



A new species of karst-associated kukri snake (Reptilia: Squamata: Colubridae: *Oligodon* Fitzinger, 1826) from southern Thailand

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Abstract

We describe a new species of kukri snake (*Oligodon* Fitzinger, 1826) from the limestone karst formations of Satun and Trang Provinces in southern Thailand. Phylogenetic analyses based on three mitochondrial DNA fragments (12S–16S ribosomal rRNA and cytochrome *b*) recover the new species within the *Oligodon cinereus* species complex, where it forms a deeply divergent yet poorly supported clade sister to *Oligodon saiyok* Sumontha et al., 2017 and another unnamed lineage currently referred to *Oligodon cinereus* (Günther, 1864) from southwest Myanmar. Morphologically, the new species is distinguished from all other members of the genus by the following combination of characters: ventral scales 189–193 with distinct lateral keeling; subcaudal scales 47–54, paired; anterior dorsal scale rows 17–19, with the reduction from 19 to 17 rows occurring above the 28th–30th ventral scale when present; maxillary teeth 8, blade-like and laterally compressed; dorsum olive–gray, plain; ventral surface white anteriorly, dark gray posteriorly; underside of tail dark gray, smeared with white. We briefly discuss the natural history and conservation status of this new species and provide observations of other kukri snakes inhabiting limestone karst habitats. Our study also incorporates genetic samples of four recently described *Oligodon* endemic to Thailand, all of which are recovered in the *O. cinereus* species complex. In agreement with previous studies, we demonstrate that species-level diversity within the *O. cinereus* species complex is underestimated, and additional sampling is necessary to revise this taxonomically challenging clade.

Keywords

Biodiversity, molecular phylogenetics, Serpentes, Southeast Asia, systematics, taxonomy, Thai–Malay Peninsula

Introduction

Oligodon Fitzinger, 1826 (family: Colubridae) is the second most speciose snake genus in the world, with the number of recognized species ranging from 87 to 90, depending on the author (Lee et al. 2023; Uetz et al. 2023; David et al. 2023). Commonly referred to as kukri snakes due to their blade-like dentition, *Oligodon* occur throughout tropical Asia and are especially diverse in the Indochinese region (Cambodia, Laos, Vietnam, and Thailand), where several new species have been described (Nguyen et al. 2017, 2022; Pauwels et al. 2017, 2021; Sumontha et al. 2017; Nguyen et al. 2020; David et al. 2022). Earlier authors had partitioned most *Oligodon* native to Indochina into two intrageneric groups based on differences in hemipenial morphology (Smith 1943; Leviton 1963). Members of the *O. cinereus* species group have hemipenes with a simple sulcus spermaticus and distinct ‘papillae’-like appendages visible on the retracted organ (henceforth termed ‘myoectases’, sensu Wagner 1975), whereas the *O. cyclurus-taeniatus* species group include members with longer hemipenes and a divided sulcus spermaticus. The presence of myoectases in the latter group varies, with species more closely related to *Oligodon cyclurus* (Cantor, 1839) lacking these structures and those to *Oligodon taeniatus* (Günther, 1861) retaining them (David et al. 2008a, 2008b; Green et al. 2010; Nguyen et al. 2020; Yushchenko et al. 2023b). Both *cinereus* and *cyclurus-taeniatus* groupings were originally conceived as phenetic classifications, though molecular phylogenies have so far recovered each as monophyletic (Green et al. 2010; Pyron et al. 2013; Nguyen et al. 2020; Yushchenko et al. 2023a).

In Thailand, four new *Oligodon* have been described within the past 10 years, and all are endemic to the country and have localized distributions (Pauwels et al. 2017, 2021; Sumontha et al. 2017). First, Pauwels et al. (2017) described *Oligodon huahin* based on a series of specimens collected near the outskirts of Kaeng Krachan National Park in Prachuap Khiri Khan Province. Then, Sumontha et al. (2017) described another species, *O. saiyok* based on two specimens found in limestone karst formations near Sai Yok National Park, Kanchanaburi Province. Most recently, Pauwels et al. (2021) described *Oligodon phangan* and *Oligodon promsombuti*, which were collected from two separate localities in Surat Thani Province. Three of these species (*O. huahin*, *O. phangan* and *O. promsombuti*) were putatively considered members of the *Oligodon cyclurus-taeniatus* species group based on their hemipenial morphology, which were bilobed in shape when partially everted. However, the assignment of *O. phangan* to this species group was considered tentative, as no male specimens were known at the time of its description. Likewise, the species group assignment of *O. saiyok* was not evaluated, since the hemipenis of the male holotype was left retracted inside the tail base, preventing an assessment of its shape and ornamentation. Thus, all four recently

described species of Thai *Oligodon* were described exclusively from morphology, and their phylogenetic positions have remained untested, pending the acquisition of molecular data.

