TAPROBANICA, ISSN 1800–427X. November, 2023. Vol. 12, No. 02: pp. 37–47, pl. 21.

http://www.taprobanica.org
https://doi.org/10.47605/tapro.v12i2.306

urn:lsid:zoobank.org:pub:9C0E24FA-AC32-47E1-A1A7-20CE339C038E

A NEW BLINDSNAKE SPECIES (SQUAMATA: SCOLECOPHIDIA: TYPHLOPIDAE: *Indotyphlops*) FROM THE DRY ZONE OF SRI LANKA

Section Editor: Ivan Ineich *Submitted*: 14 October 2023, *Accepted*: 12 November 2023

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Abstract
Based on both morphological and genetic evidence, we describe a new species of typhlopid snake from the dry zone of Sri Lanka, the first scolecophidian snake species to be described from Sri Lanka for nearly 75 years. Being the ninth member to the genus from the island, the new species can be distinguished from its congeners by the following combination of characteristics: small body (total length 94–131 mm, snout–vent length 91–128 mm, tail length 2.1–2.8 mm); 20 longitudinal body scale rows; narrow rostral, longer than wide in dorsal aspect (rostral width/rostral length 0.55–0.57), not extending to level of eye; frontal shield extending to upper level of eye; 322–352 middorsal scales (not including intercalary scales); 306–342 midventrals; divided nasal scale; first gland line across head straight, not extending to ocular level; second gland line convex, midpoint reaching midlevel of eye. We have provided molecular phylogenetic evidence to support its distinctiveness from the phenotypically similar *I. braminus*.

***Key words*:** herpetology, *Indotyphlops braminus*, molecular phylogenetics, systematics, taxonomy

Introduction

Sri Lanka has a fauna of 10 currently recognised species of scolecophidians ('blindsnakes'), all but two of which are considered endemic to the island (Wickramasinghe *et al*. 2022). Of these 10 species, eight are species of the typhlopid genus *Indotyphlops* Hedges *et al*. 2014 and two are species of the gerrhopilid genus *Gerrhopilus* Fitzinger, 1843 (Wickramasinghe *et al*. 2022). The most recent description of a blindsnake species from Sri Lanka was 75 years ago by Taylor (1947), who described five new species endemic to the island, all from a single location (Trincomalee, on the northeast coast).

Although 10 species of blindsnakes are known from the island, this fauna has never been thoroughly explored or systematically assessed. Because they are small (typically 10–15 cm long and with few distinguishing external characters) and ecologically cryptic, usually living in leaf

litter and soil or beneath logs and stones, these snakes have hitherto been largely understudied.

Several species of Sri Lankan blindsnake have not been reported for decades and there is a general lack of knowledge of the distribution and natural history of most taxa (Wickramasinghe *et al*. 2022). As a result, conservation status of Sri Lankan blindsnakes have been assessed in the most recent national Red List of Threatened Species of Sri Lanka (Gibson *et al*. 2020) as: (1) three species Critically Endangered (CR): *Indotyphlops lankaensis* (Taylor, 1947), *I. leucomelas* (Boulenger, 1890) and *Gerrhopilus mirus* (Jan, 1860); (2) two species Endangered (EN): *G. ceylonicus* (Smith, 1943) and *I. malcolmi* (Taylor, 1947); (3) three species Data Deficient (DD): *I. tenebrarum* (Taylor, 1947), *I. veddae* (Taylor, 1947) and. *I. violaceus* (Taylor, 1947); and (4) two non-endemic species of Least Concern (LC): *I. porrectus* (Stoliczka, 1871) and *I. braminus* (Daudin, 1803). Here we describe a new species of *Indotyphlops*, based on morphological and molecular analysis of three recently collected specimens from Giritale, Polonnaruwa District, North Central Province, in the dry zone (rainfall <2,000 mm/year) of Sri Lanka.

Material and methods

Fieldwork and specimen preservation. Field sampling of scolecophidians, and preservation of euthanised specimens follows methods reported by Wickramasinghe *et al*. (2022). Three specimens of an unidentified blindsnake were collected from Giritale, Polonnaruwa District, North Central Province, Sri Lanka (Fig. 1).

Thirteen measurements were taken with a Mitutoyo digital point vernier caliper (to the nearest 0.1 mm), on the left side of specimens for bilateral features. Each measurement was taken three times and the mean value was used. Shield terminology was referred to the most recent scolecophidian publication by O'Shea *et al*. (2023), where the first shield behind rostral is termed frontal, however this is also termed as prefrontal by others (e.g., Stoliczka 1871, Wall 1919, Taylor 1947, Khan 1999, Wallach 1999). Nomenclature of external features abbreviated in the text, and definitions of external measurements taken, are as follows: body depth (BD, maximum depth of body, measured at midbody), body width (BW, maximum width of body, across midbody), distance between eyes (IO, shortest distance between eyes), head depth (HD, maximum depth of head, at mid-eye level),

