie Kardos, and Elisabeth Rochel for laboratory assistance and those persons and institutions who contributed some of the tissue and DNA samples used in these studies or assisted us in the field: Ken Aplin, Aaron Bauer, Christopher Austin, William Branch, L. Chirio, Carla Cicero (MVZ), K. Coate, Ronald Crombie, K. Daoues, Donna Dittmann (LSUMZ), Stephen Donnellan, Paul Doughty, Sandy Echternacht, Julie Feinstein (AMNH, Ambrose-Monnell), Eli Greenbaum, Carla Hass, T. Heger, Robert Henderson, Mark Hutchinson, James Lazell, C. Marty, Greg Mayer, Robert Murphy (ROM), Renata Platenberg, Robert Powell, Nicolas Puillandre, S. Richards, Charles Ross, Richard Thomas, S. Thomson, Sébastien Trape, Miguel Vences, Jens Vindum (CAS), Laurie Vitt, L. Whitsed, and Addison Wynn (USNM). SBH thanks the governments of the Cayman Islands, Cuba, Dominica, Dominican Republic, Guadeloupe, Haiti, Jamaica, Puerto Rico, St. Kitts and Nevis, Turks and Caicos, and the U.S. Virgin Islands for scientific collecting permits. Patrick David provided critical comments on the manuscript.

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Appendix 1: samples used in the molecular analyses

The following is a list of samples and localities used in the molecular analyses (Figs. 1-3), excluding those already detailed in our previous global study (Vidal *et al.* 2010). Besides the samples listed below, we include in Fig. 1 sequences, from GenBank, of *Xerotyphlops vermicularis* ("A"), two samples of *X. socotranus,* two of *Letheobia episcopa*, and one of *L. simonii* published in a recent study (Kornilios *et al.* 2013). Abbreviations are: CAS (California Academy of Sciences, USA), EBG and ELI (Eli B. Greenbaum), SBH (S. Blair Hedges, Pennsylvania State University, USA), and USNM (National Museum of Natural History, Washington, D.C., USA).

Afrotyphlopinae. *Afrotyphlops elegans* 1 (CAS 219176; Fonta de Tchipique, Principe Island, Sao Tome and Principe), *Afrotyphlops elegans* 2 (CAS 238870; Principe Island, Sao Tome and Principe), *Afrotyphlops elegans* 3 (CAS 238880; abandoned Rosa, Nova Cuba, Principe Island, Sao Tome and Principe), *Afrotyphlops sp.* 1 (USNM 576137; Impongui, Likouala Dept., Republic of Congo), *Afrotyphlops sp.* 2 (ELI 158; Katanga Prov., Kasongomwana, Democratic Republic of the Congo), *Afrotyphlops* cf *angolensis* (EBG 2220; Force Bendera, on west side of Mt. Kabobo, 30-40 km N Kalemie, Democratic Republic of the Congo), *Letheobia feae* 1 (CAS 218907; on road between Bombaim and Santa Adelaide at Rio Abade bridge, Sao Tome Island, Sao Tome and Principe), *Letheobia feae* 2 (CAS 219310; Cruzeiro, Sao Tome Island, Sao Tome and Principe), *Letheobia feae* 3 (CAS 219335; trail between Born Sucesso to Lago Ameilia, Sao Tome Island, Sao Tome and Principe).