Two more studies (Yushchenko et al. 2023a; David et al. 2023) made taxonomic changes relevant to *Oligodon* in Thailand. Most pertain to *Oligodon cinereus* (Günther, 1864), a widespread species that contains multiple color morphs and junior synonyms across its range (Smith 1943; Green et al. 2010; David et al. 2011). Based on molecular data, Yushchenko et al. (2023a) found that *O. cinereus* was not monophyletic. They restricted ‘true’ *O. cinereus* to populations in southern Indochina (Cambodia, Laos, and Vietnam) and transferred the recently described *Oligodon cattienensis* Vassilieva et al., 2013 to its synonymy. In addition, Yushchenko et al. (2023a, 2023b) demonstrated that the hemipenial morphology of *O. cinereus*, and other newly named *Oligodon*, had been improperly described by past studies, leading earlier authors to assign taxa into incorrect species groups. While Yushchenko et al. (2023a) did not propose any other changes, their results showed that *O. “cinereus”* (as previously conceived) represents a composite of species-level lineages, a finding that was also hinted by earlier works (Green et al. 2010; David et al. 2011).

Subsequently, David et al. (2023) made additional re-arrangements to *O. cinereus*. While they agreed with the results of Yushchenko et al. (2023a), David et al. (2023) diverged from those authors by resurrecting *Simotes multifasciatus* Jan in Jan and Sordelli, 1865 and *Simotes swinhonis* Günther, 1864 (both junior synonyms of *O. cinereus*) to species species, and synonymizing *Oligodon condaoensis* Nguyen et al., 2016 with *O. cinereus*. The classification suggested by David et al. (2023) is not unwarranted, and in this study, we adopt their latter change (synonymizing *O. condaoensis*). However, in contrast to David et al. (2023), we are more conservative regarding *O. multifasciatus* and *O. swinhonis* and prefer to recognize *O. “cinereus”* as a single unit that encompasses both of these taxa. Our hesitation is due to the fact that *O. cinereus*, *O. multifasciatus* and *O. swinhonis* (sensu David et al. 2023) do not correspond with the phylogenetic clades delimited by Yushchenko et al. (2023a). In recognition of the changes proposed by David et al. (2023), the term “species complex” is used hereafter to describe the clade containing *O. “cinereus”* and related taxa (see Fig. 1).

During herpetological surveys targeting limestone karst formations in Trang and Satun provinces, Thailand, we observed three *Oligodon* that were referable to the *O. cinereus* species complex. A closer examination of the Trang and Satun province specimens revealed additional genetic and morphological differences that separate them from all other members of the genus. In this study, we describe these specimens as a new species and use this opportunity to investigate the phylogenetic position of the four recently described *Oligodon* from Thailand (*O. huahin*, *O. phangan*, *O. promsombuti* and *O. saiyok*), all of which have not been included within published molecular datasets until now.