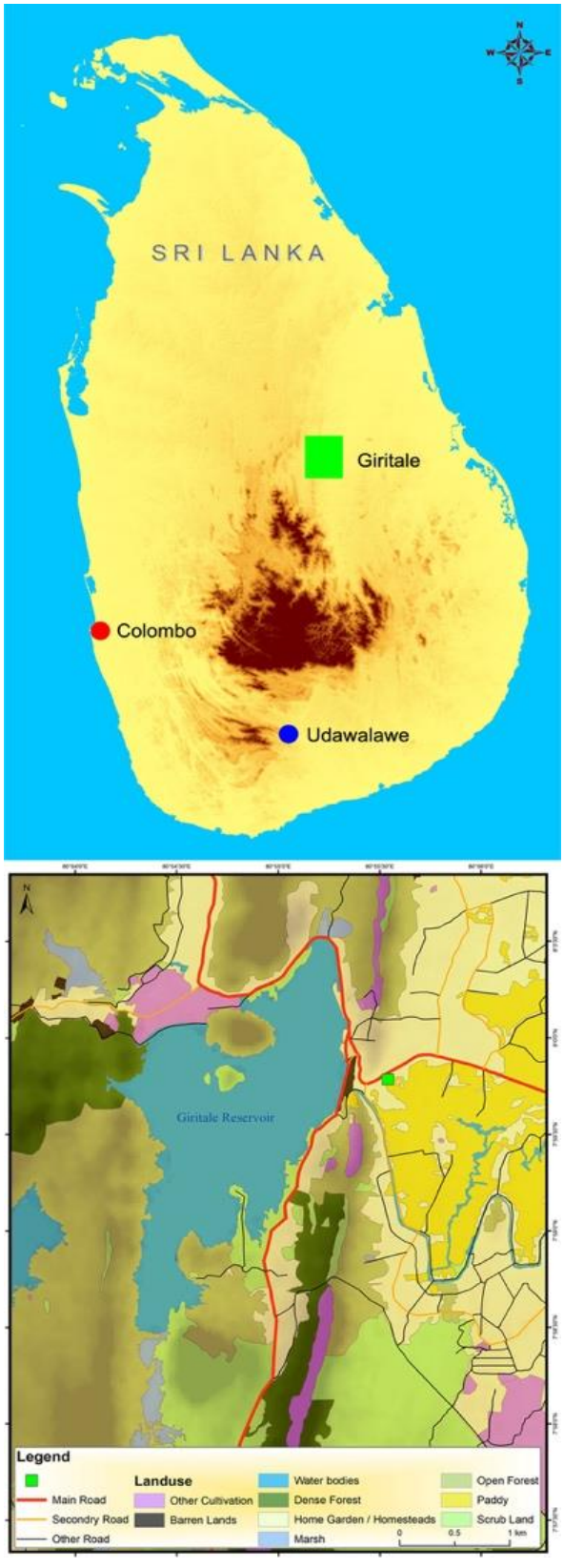

Figure 1. Map of Sri Lanka showing the type locality of *Indotyphlops combank* sp. nov., Giritale, (green square); the red and blue circles are the two possible localities for the genetically and phenotypically very similar (and possibly conspecific) specimen USNM 297493 [previously identified as *I.* cf. *pammeces* by Vidal *et al*. (2010) and Wickramasinghe *et al*. (2022).

head width (HW, maximum width of head), nostril to eye distance (NE, shortest distance between eye and nostril); rostral length (RL, snout tip to posterior end of rostral shield), rostral width, dorsally (RW, maximum width of rostral dorsally), rostral width, ventrally (RWV, maximum width of rostral ventrally), snout tip–eye distance (SE, shortest distance between tip of snout and eye), snout–vent length (SVL, tip of snout to end of cloacal shield), tail depth (TD, depth of tail measured at TL/2), tail length (TL, from vent to tip of tail), total body length (TOL, SVL+TL), longitudinal scale rows (LOS, number of scale rows around midbody), middorsal scale count (MDS, number of middorsal scales between the rostral shield and terminal spine of the tail), ventrals (VEN, number of midventral scales from postmental to precloacal shield), subcaudal scale count (SUB, number of subcaudal scales, the minimum number of midventral scales between the vent and terminal spine), supralabial shields (SUL, number of supralabials on each side).

Photographs of all the live specimens were made using the following equipment: Canon EOS 7D, Canon 100 mm F2.8 L USM, and Canon MT 24+Flash dome diffuser (1/200 Sec, f/13, ISO 100). Collection locality coordinates were recorded with a Garmin E-trex Venture GPS. We have examined type specimens of eleven of the 23 currently recognised species of *Indotyphlops* (Appendix 1). For information on species for which we were unable to examine types, we relied on original descriptions in Wallach (2009, 2020), Wickramasinghe *et al*. (2022), Wynn *et al*. (2016), and O'shea *et al*. (2023). The type specimens of the new species are deposited in the National Museum of Sri Lanka, Colombo, Sri Lanka (NMSL) and the National Wildlife Research and Training Center, Department of Wildlife Conservation, Giritale, Sri Lanka (DWC). Additional sources of comparative taxonomic information include Daudin (1803), Jan (1864), Peters (1864), Stoliczka (1871), Wall (1919), Constable (1949), Auffenberg (1980), Khan (1999), Wallach (1999, 2020), Wallach & Pauwels (2004), and O'Shea *et al*. (2023). Other institutional catalogue number prefixes: Field Museum of Natural History, Chicago, USA (FMNH); Natural History Museum, London, UK (NHMUK); Muséum national d'Histoire naturelle, Paris, France (MNHN), Smithsonian National Museum of Natural History, Washington, USA (USNM); Museum acronyms are those of Sabaj (2020).

***Molecular phylogenetics*.** Whole-genomic DNA was extracted from tissues using a Qiagen DNeasy blood and tissue extraction kit following the manufacturer's protocol. Extracted samples were tested for presence of high molecular weight DNA using electrophoresis on 0.8% agarose gel. Based on comparative data available for other typhlopids, we selected parts of four nuclear (*nu*) genes for amplification using the Polymerase Chain Reaction (PCR). The *nu* genes are brain-derived neurotrophic factor (*bdnf* ~630 bp), Amelogenin (*amel* ~372 bp), Recombination-activating gene 1 (*rag1* ~516), and bone morphogenetic protein 2 (*bmp2* ~588 bp). PCR primers are reported in Appendix 2.

All PCRs were carried out in 25 µL reactions, using 1 µL of each primer (2 mM), 2 µL of 25 mM $MgCl_2$, 2 µL of 10 mM dNTP, 0.5 µL of 5 u/µL GoTaq polymerase (Promega), 12.5 µL of nuclease free water (Norgen Biotek Canada), 1 mL of template DNA (*ca*. 250 ng/mL). PCRs were run on an Eppendorf Mastercycler with an initial denaturation at 95°C for 2 min followed by 35 cycles of denaturation at 95°C for 30 sec, annealing at 48°C for 45 sec, extension at 72 °C for 60 sec, and a final extension of 72 °C for 5 min. PCR product purification and Sanger sequencing were carried out by the Molecular Biology Laboratories, NHMUK.