Asiatyphlopinae. *Acutotyphlops subocularis* (ABTC104792; Vuovo Camp, West New Britain, PNG). All *Anilios* are from Australia: *Anilios affinis* SH1 (SAMAR55645; Blackdown Tableland Road, 2k S Jnctn, QLD), *Anilios ammodytes* SH10 (WAMR127760; 5k S Mount Tom Price Mine, WA), *Anilios ammodytes* SH11 (WAMR104109; 1.4k NNE Woodstock, WA), *Anilios ammodytes* SH2 (WAMR170658; 31k WSW Mt Elvire, WA), *Anilios ammodytes* SH3 (WAMR121995; Weeli Wolli Spring, WA), *Anilios* ammodytes SH4 (WAMR102560; Barlee Range Nature Reserve, WA), *Anilios ammodytes* SH5 (WAMR165282; 16.6k ENE Karratha, WA), *Anilios ammodytes* SH6 (WAMR139430; Mount Minnie Homestead, WA), *Anilios ammodytes* SH7 (WAMR162120; 16k W Mt De Courcey, WA), *Anilios ammodytes* SH8 (WAMR141306; Cape Preston area, WA), *Anilios ammodytes* SH9 (WAMR158097; 5k NNE Python Pool, WA), *Anilios australis* SH12 (WAMR132329; 2k NE Wonnerup Siding, WA), *Anilios australis* SH13 (WAMR154969; East Wallabi Island, WA), *Anilios bicolor* SH14 (SAMAR61971; near Boolcoomata HS, SA), *Anilios bicolor* SH15 (WAMR165618; Ora Banda, WA), *Anilios bituberculatus* SH16 (SAMAR48359; 3.5k W Inkerman, SA), *Anilios bituberculatus* SH17 (SAMAR62428; 20k NE Mount Penrhyn, SA), *Anilios bituberculatus* SH18 (SAMAR44731; Welbourne Hill Station, SA), *Anilios bituberculatus* SH19 (ANWCR06665; Berrigan State Forest, 11k E Berrigan, NSW), *Anilios bituberculatus* SH20 (SAMAR18867; Burke's Grave, near Innamincka, SA), *Anilios centralis* SH21 (SAMAR56511; 8k ENE Mount Chandler, SA), *Anilios centralis* SH22 (ABTC24079; MacDonnell Ranges, NT), *Anilios diversus* SH23 (WAMR157402; Tanami Desert, WA), *Anilios diversus* SH24 (NTMR16427; Supplejack Station, 8 Mile Bore, NT), *Anilios diversus* SH25 (WAMR126054; ~5k S Carlton Hill Homestead, WA), *Anilios diversus* SH26 (WAMR151035; Lake Argyle, WA), *Anilios diversus* SH27 (WAMR119543; Mirima National Park, WA), *Anilios diversus* SH28 (ABTC102746; 176 Camooweal Street, Mount Isa, Qld), *Anilios diversus* SH29 (ABTC70684; Tennant Creek, NT), *Anilios diversus* SH30 (WAMR112027; Beagle Bay Aboriginal Community, WA), *Anilios diversus* SH31 (NTMR19058; Guluwuru Island, NT), *Anilios endoterus* SH32 (SAMAR21202; Olympic Dam Site, SA), *Anilios endoterus* SH33 (WAMR102627; Little Sandy Desert, WA), *Anilios endoterus* SH34 (WAMR135151; near Telfer Dome, WA), *Anilios endoterus* SH35 (WAMR115000; 38k ENE Laverton, WA), *Anilios ganei* SH36 (WAMR140003; Millstream, WA), *Anilios ganei* SH37 (WAMR162129; 27k ESE Mt De Courcey, WA), *Anilios ganei* SH38 (WAMR124835; 30k W Newman, Cathederal Gorge, WA), *Anilios ganei* SH39 (WAMR156328; Chichester Range, WA), *Anilios grypus* SH40 (WAMR114909; Marble Bar, WA), *Anilios grypus* SH41 (WAMR108596; 8k E Yarra Bluff, WA), *Anilios grypus* SH42 (WAMR157403; Tanami Desert, WA), *Anilios grypus* SH43 (WAMR108923; 25k SE Telfer, WA), *Anilios grypus* SH44 (WAMR110716; Brockan Mine, WA), Anilios *grypus* SH45 (WAMR114282; Wittenoom, WA), *Anilios grypus* SH46 (WAMR127522; 10k S Onslow, WA), *Anilios grypus* SH47 (WAMR102679; Little Sandy Desert, WA), *Anilios grypus* SH48 (SAMAR55272; Phosphate Hill, Buffel site, Qld), *Anilios guentheri* SH49 (WAMR105974; Kingston Rest, WA), *Anilios guentheri* SH50 (WAMR108431; 32k N Ord River crossing, WA), *Anilios*