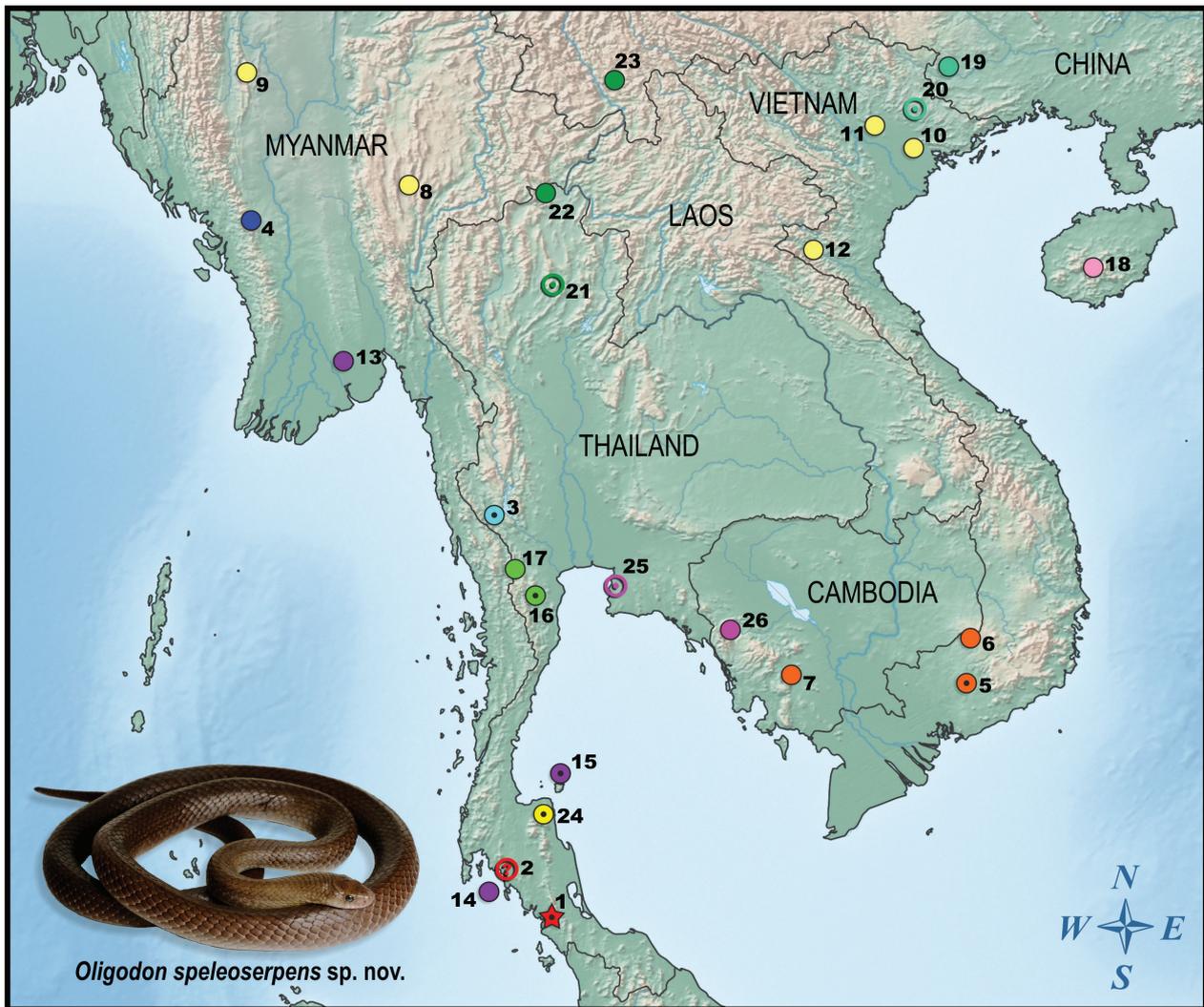


Figure 1. Sampled localities of the *Oligodon cinereus* species complex used in this study, including *Oligodon speleoserpens* sp. nov., *O. huahin*, *O. phangan*, *O. promsombuti*, *O. purpurascens*, *O. sai yok*, *O. joynsoni*, *O. inornatus*, *O. nagao*, *O. cinereus* s. str., and unnamed lineages of *O. “cinereus”* labeled by clade. Base map created using simplemappr.net. Filled icons denote populations included in phylogenetic analyses; empty icons denote populations not included in the phylogenetic analyses; type localities are indicated by a dot at the center of an icon. Colors and locality numbers correspond to Figure 2 and Table S1. **Localities.** *Oligodon speleoserpens* sp. nov.: (1) Tham Khao Ting Cave, Trang Prov., and Tham Le Stegodon Cave, Satun Prov., Thailand; *Oligodon* sp.: (2) Krabi Prov., Thailand (unconfirmed locality); *O. sai yok*: (3) Sai Yok Distr., Kanchanaburi Prov., Thailand; *O. cinereus* clade 4: (4) Rakhine Yoma Mts., Rakhine St., Myanmar; *O. cinereus* clade 1 (sensu stricto): (5) Cat Tien NP, Dong Nai Prov., Vietnam (type locality of *O. cattienensis*); (6) Bu Gia Map NP, Binh Phuoc Prov., Vietnam; (7) Kirirom NP, Kampong Speu Prov., Cambodia; *O. cinereus* clade 2: (8) Kalaw, Shan St., Myanmar; (9) Alaungdaw Kathapa NP, Sagaing Div., Myanmar; (10) Chi Linh, Hai Duong Prov., Vietnam; (11) Tam Dao NP, Vinh Phuc Prov., Vietnam; (12) Pu Mat NP, Nghe An Prov., Vietnam; *O. phangan*: (13) Mingalar-don, Hlawga WP, Yangon Div., Myanmar; (14) Ko Phi Phi Don Isl., Krabi Prov., Thailand; (15) Ko Pha Ngan Isl., Surat Thani Prov., Thailand; *O. huahin*: (16) Kaeng Krachan NP, Phetchaburi, Thailand; (17) Suan Phueng, Ratchaburi, Thailand; *O. nagao* and *O. cinereus* clade 3: (18) Hainan Isl., Hainan Prov., China; (19) Nonggang NR, Guangxi Prov., China; (20) Huu Lien, Lang Son Prov., Vietnam (type locality of *O. nagao*); *O. joynsoni*: (21) Ngao Dist., Lampang Prov., Thailand (type locality); (22) Doi Tung, Chiang Rai Prov., Thailand; (23) Xishuanhbanna NP, Yunnan Prov., China; *O. promsombuti*: (24) Khao Phanom Wang, Surat Thani Prov., Thailand; *O. inornatus*: (25) Nong Kai Ploi, Chonburi Prov., Thailand (type locality); (26) Samkos WS, Pursat Prov., Cambodia.

Materials and methods

Sampling and species delimitation

Fieldwork that resulted in the collection of *Oligodon* was performed across southern Thailand in Kanchanaburi,

Phetchaburi, Satun, Surat Thani, and Trang Provinces between 2018 and 2023. Geographic coordinates and altitude of all specimens were obtained using a Garmin GPSMAP 60CSx GPS receiver (USA) and recorded in WGS84 datum. Collected snake specimens were captured by hand and euthanized via injection using a 20% solution of benzocaine, then fixed in formalin before be-

ing transferred into 70% ethanol for preservation. Prior to fixation, a small sample of muscle tissue was taken from each specimen and stored in 95% ethanol for molecular analyses. The uncollected specimen of the new species was measured and photographed on-site to examine relevant morphological features and was subsequently released at the point of capture. Specimens and their tissue samples were deposited in the herpetological collections of the School of Agriculture and Natural Resources, University of Phayao, Phayao, Thailand (AUP) and the Zoological Museum of Moscow University, Moscow, Russia (ZMMU).