Consensus sequences from forward and reverse reads were aligned using Geneious Prime 2023.0.4 (Kearse *et al*. 2012) and then manually edited and refined by eye. Sequences were aligned for each gene separately using MUSCLE (Edgar 2004) implemented in Geneious Prime 2023.0.4 (Kearse *et al*. 2012), employing default parameters. Aligned sequences of the protein-coding genes were translated into amino acid sequences to check for premature stop codons (that might indicate accidental sequencing of pseudogenes) and to determine the correct reading frame. Two concatenated datasets were prepared using Geneious Prime. One data set comprised the four sampled *nu* genes consisting 1586 bp (*amel* 317 bp; *bdnf* 577 bp; *bmp2* 422 bp; *rag1* 256 bp), and the other one comprising the four *nu* genes plus partial sequences for the mitochondrial (*mt*) gene cytochrome b (*cytb*), with its final aligned, concatenated dataset of markers consisting of 2234 bp (*cytb* 648 bp; *bdnf* 577 bp; *bmp2* 422 bp; *amel* 317 bp; *rag1* 256 bp).

The best-fitting nucleotide substitution model and partitioning scheme for phylogenetic

analyses was determined using PartitionFinder 2 (Lanfear *et al*. 2017) providing each codon position of each gene as the initial scheme, and using the 'greedy' algorithm (Lanfear *et al*. 2012), branch lengths as 'linked', and model selection as determined by the corrected Akaike Information Criterion (AICc). We conducted phylogenetic analyses using Bayesian inference (BI) as implemented in MrBayes v 3.2.6 (Ronquist *et al*. 2012) and Maximum likelihood (ML) as implemented in IQ-TREE (Nguyen *et al*. 2015). MrBayes analysis involved two Metropolis coupled Markov chain Monte Carlo (MCMCMC) chains in two independent runs with a sample frequency of 1,000, run for 8 million generations. Convergence between the two runs was assessed using Tracer 1.7 (Rambaut *et al*. 2018) and the first 25% of generations were discarded as burn-in.

Support for internal branches for BI trees was quantified with posterior probability values, and for ML trees with bootstrap support determined from 1,000 bootstrap replicates. For IQ-TREE analyses we implemented the ultrafast bootstrap. BI and ML analyses were conducted for each independent data set, and for the concatenated data set of *amel-bdnf-bmp2-cytb-rag1* (2234 bp). The concatenated data set was prepared using Geneious Prime 2023.0.4.

Uncorrected pairwise (*p*) distances between individuals and taxa were calculated using MEGA11 (Kumar *et al*. 2016). Distances were calculated using the Jukes–Cantor model (Jukes & Cantor 1969). The sequences newly generated in this study were deposited in GenBank under accession codes: QR770616, QR770617, and QR770618 (Appendix 3). In addition to our newly generated sequences, we analysed comparative data for 70 other typhlopoids of the family Typhlopidae and the xenotyphlopid *Xenotyphlops grandidieri* (as an outgroup) available in GenBank. These additional sequences are listed in Appendix 3. The two datasets included 58 leaves for the *nu*-only and 67 leaves for the *nu+mt* alignments.

Results

***Fieldwork*.** All three specimens of the new species were collected from a single location within an area of 1 m radius from Giritale, Polonnaruwa District, in a typical dry zone home garden, under a pile of stone chips. The species has also been observed in the nearby dry forested areas (Fig. 4) including Giritale Nature Reserve.

***Molecular systematics*.** Phylogenetic analyses of the concatenated data set for the 58-leaf *nu* dataset using both BI and ML analyses recovered similar relationships (Fig. 2A), and the well supported relationships in these trees are also compatible with those inferred from the 67-leaf *nu+mt* dataset analysed with both BI and ML (Fig. 2B). All four currently recognized subfamilies of Typhlopidae were recovered as monophyletic. As in previous analyses (see Wickramasinghe *et al*. 2022) support for the monophyly of *Indotyphlops* is uncompelling.

The new species is deeply nested within a maximally supported clade of *Indotyphlops* from South Asia (India + Sri Lanka), among samples variously identified as *I. braminus*, *I. pammeces* (Günther, 1864), and *I.* cf. *pammeces*. This clade is moderately well supported as a sister to a maximally supported clade comprising *I. albiceps* (Boulenger, 1898) and a northeast Indian *I.* sp. The new species is strongly supported as sister to a sample from Sri Lanka previously identified as *I.* cf. *pammeces* (Vidal *et al*. 2010, Wickramasinghe *et al*. 2022). The closest relative of this sister pair is not clearly resolved in our analyses, but it is seemingly not most closely related to specimens from southern India identified as *I. pammeces* (by Sidharthan *et al*. 2022). As reported by Sidharthan *et al*. (2022), samples from South Asia identified as *I. braminus* are polyphyletic. *P*-distances for the four *nu* genes, between *I. combank* sp. nov. and the most closely related South Asian lineages are reported in Table 1 and Supplement.

Table 1. Uncorrected pairwise (*p*) distances (%) between the new species and genetically close *I.* cf. *pammeces*, and phenotypically similar *I. braminus*.

	The new species			
	amel	*bdnf*	*bmp2*	*rag1*
I. cf. *pammeces*	0.6	0.3	0	0.9
I. braminus	1.3	0.9	0.4	2.7

Systematics

Indotyphlops ***combank*** sp. nov.
[urn:lsid:zoobank.org:act:01EEC18B-9465-4399-8D40-D06DA83729D1]
(Fig. 3, Table 2)

***Holotype*.** NMSL 2023.07.01 (SVL 123.5 mm), collected from Giritale (7°59'47"N, 80°55' 32"E; alt. 85m a.s.l.), Polonnaruwa District, North Central Province, Sri Lanka, by L.J.M. Wickramasinghe, M.C. De Silva, and D.R. Vidanapathirana on 13 September 2011.