guentheri SH51 (NTMR16488; Top Springs, Tanami Desert, NT), *Anilios guentheri* SH52 (NTMR13611; Katherine Gorge, NT), *Anilios guentheri* SH53 (ABTC67980; Bradshaw Station, NT), *Anilios guentheri* SH54 (SAMAR53885; 40k S Tunnel Creek Gorge, WA), *Anilios hamatus* SH55 (WAMR136817; Lake Mason Station, WA), *Anilios hamatus* SH56 (WAMR156249; Onslow area, WA), *Anilios hamatus* SH57 (WAMR145266; 5k S Mount Tom Price Mine, WA), *Anilios hamatus* SH58 (WAMR120619; unknown locality, WA), *Anilios hamatus* SH59 (WAMR111862; 26k SE Wheelarra Hill, WA), *Anilios hamatus* SH60 (WAMR136276; Muggon Station, WA), *Anilios hamatus* SH61 (WAMR131753; Mount Robinson, West Angelas, WA), *Anilios howi* SH62 (WAMR141536; Kalumburu, WA), *Anilios kimberleyensis* SH63 (WAMR165559; Koolan Island, WA), *Anilios kimberleyensis* SH64 (ABTC29484; Litchfield NP, NT), *Anilios kimberleyensis* SH65 (WAMR165885; South Maret Island, WA), *Anilios kimberleyensis* SH66 (WAMR125981; Wyndham, WA), *Anilios leptosoma* SH67 (WAMR114894; Geraldton, WA), *Anilios leptosoma* SH68 (WAMR129778; 22k S Kalbarri, WA), *Anilios ligatus* SH69 (SAMR31019; 21k E Narrabri, NSW), *Anilios ligatus* SH70 (NTMR13753; Keep River NP, NT), *Anilios ligatus* SH71 (NTMR35156; Tableland Highway, NT), *Anilios ligatus* SH72 (NTMR19109; Raragala Island, NT), *Anilios longissimus* SH73 (WAMR120049; Bandicoot Bay, Barrow Island, WA), *Anilios nigrescens* SH74 (AMSR146228; Castlereagh waste depot, near Penrith, NSW), *Anilios nigrescens* SH75 (SAMAR31025; 8k W Woolbrook, NSW), *Anilios nigrescens* SH76 (AMSR157200; Torrington State Recreation area, Butler, NSW), *Anilios nigrescens* SH77 (ABTC03939; 8k W McAfees Lookout, Qld), *Anilios nigrescens* SH78 (AMSR157267; Red Range to Kingsgate Road, NSW), *Anilios pilbarensis* SH79 (WAMR110939; 22.1k WSW Pannawonica, WA), *Anilios pinguis* SH80 (WAMR146995; Helena Valley, WA), *Anilios proximus* SH83 (ANWCR06668; Sloane Reserve, 28.5k N Mulwala, Savernake Hall, NSW), *Anilios silvia* SH84 (QMJ46128; 25k N Pomona, Qld), *Anilios torresianus* SH82 (QMJ60625; Mt Hartley, Qld), *Anilios troglodytes* SH85 (WAMR146048; Oobagooma Homestead, WA), *Anilios unguirostris* SH86 (WAMR146958; Kalumburu, WA), *Anilios unguirostris* SH87 (NTMR21669; Dundee Beach, Fog Bay, NT), *Anilios unguirostris* SH88 (SAMR54430; Burke Development Road 10k ENE, Qld), *Anilios unguirostris* SH89 (WAMR117861; near Mount Percy, WA), *Anilios waitii* SH90 (WAMR120315; unknown locality, WA), *Anilios waitii* SH91 (WAMR165022; 1k N Mulga Downs Outcamp, WA), *Anilios wiedii* SH92 (AMSR154152; Poison Gate road, on road to Poison, NSW). *Asiatyphlops diardii* (USNM, uncataloged; Myanmar), *Asiatyphlops muelleri* (CAS 222410; Nat Ma Taung National Park, Min Dat Township, Min Dat District, Chin State, Myanmar), *Asiatyphlops sp.* 1 (CAS 224653; Nagmung Town, Nagmung Township, Putao District, Kachin State, Myanmar), *Asiatyphlops sp.* 2 (CAS 224658; Nagmung Town, Nagmung Township, Putao District, Kachin State, Myanmar), *Asiatyphlops sp.* 3 (CAS 224750; between Nagmung Town and Ta Se Htu Village, Nagmung Township, Putao District, Kachin State, Myanmar), *Asiatyphlops sp.* 4 (CAS 225173; Ba Bawt village, Nagmung Township, Putao District, Kachin State, Myanmar), *Asiatyphlops sp.* 5 (CAS 230225; Machanbaw Town, Machanbaw Township, Putao District, Kachin State, Myanmar), *Asiatyphlops sp.* 6 (CAS 235322; near Myin Che Taung, Mintatt Township, Mindat District, Chin State, Myanmar), *Asiatyphlops sp.* 7 (CAS 235378; between Sawn Taung village and Ba Late Htwe village, Mintatt Township, Mindat District, Chin State, Myanmar), *Sundatyphlops polygrammicus* (WAM R98715; Brang Kua, Moyo Island, Indonesia), *Xerotyphlops vermicularis* 1 (CAS 228715; Harzevil Village in Old Manjil, Gilan Province, Iran), *Xerotyphlops vermicularis* 2 (CAS 228716; Harzevil Village in Old Manjil, Gilan Province, Iran).