Two tissues of the new species, topotypic specimens of *O. huahin*, and the name-bearing type specimens of *O. phangan*, *O. promsombuti* and *O. saiyok* were sampled for molecular analyses, in addition to 57 samples of *Oligodon* from GenBank. One sample each of the snake species *Oreocryptophis porphyraceus* (Cantor, 1839) (subfamily Colubrinae) and *Hebius vibakari* (Boie, 1826) (subfamily Natricinae) were used as outgroup taxa to root the tree. Both outgroups represent colubrid species that are highly divergent from *Oligodon* and have been used in past phylogenetic investigations (Nguyen et al. 2020; Lee et al. 2023; Yushchenko et al. 2023a, 2023b). Accession numbers, voucher specimens, and localities are included in Table S1. Our guidelines for delimiting and defining species follow the General Lineage Concept (de Queiroz

2007), where a species is considered to be a single independent lineage that has a separate evolutionary trajectory relative to its congeners. We follow the guidelines set by Padiál et al. (2010) for integrative taxonomy, and use discrete morphological separation, substantial genetic divergence, and monophyletic resolution in phylogenetic analyses as evidence indicative of a distinct species.

Museum acronyms mentioned in-text follow Sabaj (2020) except for the following institutions: **AUP**: Herpetological Collection, School of Agriculture and Natural Resources, University of Phayao, Phayao, Thailand; **CESS**: Center for Ecological Sciences, Indian Institute of Science, Bangalore; **CUHC**: Comenius University Herpetological Collection, Bratislava, Slovakia; **WII-ADR**: Wildlife Institute of India—Abhijit Das Reptile collection, Dehra Dun, India. Additional acronyms are explained in Table S1.

Molecular analyses

We extracted total genomic DNA of novel samples from muscle or skin tissues preserved in 95% ethanol using a Qiagen DNAeasy Blood and Tissue Kit following manufacturers protocols. We performed polymerase chain reactions (PCRs) on extracted DNA and amplified two fragments of mitochondrial DNA (mtDNA): the first in-