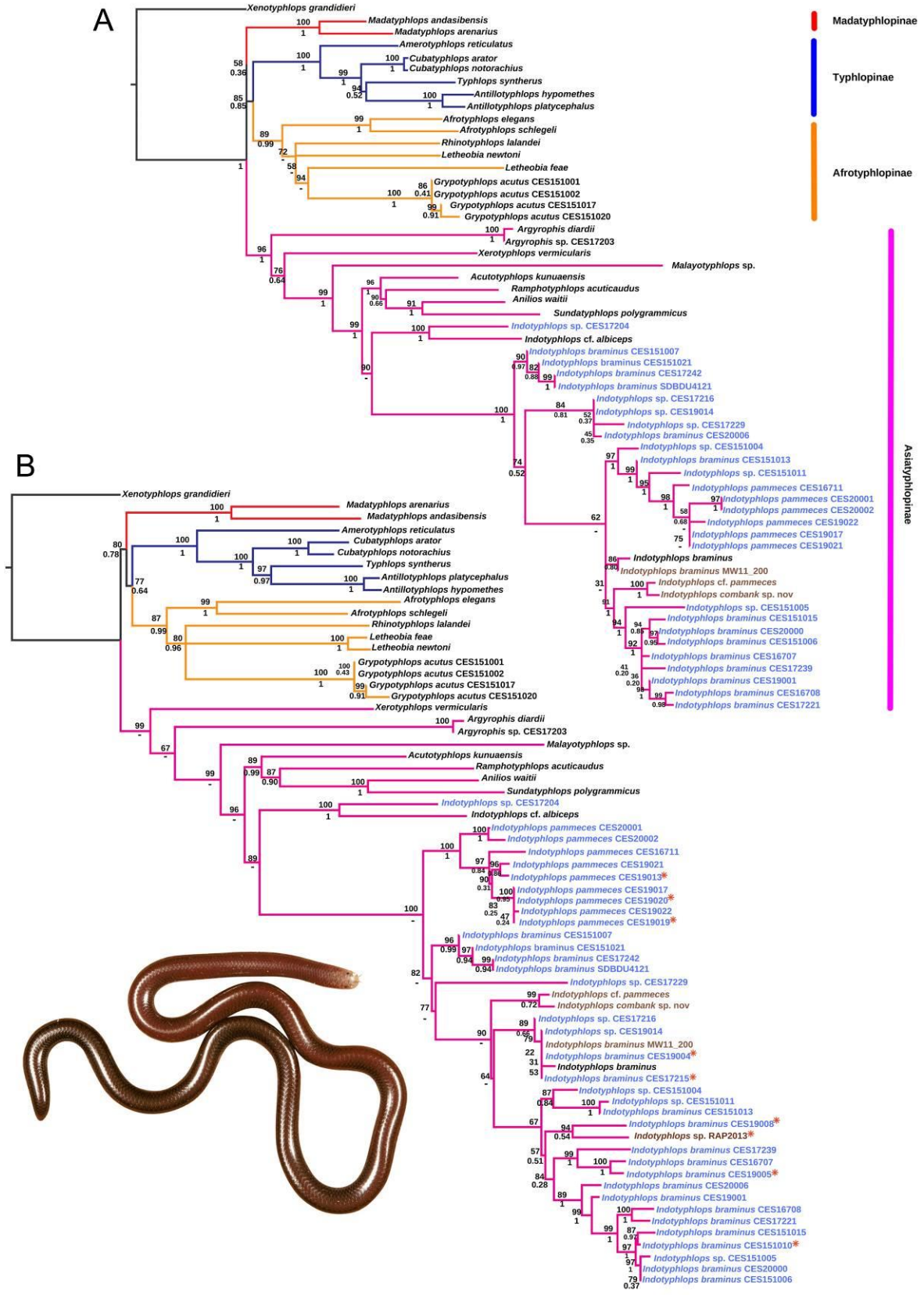

Figure 2. Molecular phylogenetic relationships of the family Typhlopidae based on analyses of the concatenated datasets with IQ tree bootstrap support values (ultrafast) above, and Bayesian posterior probabilities below internal branches; (A) four *nu* markers of 1586 bp (*amel* 317 bp; *bdnf* 577 bp; *bmp2* 422 bp; *rag1* 256 bp); (B) having one *mt* and four *nu* markers of 2234 bp (*cytb* 648 bp; *bdnf* 577 bp; *bmp2* 422 bp; *amel* 317 bp; *rag1* 256 bp). Specimens indicated with an asterisk have only *cytb*, sequences. *Indotyphlops* specimens sampled from India are indicated in blue, while those sampled from Sri Lanka are indicated in brown.

***Paratypes*.** NMSL 2023.07.02 (SVL 93.6 mm) and DWC 2023.05.01 (SVL 131.1 mm); the same collection data as holotype.

***Diagnosis*.** *Indotyphlops combank* sp. nov. can be distinguished from all known congeners by the following combination of characters. A small sized snake (total length 94–131 mm, SVL 91–128 mm, TL 2.1–2.8 mm); slender (TOL/BW 49.3–57); 20 longitudinal scale rows along the body; rostral narrow, longer than wide in dorsal aspect (RW/RL 0.55–0.57), not extending posteriorly to level of eye; frontal shield extends to upper level of eye; middorsal scales 322–352 (not including intercalary scales); midventrals 306–342; nasal scale divided; first gland line across head straight, not reaching level of eye; second gland line convex, midpoint reaching midlevel of eye.