Typhlopinae. *Antillotyphlops geotomus* (SBH 172760; ca. 1.5 km NE New River, Nevis, St. Kitts and Nevis), *Antillotyphlops granti* (SBH 172155; 4.0 km E Guanica in Bosque Estatal de Guanica, Campamento Santiago, Puerto Rico, USA), *Antillotyphlops guadeloupensis* (SBH 102276; Pointe de la Grande Anse near Trois Rivieres, Basse-Terre, Guadeloupe), *Typhlops hectus* (SBH 191789; 2.4 km N of Ducis, Dept. Du Sud, Haiti), *Antillotyphlops hypomethes* (SBH 172150; Rio Piedras on campus of UPR, Puerto Rico, USA), *Typhlops jamaicensis* (SBH 172445; 6.2 km W Oracabessa, St. Mary, Jamaica), *Antillotyphlops naugus* (SBH 172758; Upper Quail Dove Ghut, Guana Island, British Virgin Islands), *Cubatyphlops perimychus* (SBH 161981; W. T. Sampson High School, Guantanamo Bay USNS, Cuba), *Antillotyphlops platycephalus* (SBH 172180; 12.3 km SSE Arecibo, Puerto Rico, USA), *Typhlops proancylops* (SBH 103605; N of Fond Verrettes, Soliette, l'Ouest, Haiti), *Typhlops pusillus* (SBH 192420; 19.5 km N of Ca Soleil, Dept. de l'Artibonite, Haiti), *Antillotyphlops richardii* (SBH 266855; 0.2 km S St. Peter's Peak along roadside, St. Thomas,

US Virgin Islands), *Amerotyphlops tasymicris* (SBH 269088; Grenadines, Union Island, Chatham Bay), *Typhlops titanops* (SBH 160293; 22 km N Pedernales at the Rio Mulito, Pedernales, Dominican Republic), *Typhlops sp.* 01 (SBH 190612; 1.5 km WSW La Tabla, Santiago de Cuba, Cuba), *Typhlops sp.* 02 (SBH 190943; ca 0.5 km N La Hembrita, Guantanamo, Cuba), *Typhlops sp.* 03 (SBH 193810; grounds of Hotel Punta de Piedra, Granma, Cuba), *Typhlops sp.* 04 (SBH 194029; 8.5 km SW of Loma Mensura, Holguin, Cuba), *Typhlops sp.* 05 (SBH 193770; 2.4 km SE of Ojo del Toro, Granma, Cuba), *Typhlops sp.* 06 (SBH 193733; 1.6 km N of Camaron Grande, Granma, Cuba), *Typhlops sp.* 07 (SBH 193614; 1.4 km N of Minas del Frio, Granma, Cuba), *Typhlops sp.* 08 (SBH 191419; 1.5 km WSW La Tabla, Santiago de Cuba, Cuba), *Typhlops sp.* 09 (SBH 191538; Narigon, La Habana, Cuba), *Typhlops sp.* 11 (SBH 190202; SW slope of El Yunque de Baracoa, Guantanamo, Cuba), *Typhlops sp.* 12 (SBH 190231; 15.8 km NW Baracoa on coast road, Guantanamo, Cuba), *Typhlops sp.* 13 (SBH 190565; 1.5 km NE La Cantera, Santiago de Cuba, Cuba), *Typhlops sp.* 14 (SBH 190941; Rio Cuzco Canyon, ca. 3 km N Los Oasis, Guantanamo, Cuba), *Typhlops sp.* 15 (SBH 191018; near La Fangosa, 10.1 km W Vega Grande, Guantanamo, Cuba), *Typhlops sp.* 16 (SBH 102370; ca. 15 km W El Valle, Hato Mayor, Dominican Republic), *Typhlops sp.* 17 (SBH 193206; 8.8 km N thence 0.5 km W Tenares, Los Tabucos, Dominican Republic), *Typhlops sp.* 18 (SBH 267752; ca. 1 km SW Los Limones, Monte Plata, Dominican Republic), *Typhlops sp.* 19 (SBH 266322; 1.6 mi. NNE El Azul, San Juan, Dominican Republic), *Typhlops sp.* 20 (SBH 191839; 5.0 km S of Pestel, Dept. de la Grand'Anse, Haiti).

Leptotyphlopidae. *Leptotyphlops* cf *emini* (EBG 2280; Goma, Democratic Republic of the Congo).