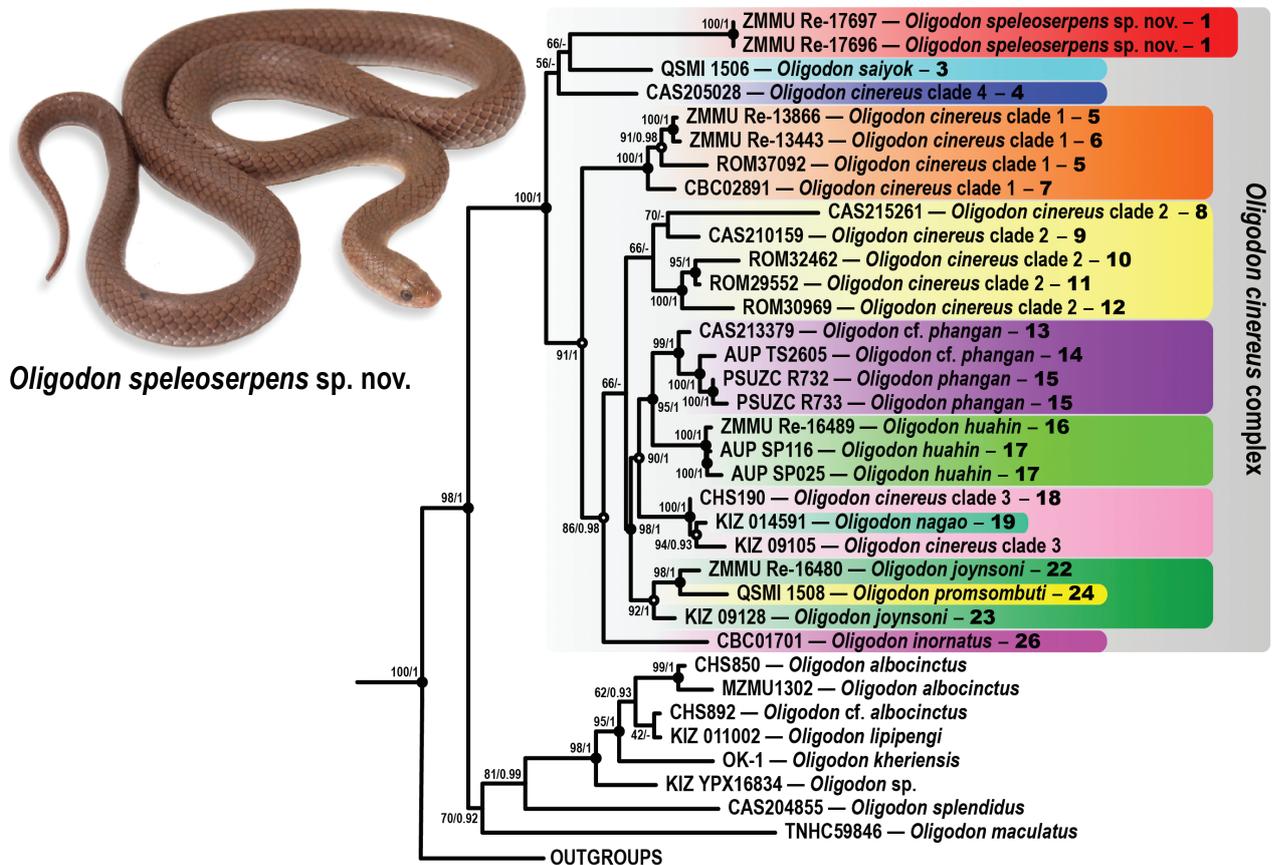


Figure 2. Phylogenetic tree of *Oligodon* from the analysis of 12S rRNA–16S rRNA and *cyt b* mitochondrial DNA gene sequences. For voucher specimen information and GenBank accession numbers see Table S1. Numbers at tree nodes correspond to ML UFBS / BI PP support values, respectively; an en-dash denotes no support. Colors of clades and locality numbers correspond to those in Figure 1.

cluding partial sequences of 12S ribosomal RNA (rRNA), transfer RNA (tRNA)-Valine and 16S rRNA (total length up to 1981 bp), and a second fragment including the complete sequence of the gene cytochrome *b* (*cyt b*) (1091 bp). Primers used for PCRs and sequencing are summarized in Table S2. PCR protocols for 12S–16S rRNA fragments were adapted from Green et al. (2010), whereas a modified procedure from Chen et al. (2014) was used for *cyt b* (see Yushchenko et al. 2023a for more details). All PCR products were sequenced in both directions by the “Evrogen” company at the Institute of Bioorganic Chemistry, Russian Academy of Sciences (Moscow, Russia), and were assembled and checked using Sequencher 4.9 (GeneCodes). Nucleotide sequences were initially aligned in MAFFT v.7 (Katoh and Standley 2013) with default parameters then checked by eye in BioEdit 7.0.5.2 (Hall 1999) and slightly adjusted for translation when appropriate. Mean uncorrected genetic distances (p distances) were calculated in MEGA 7.0 (Kumar et al. 2016). Obtained sequences were deposited in GenBank under accession numbers PP505895–PP505904, PP512957–PP512966 (Table S1).

Phylogenetic analyses were performed using 67 samples of *Oligodon* and the two outgroup taxa *O. porphyraeus* and *H. vibakari*. Both Bayesian inference (BI) and maximum likelihood (ML) approaches were used to estimate phylogenetic trees based on mtDNA sequence data. We used IQ-TREE 2 (Minh et al. 2020) to estimate optimal evolutionary models for dataset analyses based on suggestions from the Akaike information criterion (AIC). The best-fitting model for both BI and ML analyses for the 12S–16S rRNA fragments and the second codon partition of *cyt b* was the GTR+G+I model of DNA evolution. For *cyt b*, the AIC suggested the GTR+G model for the first codon partitions, and the HKY+G+I model for the third codon partition. ML analysis was conducted using IQ-TREE 2, and BI analysis was conducted in MrBayes 3.2.2 (Ronquist et al. 2012). For the ML analysis, confidence in nodal topology was estimated via the ultrafast bootstrap approximation algorithm (UFBS; Hoang et al. 2018) with 1000 bootstrap pseudoreplicates. For the BI analysis, Metropolis-coupled Markov chain Monte Carlo (MCMC) analyses were run with one cold chain and three heated chains for one million generations and sampled every 1000 generations. Two independent MCMC run iterations were performed and 100 trees were discarded as burn-in. The convergence of the runs was checked by exploring and examining likelihood plots in TRACER v1.6 (Rambaut et al. 2020), with effective sample sizes (ESS) all above 200. Internal nodes having ML UFBS values of 95 and above were a priori considered highly supported, while nodes with values of 90–94 were considered well-supported, and nodes with values of 70–89 were considered as tendencies. Lower values were regarded as indicating unresolved nodes (Huelsenbeck and Hillis 1993). Nodal support for BI was assessed by calculating posterior probabilities (BI PP), with nodes containing values over 0.95 considered sufficiently resolved, while BI PP values between 0.95 and 0.90 were regarded as tendencies.