***Comparison*.** Currently there are 23 recognized species in the genus *Indotyphlops* (Uetz *et al*. 2023). Of these, *I. combank* sp. nov. superficially resembles *I. braminus* in its similar body size, overlapping middorsal scale count, 20 LOS, and overlapping geographical distribution because both species occur in Giritale (this report; Wickramasinghe *et al*. 2022). However, *I. combank* sp. nov. differs from *I. braminus* in that the second supralabial contacts the posterior nasal shield (*vs* not in contact), and the infranasal suture does not contact the preocular (*vs* contacting the preocular).

Indotyphlops combank sp. nov., is similar to the five Sri Lankan endemics *I. lankaensis*, *I. malcolmi*, *I. tenebrarum*, *I. veddae*, and *I. violaceus* in having 20 LOS. Except for *I. pammeces* and *I. tenebrarum*, all these other species differ from *I. combank* sp. nov. in having 229–295 MDS (*vs* 306–342). The new species differs from *I. lankaensis* by its interoccipital shield (fourth middorsal shield behind rostral) being notably larger than the interparietal shield, wider than long (*vs* interparietal shield larger than the interoccipital shield), fourth gland line across body which lies beneath the interoccipital shield being the longest gland line across body (*vs* insignificant in size); differs from *I. malcolmi* by its rostral not extending to anterior level of eye (*vs* rostral extending to anterior level of eye), postnasal shield not extending to anterior level of eye (*vs* extending to posterior level of eye), frontal smaller than interoccipital shield (*vs* larger than interoccipital shield); differs from *I. veddae* by its frontal shield extending only slightly beyond the posterior level of the eye (*vs* reaching anterior level of eye); from *I. violaceus* by its slender body TOL/TW 49.3–57 (*vs* robust, TOL/TW *ca*. 27). The new species differs from *I. pammeces* in that its rostral does not extend posteriorly beyond the anterior level of the eye (*vs* rostral reaching the anterior level of eye), and by its frontal shield extending only slightly beyond the posterior level of the eye (*vs* frontal shield larger, extending nearly half of its length beyond the posterior level of eye). The new species differs from *I. tenebrarum* in having a frontal shield that extends slightly beyond the posterior level of eye (*vs* frontal shield reaching midlevel of eye), and posterior margin of frontal shield extending beyond posterior level of eye (*vs* reaching midlevel of eye). The Indian *I. fletcheri* (Wall, 1919) has been considered a junior synonym of *I. braminus* (see Wallach 2009, Wallach *et al*. 2014), the whereabouts of the type series is unknown (Wallach 2009), and MDS or VEN were not presented in Wall's original description; however, the types were reported to be less slender than *I. combank* sp. nov. (TOL/BW 40–45 *vs* 49.3–57). The new species differs from *I. albiceps* (Boulenger, 1898) and *I. schmutzi* (Auffenberg, 1980) in having a brown head, anterior end of body, and tail tip (*vs* whitish) and in being less slender (TOL/BW 49.3–57 *vs* 64 and 70, respectively).

In having 20 LOS, the new species differs from *I. ahsanai* (Khan, 1999), *I. exiguus* (Jan, 1864), *I. filiformis* (Duméril & Bibron, 1844), *I. laca* O'Shea, Wallach, Hsiao & Kaiser, 2023, *I. lazelli* (Wallach & Pauwels, 2004), *I. loveridgei* (Constable, 1949), *I. madgemintonae* (Khan, 1999), *I. meszoelyi* (Wallach, 1999), and *I. porrectus* which have 18 LOS; and from *I. leucomelas*, *I. jerdoni* (Boulenger, 1890), *I. longissimus* (Duméril & Bibron, 1844) and *I. tenuicollis* (Peters, 1864), all of which have 22 LOS.

***Description of holotype*.** Small snake in good condition, total length 126.3 mm (SVL 123.5 mm, TL 2.8 mm), elongate (SVL/HW 53.7); head slightly wider than anterior of body (HW/BD 0.97), convex above; snout elliptical in lateral aspect, subrectangular in dorsal and ventral aspects (HL/HW 1.6), rostral narrow, longer than wide in dorsal aspect (RW/RL 0.55); rostral not extending back to anterior level of eye, broadly rounded at the snout tip in dorsal view; frontal shield extends to upper level of eye; first gland line across head straight, not extending to eye level; second gland line convex, midpoint reaching midlevel of eye; nostrils smaller than eyes; superior internasal suture