Morphological analyses

We examined morphological features of the new species and compared them with 239 *Oligodon* specimens from natural history collections (Appendix S1) and literature descriptions (David et al. 2008a, 2008b, 2011, 2012; Jiang et al. 2012, 2020; Nguyen et al. 2016, 2017, 2022; Pauwels et al. 2017, 2021; Sumontha et al. 2017; Nguyen et al. 2020; Lalbiakzuala and Lalremsanga 2020; David et al. 2022; Yushchenko et al. 2023a, 2023b; David et al. 2023). Coloration was documented based on field observations, photographs taken in life, or collected specimens in preservative. Methodology for counting ventral scales followed Dowling (1951). Dorsal scale row reductions were noted by their positions relative to each ventral scale. The tail tip was not included in the number of subcaudals. Head scale suture angle terminology was adapted from Kaiser et al. (2019). Maxillary teeth were counted by carefully reflecting the soft tissue surrounding the upper jaw to reveal each tooth socket. Sex was determined by ventral incision below the vent to detect the presence or absence of hemipenes and subsequently confirmed in the type series of the new species by another incision anterior to the cloaca to detect whether testes/ductus deferens or oviducts were present. The hemipenis of the new species was partially everted in the field after euthanasia by injecting water immediately posterior to the tail base, a procedure partially adapted from Jiang (2010). Terminology used for the hemipenial description follows Dowling and Savage (1960) and Wagner (1975).

Linear measurements and morphological characters follow Yushchenko et al. (2023b), with some exceptions explained below. All measurements except body and tail lengths were taken under a dissecting microscope using Mitutoyo digital slide-calipers to the nearest 0.1 mm. Body and tail lengths were measured to the nearest millimeter by straightening specimens along a flexible ruler. The following linear measurements (all in mm) were taken: snout to vent length (SVL); tail length (TailL); total length (TotalL); relative tail length (TailLR), the ratio between tail length and total length given in decimal form; head length (HeadL) from the tip of the snout to the retroarticular process of the mandible; head width (HeadW); head depth (HeadD), measured between the dorsal and ventral surface of the head in lateral view; snout length (SnoutL); eye diameter (EyeD); frontal scale length (FrontalL); frontal scale width (FrontalW); interorbital distance (IOD); internarial distance (IND); and rostral width (RostralW), the maximum width of the rostral scale in dorsal view. Additional morphological characters examined include the number of maxillary teeth (MT); anterior dorsal scale rows, counted 15 ventral scales posterior to the head (ASR); midbody dorsal scale rows (MSR), counted halfway down the body based on snout-vent-length; posterior scale rows (PSR), counted 15 ventral scales anterior to the vent; dorsal scale row formula (DSR) summarizing the three dorsal scale row counts (i.e., ASR–MSR–PSR); ventral scales (VEN); subcaudal scales (SC); total body scales (TOTAL) including the cloacal plate (counted as one scale regardless of whether

the plate is entire or divided); subcaudal ratio (SCR), the ratio between the number of subcaudals and the number of total body scales; cloacal plate (CP), given as entire (one scale) or paired (divided into two scales); condition of nasal scale (NASAL), given as divided, subdivided or entire; condition of loreal scale (LOREAL), given as present or absent; number of supralabials (SL); number of supralabials in contact with the eye (SL-Eye); number of infralabials (IL); condition of the first pair of infralabials as separate or in-contact (IL-contact); number of infralabials in contact with the anterior pair of chin shields (IL-CS); number of preocular scales (PrO); number of presubocular scales (PrsO); number of postocular scales (PtO); number of anterior temporals (Ate); and number of posterior temporals (Pte). Abbreviations for these characters are used in Tables 3, 4. Symmetric characters are given in left/right order.

Results

Both the ML and BI analyses agree with previously published phylogenies of *Oligodon* (Che et al. 2020; Nguyen et al. 2020; Mirza et al. 2021; Qian et al. 2021; Das et al. 2022; Yushchenko et al. 2023a, 2023b; Lee et al. 2023) (Fig. 1 and Appendix S2). Members of the *O. cinereus* species complex were monophyletic in both analyses (Fig. 1), and were sister to a poorly supported clade (70 / 0.92, corresponding to ML UFBS / BI PP support values, respectively) containing *Oligodon maculatus* (Taylor, 1918), *Oligodon splendidus* (Günther, 1875), *O. kheriensis* Acharji and Ray, 1936, *Oligodon lipipengi* Jiang et al., 2020 and *Oligodon albocinctus* (Cantor, 1839), with the latter species rendered paraphyletic by *O. lipipengi*. In the *O. cinereus* species complex, we recovered four separate lineages containing specimens previously identified as *O. "cinereus"* that were spread out across the phylogeny.