Plate 21

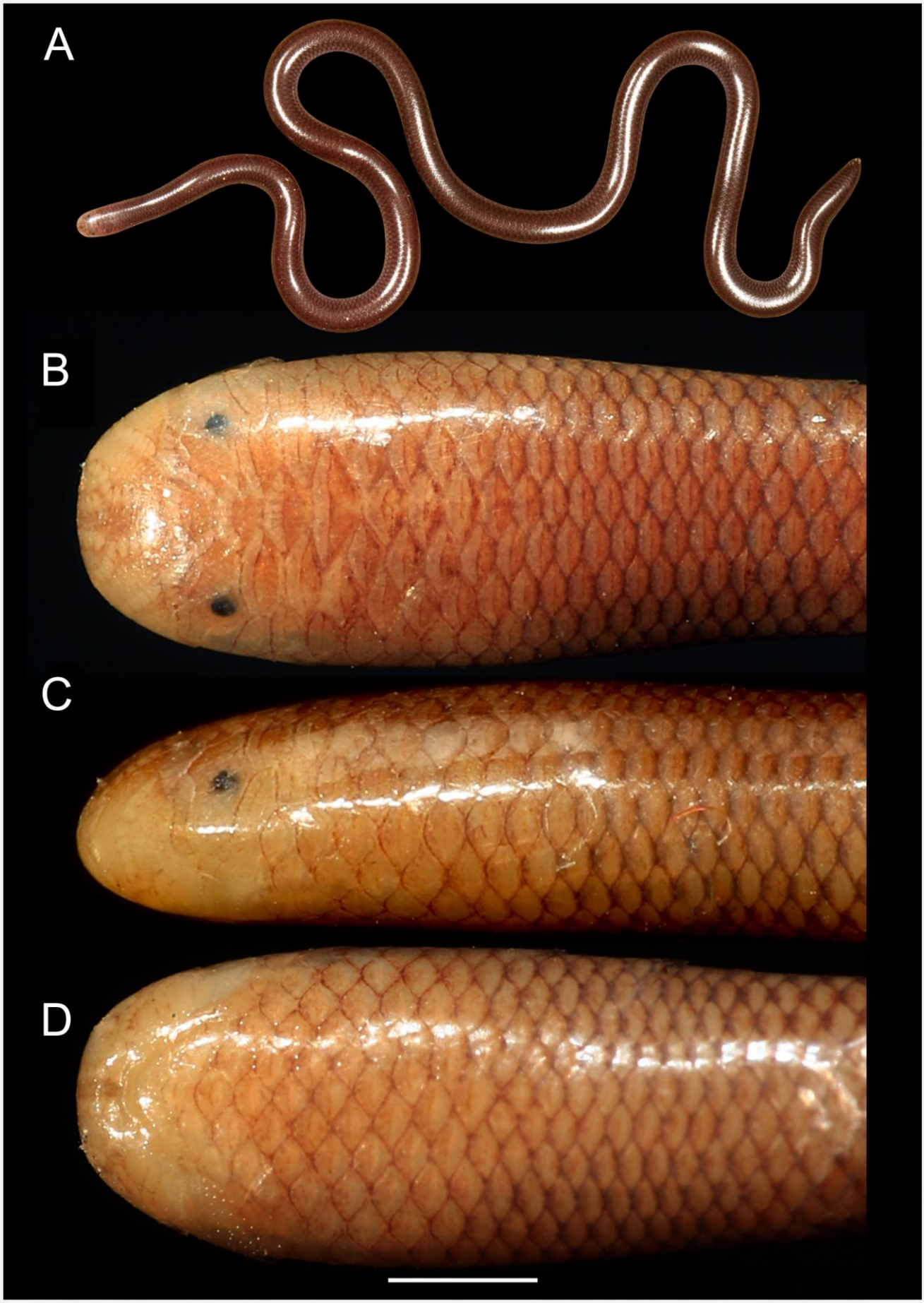

Figure 3. The holotype of *Indotyphlops combank* sp. nov. (NMSL 23001) in life from Giritale, Sri Lanka: **(A)** dorsal aspect of full body; and **(B)** dorsal, **(C)** lateral, and **(D)** ventral aspects of head; scale: 1 mm

short; nasal scale completely divided; postnasal shield not extending to anterior level of eye; eye small and visible; pupil horizontally elliptical (in preservation); four supralabials, increasing in size from first to last; 351 middorsal scale rows; 20 longitudinal scale rows around body; 351 ventral scales; 14 middorsocaudal scales; tail tapers only slightly for first three-quarters of its length posterior to vent, after which it tapers more abruptly to tail tip; terminal scale cone-shaped with sharply pointed keratinized spine.

***Colour in life*.** Dorsal body dark brown. On closer examination, all dorsal scales have a darker basal pigmentation. Head region slightly paler in colour, pinkish brown, with glandular edges off white. Venter pinkish, with darker pigmentation on scale margins, giving a chequered appearance.

***Colour in alcohol*.** Entire specimen has faded in colouration and lacks pigmentation, appearing creamish off-white. Darker pigmented regions paler brown than in life.

***Variation in paratypes*.** Paratype NMSL 2023.07.02 has fewer MDS and VEN, 322 and 306 respectively. Paratype DWC 2023.05.01 has slightly more VEN (342) than the holotype. Paratypes resemble holotype in major scalation features, including the extent of and sutural contacts among head shields.

Table 2. Morphometric (in mm) and meristic data for the type series of *Indotyphlops combank* sp. nov.

	Holotype	Paratypes	
Character	NMSL 2023. 07.01	NMSL 2023. 07.02	DWC 2023. 05.01
Middorsal scales	351	322	352
Ventrals	336	306	342
Subcaudals	14	14	10
Longitudinal scale rows	20	20	20
Supralabials (L/R)	4/4	4/4	4/4
Total body length	126.3	93.5	131.1
Snout–vent length	123.5	91.5	128.5
Tail length	2.8	2.1	2.7
Rostral length	1.0	0.8	1.1
Rostral width (dorsally)	0.5	0.5	0.6
Rostral width (ventrally)	0.5	0.4	0.5
Snout–eye distance	1.1	1.0	1.2
Distance between eyes	1.1	01	1.1
Head width	2.0	1.6	1.9
Head depth	1.3	1.1	1.4
Body depth	2.0	1.9	2.2
Body width	2.3	1.9	2.3
Tail depth	1.8	1.6	1.8
Nostril–eye distance	0.8	0.7	0.8

***Etymology*.** The specific epithet (*combank* in English) is a noun in apposition, which refers to Commercial Bank (PLC) Sri Lanka. The name is in recognition of the bank's support for Sri Lankan biodiversity discovery and conservation.

Figure 4. An aerial photograph showing one of the dry forested habitats where *Indotyphlops combank* sp. nov. has been observed.

Discussion

Indotyphlops combank sp. nov., is the first species of blindsnake to be described from Sri Lanka after Edward Harrison Taylor's description of five novel species in 1947. This brings to nine the number of species of *Indotyphlops* in Sri Lanka, all but two of which are endemic. As discussed by Wickramasinghe *et al*. (2022), one of the challenges of South Asian *Indotyphlops* taxonomy is that DNA sequence data are available for only a few species, and many of the available sequences are for vouchers for which morphological data have not been reported. This complicates attribution of taxon names to genetic lineages, which is further complicated by the likely hybrid origin of *I. braminus* (see Sidharthan *et al*. 2022).

The new species is morphologically similar to *I. pammeces* in being small, slender and pigmented, in having similar scale counts, and in that the second supralabial contacts the posterior nasal shield. However, the two species differ in the posterior extent of the rostral and frontal scales. Furthermore, as far as is known, *I. pammeces* is restricted to India and *I. combank* sp. nov. to Sri Lanka, and the new species is more closely related to at least one of the molecular genetic lineages that phenotypically are identified as *I. braminus*.

Other than *I. braminus*, DNA sequence data had previously been reported for only two Sri Lankan specimens of *Indotyphlops* (USNM 297493), identified as *I.* cf. *pammeces* (Vidal *et al*. 2010, see Wickramasinghe *et al*. 2022), and

Indotyphlops sp. (NMSL 2012.01.01) was referred to as such by Pyron & Wallach (2014) but as 'Typhlopidae sp.' by Pyron *et al*. (2013). The available DNA sequences of USNM 297493 are very similar to those of *I. combank* sp. nov. Based on photographs and scale counts (A. Wynn, pers. comm., 2022) that USNM specimen has 20 LOS, 375 MDS, and 14 SUB, and head scalation which closely resembles the types of *I. combank* sp. nov.: rostral narrow, not extending posteriorly to level of eyes; frontal shield extends to upper level of eye; nasal scale divided; first gland line across head straight, not extending to ocular level; second gland line convex, midpoint reaching midlevel of eye. The locality of USNM 297493 is unclear (Colombo or Udawalawe), but we consider the specimen referable to *I. combank* sp. nov.

Acknowledgements

Fieldwork was undertaken with permission from the Department of Wildlife Conservation (DWC Permit no: WL/3/2/2/13), which we gratefully acknowledge. We would like to thank C. Sooriyabandara (Director General, DWC) and R. Marasinghe (Director of Planning and Research, DWC) for their support and encouragement. Equipment and enabling museum reference work outside Sri Lanka was funded by Nagao Natural Environment Foundation, Japan, Dilmah Conservation, Sri Lanka, Wildlife and Nature Protection Society Sri Lanka and IDEA WILD. The Global Environment Facility of the United Nations Development Project (UNDP), and the Bird and Wildlife team funded the molecular studies. SYNTHESYS grants from the EU enabled examination of comparative material at the BMNH (LJMW and NW) and MNHN (LJMW). We thank P. Campbell (BMNH), A. Ohler, J. Blettery, S. Grosjean, A. Mathilde, and J. Courtois (MNHN), and A. Resetar (FMNH) for providing assistance during the visits; A. Wynn for generously providing images and data on some *Indotyphlops* specimens; M. Rathnayake, C. Bambaradeniya, R. Pethiyagoda, D.J. Gower (NHMUK), A.A.T. Amarasinghe (BRIN, Indonesia), I. Ineich (MNHN), and an anonymous reviewer for additional constructive comments; P. Samarawickrama for preparing the distribution map (figure 1); F. Sampaio and K. Ukuwela for technical mentorship to NW; and A. Abayekoon, K. Gunawardena, D. Warakagoda, U. Hettige, A. Basnayaka, D. Jayasinghe, N. Perera, J. Kanagarathnam, and colleagues from the Herpetological Foundation of Sri Lanka, and the Institute of Biochemistry, Molecular Biology, and Biotechnology of the University of Colombo for various courtesies.

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Appendix 1. Comparative type material examined.

***Indotyphlops albiceps*. Thailand:** NHMUK 1946.1.10.50 (holotype), SVL 126.6 mm.
***I. braminus*. Thailand:** FMNH 178263 (holotype of *Typhlops khoratensis*).
***I. filiformis*. Unknown:** MNHN-RA 0929 (holotype), SVL 124 mm.
***I. jerdoni*. India:** NHMUK 1946.1.10.66 (syntype), SVL 218 mm; 1946.1.10.67 (syntype; no head), 1946.1.10.68 (syntype), SVL 232 mm.
***I. lankaensis*. Sri Lanka:** FMNH 100066 (holotype), SVL 100.3 mm.
***I. leucomelas* Sri Lanka:** NHMUK 1946.1.10.46 (holotype), SVL 121 mm.
***I. longissimus*. North America (in error):** MNHN-RA 1061 (holotype), SVL 311 mm.
***I. malcolmi*. Sri Lanka:** FMNH 100132 (paratype), SVL 73.4 mm.
***I. pammeces*. India:** NHMUK 1946.1.11.34 (holotype), SVL 150 mm.
***I. tenebrarum*. Sri Lanka:** FMNH 120237–8 (paratype).
***I. veddae*. Sri Lanka:** FMNH 100033 (holotype), SVL 76.6 mm.
***I. violaceus*. Sri Lanka:** FMNH 100068 (holotype), SVL 101.1 mm.

Appendix 2. Primer sequences, sources, amplified, and aligned fragment lengths.

Primer	Primer sequence	Source	Fragment length	
			amplified	aligned
bdnf		Noonan & Chippindale (2006)	~630	418
BDNF-F	GACCATCCTTTTCCTKACTATGGTTATTTCATACTT			
BDNF-R	CTATCTTCCCCTTTTAATGGTCAGTGTACAAAC			
bmp2		Wiens *et al*. (2008)	~588	418
BMP2_f6	CAKCACCGWATTAATATTTATGAAA			
BMP2_r	ACYTTTTCGTTYTCRTCAAGGTA			
amel		Vidal *et al*. (2010)	~372	294
LAMSQ	ATGGGAGGATGGATGCACCA			
HAMSQ	GGCCATGRTTCAAGAGGYGTAT			
rag1		Vidal *et al*. (2010)	~516	414
RAG1_F	GCCCTCTTRTRGCNGAAAGRGAGGCCATGAAAA			
RAG1_R	TTCATYTTKCGRAAGCGCCTGAACAATTTGTTCCC			

Appendix 3. Genbank accession numbers of sequences used in analyses; voucher numbers are in Supplement