The first split within the species complex includes a clade containing *O. cinereus* clade 4, the new species from Trang and Satun Provinces, Thailand, and *O. saiyok*. The new species was recovered sister to *O. saiyok*, and those two species were recovered sister to *O. cinereus* clade 4 (CAS 205028, locality 4; see Fig. 1) from Rakhine State, Myanmar with low support (56 / –). *O. cinereus* sensu stricto (*O. cinereus* clade 1; restricted to southern Vietnam, Laos and Cambodia) was the next lineage to split, forming a well-supported clade (100 / 1.0) sister to all remaining members of the *O. cinereus* complex, which include *O. phangan*, *O. huahin*, *Oligodon nagao* David et al., 2012, *Oligodon joysoni* (Smith, 1917), *O. promsombuti*, and *Oligodon inornatus* (Boulenger, 1914), along with *O. cinereus* clade 2 (including samples from Myanmar and northern Vietnam, localities 8–12; see Fig. 1) and *O. cinereus* clade 3 (including samples from southern China, locality 18; see Fig. 1). Two populations of *Oligodon* from Yangon Region, Myanmar (CAS 213379, locality 13; see Fig. 1) and Phi Phi Island, Krabi Province, Thailand (AUP TS2605, locality 14; see Fig. 1) were

found to be closely related to topotypic *O. phangan* from Pha Ngan Island, Surat Thani Province, Thailand (locality 15; see Fig. 1). A sample morphologically identified as *Oligodon nagao* from Guangxi Province, China (KIZ 014591; identification by Jiang et al. 2012) was grouped with two specimens of *O. cinereus* clade 3 from southern China (one from Hainan Island and another from an unnamed locality). Lastly, *O. promsombuti* was recovered within the same clade as *O. joysoni*, rendering the latter paraphyletic (Fig. 1). Uncorrected pairwise genetic distances (hereafter p distances; given for 12S–16S and cyt *b*) between and within *Oligodon* in this species complex are presented in Table S4.

Based on morphology, the new species from Satun and Trang provinces of Thailand resemble most members of the *O. cinereus* species group, especially uniform/reticulated morphotypes of *O. "cinereus"*. Nonetheless, the specimen has a significant genetic distance compared to other clades within the *O. cinereus* species complex (mean 16S rRNA divergence 2.6% from *O. cinereus* clade 4; mean cyt *b* divergence 7.7% from *O. saiyok*; Table S4). These divergences are larger than other, well-established sister species pairs within *Oligodon*, such as *Oligodon chinensis* (Günther, 1888) and *Oligodon formosanus* (Günther, 1872) (mean 12s–16s divergence 1.8%; Nguyen et al. 2020). Furthermore, the new species can be differentiated from all other members of the *O. cinereus* species group by multiple morphological characteristics (see Comparisons and Table S3), especially its number of ventral and subcaudal scales, lower number of maxillary teeth, and the presence of 19 anterior dorsal scale rows in all but one specimen. The combined molecular and morphological data provide strong evidence that the *Oligodon* from Satun and Trang represents a new species, which we describe below.

Oligodon speleoserpens sp. nov.

<https://zoobank.org/37DE18D9-FD02-4DD3-9176-BD1A3655955B>

Figures 3–5, Tables 1, S3

Holotype. ZMMU Re-17696 (field number ISS-128), adult male collected on 20 January 2023 at the entrance of Tham Le Stegodon Cave, Satun Province, Thailand (7.158315°N, 99.802631°E, 28 meters elevation), by Parinya Pawangkhanant and Sabira S. Idiiatullina.

Paratype. ZMMU Re-17697 (field number NAP-13128), adult female collected 24 September 2022 inside Tham Khao Ting Cave, Trang Province, Thailand (7.158315°N, 99.802631°E, 12 meters elevation), by Nikolay A. Poyarkov, Nikita S. Kliukin, Chatmongkon Suwannapoom and Parinya Pawangkhanant.

Diagnosis. *O. speleoserpens* sp. nov. is referred to the genus *Oligodon* based on the presence of enlarged blade-shaped maxillary teeth without a diastema, an elongate and subcylindrical body, and the presence of a large in-

flated rostral scale that blocks the internasal scales from contacting anteriorly (Wall 1923; Smith 1943; David et al. 2023). It is distinguished from all other *Oligodon* by the following combination of morphological characters: 1) head oblong-shaped with a truncated snout and slightly inflated rostral scale; 2) 8 maxillary teeth, with the posterior three teeth enlarged and blade-like; 3) dorsal scales in 19–17–15 rows (17–17–15 rows in one specimen); 4) reduction from 19 dorsal scale rows to 17 dorsal scale rows occurring at the 28th–30th ventral scale; 5) reduction from 17 dorsal scale rows to 15 dorsal scale rows occurring at the 100th–113th ventral scale; 6) cloacal plate entire; 7) 189–193 ventral scales (189–190 in male; 193 in female), distinctly keeled; 8) 47–54 paired subcaudal scales (47–54 in male; 48 in female); 9) 238–244 total body scales; 10) relative tail length 0.136–0.139 and subcaudal ratio 0.198–0.221; 11) 8 supralabials on either side of the head, with the fourth and fifth scales in contact with the orbit; 12) 9 infralabials on either side of the head with the first four scales in contact with the first pair of chin shields; 13) one loreal and one presubocular present; 14) 1+2 temporal scales; 15) dorsal color pattern uniform gray or grayish–brown without any markings or reticulations; 16) anterior half of ventral surface white with gray–brown irregularly shaped spots, posterior half immaculate dark gray, underside of tail splashed with white markings; 17) hemipenis bilobed with broad, awn-shaped lobes, simple sulcus spermaticus and smooth calyces.