Taxon	**Country**	***cytb***	***bdnf***	***bmp2***	***amel***	***rag1***
Acutotyphlops kunuaensis	Papua New Guinea	KT316466	GU902419	GU902499	GU902339	GU902669
Afrotyphlops elegans	São Tome & Principe	KT316472	GU902391	GU902471	GU902314	GU902641
Afrotyphlops schlegelli	South Africa	–	GU902449	–	–	–
Amerotyphlops reticulatus	Guyana	KT316483	MH925784	GU902476	GU902319	GU902646
Anilios waitii	Australia	KT316499	GU902402	GU902482	GU902324	GU902652
Antillotyphlops hypomethes	Puerto Rico	KF993258	GU902431	GU902511	GU902351	GU902679
Antillotyphlops platycephalus	Puerto Rico	KF993269	GU902437	GU902517	GU902357	GU902683
Argyrophis diardii		KT316507	KF992877	KF992898	KF992856	KF992940
Argyrophis sp.	India	–	MW442101	–	MW442090	MW442133
Cubatyphlops arator	Cuba	JQ910546	GU902424	GU902504	GU902344	GU902674
Cubatyphlops notorachius	Cuba	KF993264	GU902436	GU902516	GU902356	GU902682
Grypotyphlops acutus	India	–	MW442107	–	MW442095	–
Grypotyphlops acutus	India	–	MW442106	–	–	–

Grypotyphlops acutus	India	–	MW442105	–	MW442094	–
Grypotyphlops acutus	India	–	MW442104	–	MW442093	–
Indotyphlops braminus	Florida ?	JQ910548	FJ433959	GU902463	GU902306	GU902633
Indotyphlops braminus	India	OP056484	ON806735	–	ON806710	ON806835
Indotyphlops braminus	India	OP056485	ON806736	–	ON806711	ON806836
Indotyphlops braminus	India	OP056487	–	–	–	–
Indotyphlops braminus	India	OP056488	ON806745	–	ON806720	ON806845
Indotyphlops braminus	India	OP056492	ON806737	–	ON806712	ON806837
Indotyphlops braminus	India	OP056494	ON806738	–	ON806713	ON806838
Indotyphlops braminus	India	OP056495	ON806746	–	ON806721	ON806846
Indotyphlops braminus	India	OP056496	ON806739	–	ON806714	ON806839
Indotyphlops braminus	India	OP056497	–	–	–	–
Indotyphlops braminus	India	OP056498	–	–	–	–
Indotyphlops braminus	India	OP056499	–	–	–	–
Indotyphlops braminus	India	OP056501	ON806740	–	ON806715	ON806840
Indotyphlops braminus	India	OP056502	ON806741	–	ON806716	ON806841
Indotyphlops braminus	India	OP056477	ON806731	–	ON806706	ON806831
Indotyphlops braminus	India	OP056478	ON806743	–	ON806718	ON806843
Indotyphlops braminus	India	OP056479	–	–	–	–
Indotyphlops braminus	India	OP056481	ON806733	–	ON806708	ON806833
Indotyphlops braminus	India	OP056482	ON806734	–	ON806709	ON806834
Indotyphlops braminus	India	OP056483	ON806744	–	ON806719	ON806844
Indotyphlops braminus	India	OP056503	ON806748	–	ON806723	ON806848
Indotyphlops braminus	Sri Lanka	OM936925	OM936944	OM936959	OM936960	–
Indotyphlops cf. *albiceps*	Myanmar	KT316509	GU902382	GU902462	GU902305	GU902632
Indotyphlops cf. *pammeces*	Sri Lanka	–	GU902458	GU902551	GU902378	GU902703
Indotyphlops combank	Sri Lanka	–	OR770616	OR770617	OR770615	OR770618
Indotyphlops pammeces	India	OP056504	ON806749	–	ON806724	ON806849
Indotyphlops pammeces	India	OP056505	–	–	–	–
Indotyphlops pammeces	India	OP056506	ON806750	–	ON806725	ON806850
Indotyphlops pammeces	India	OP056507	–	–	–	–
Indotyphlops pammeces	India	OP056508	–	–	–	–
Indotyphlops pammeces	India	OP056509	ON806751	–	ON806726	ON806851
Indotyphlops pammeces	India	OP056510	ON806752	–	ON806727	ON806852
Indotyphlops pammeces	India	OP056511	ON806753	–	ON806728	ON806853
Indotyphlops pammeces	India	OP056512	ON806754	–	ON806729	ON806854
Indotyphlops sp.	India	–	MW442111	–	MW442099	MW442139
Indotyphlops sp.	India	–	MW442112	–	MW442100	MW442140
Indotyphlops sp.	India	–	MW442110	–	MW442098	MW442138
Indotyphlops sp.	India	–	MW442109	–	MW442097	MW442137
Indotyphlops sp.	India	–	MW442108	–	MW442096	MW442136
Indotyphlops sp.	Sri Lanka	KC347488	–	–	–	–
Letheobia feae	São Tome & Principe	–	–	–	KF992848	–
Letheobia newtoni	São Tome & Principe	KT316514	GU902388	GU902468	GU902311	GU902638
Madatyphlops andasibensis	Madagascar	KT316516	GU902453	GU902545	GU902373	GU902698
Madatyphlops arenarius	Madagascar	KT316515	GU902455	GU902547	GU902374	GU902699
Malayotyphlops luzonensis	Philippines	KT316544	GU902393	GU902473	GU902316	GU902643
Ramphotyphlops acuticaudus	Palau	JQ910543	GU902381	GU902461	GU902304	GU902631
Rhinotyphlops lalandei	South Africa	–	GU902386	GU902466	GU902309	GU902636
Sundatyphlops polygrammicus	Indonesia	JQ910612	GU902421	GU902501	GU902341	GU902671
Typhlops syntherus	Dominican Republic	KF993282	GU902443	GU902522	GU902363	GU902689
Xenotyphlops grandidieri	northern Madagascar	KF770842	GU902456	GU902550	GU902377	GU902702
Xerotyphlops vermicularis	Armenia	JQ910544	GU902397	GU902477	GU902320	GU902647

Published date: 18 November 2023