Comparisons. We compared *Oligodon speleoserpens* **sp. nov.** with all other members of the *O. cinereus* species group and use Table S3 to compare it with other *Oligodon* native to Thailand. Its uniform gray dorsum distinguishes most members of the *O. cinereus* species group that have banded, cross-barred, or blotched dorsal color patterns; namely, *O. albocinctus*, *Oligodon ancorus* (Girard, 1857), *Oligodon kampucheanensis* Neang, Grismer and Daltry, 2012, *O. lipipengi*, *O. nagao*, *Oligodon purpurascens* (Schlegel, 1837), *O. saiyok*, and *Oligodon teyniei* David, Hauser, and Vogel, 2022. Exceptions include *O. “cinereus”*, *O. huahin*, *O. joysoni*, *O. inornatus*, and *O. phangan*, which have variable color patterns, or are uniform/reticulated dorsally. Between these congeners, *Oligodon speleoserpens* **sp. nov.** is most easily distinguished by usually having 19 anterior scale rows (vs. no more than 15 or 17 scale rows anywhere on the body; only one specimen of *Oligodon speleoserpens* **sp. nov.** with 17 anterior scale rows) with the reduction from 19 to 17 rows occurring between ventral scales 28 and 30.

More specifically, *O. speleoserpens* **sp. nov.** is distinguished from *O. huahin* by having 189–193 ventrals (vs. 166–173 in males), 47–54 subcaudals (vs. 35–41 in males), 9 infralabials (vs. 7–8), dorsum dark gray (vs. dorsum uniform but lighter gray, tan or orange), and a dark gray venter without conspicuous dark spots or rectangular blotches on the posterior half (vs. venter plain white); from *O. inornatus* by having 189–193 ventrals (vs. 169–173), 47–54 subcaudals (vs. 31–43), 8 maxillary teeth (vs. 10–11), and a ventral coloration without conspicuous dark spots or rectangular blotches on the

posterior half (vs. ventral surface with small square or rectangular spots); from *O. joysoni* by having 54 subcaudals in females (vs. 37–41 in females), relative tail length (TailLR) 0.139 in females (vs. 0.125–0.129 in females), 8 maxillary teeth (vs. 11–12), and a uniform gray or grayish–brown dorsum without crossbars or reticulations (vs. light tan, ochre brown or gray, narrow irregular shaped crossbars present on dorsal surface of body and tail); from *O. phangan* by having 189–193 ventrals (vs. 163–166), 47–54 subcaudals (vs. 33–42), 8 maxillary teeth (vs. 12), 9 infralabials (vs. 8), presubocular present (vs. absent), dorsum uniform gray or grayish–brown (vs. dorsum uniform orange–gray with indistinct vertebral lines present), and a ventral coloration without conspicuous dark spots or rectangular blotches on the posterior half (vs. ventral surface plain white); and from *O. promsombuti* by having 189–193 ventrals (vs. 177), 47–54 subcaudals (vs. 40), 8 maxillary teeth (vs. 12), 9 infralabials (vs. 8), presubocular present (vs. absent), and a ventral coloration without conspicuous dark spots or rectangular blotches on the posterior half (vs. venter with large rectangular blotches across entire ventral surface). *O. speleoserpens* **sp. nov.** differs from all clades hitherto referred to as *O. “cinereus”* (including *O. cinereus* sensu stricto) by having 189–193 ventral scales (vs. no more than 186), 47–54 subcaudals (vs. no more than 45), 8 maxillary teeth (vs. 10–13), and 9 infralabials (vs. usually 7–8, rarely 9). Moreover, the posterior portion of the venter is dark and uniform colored in *O. speleoserpens* **sp. nov.**, whereas uniform or reticulated colored populations of *O. “cinereus”* we examined (Appendix S1) have an immaculate venter with rectangular spots or blotches on the lateral edge of each ventral scale. The ventral underside of the tail, which is dark gray smeared with minimal white markings, is found in all specimens of *O. speleoserpens* **sp. nov.** and is absent in all uniformly patterned *O. “cinereus”*, as well as most other members of the *O. cinereus* species complex.

Five additional species of *Oligodon* outside of the *O. cinereus* species group may occur in close proximity with *O. speleoserpens* **sp. nov.** and are thus compared here. *Oligodon speleoserpens* **sp. nov.** differs from members of the *O. cyclurus-taeniatus* species group found in the same area of southern Thailand, namely *Oligodon fasciolatus* (Günther, 1864), *Oligodon mouhoti* (Boulenger, 1914) and *O. taeniatus*, by its uniform dark-olive dorsum without any conspicuous head markings (vs. lighter brown dorsum with a well-defined series of vertebral stripes [*O. mouhoti* and *O. taeniatus*] or series of large blotches [*O. fasciolatus*], in addition to the presence of conspicuous nuchal and temporal markings on the head). Next, *O. speleoserpens* **sp. nov.** most easily differs from *Oligodon signatus* (Günther, 1864), restricted to a few provinces at the southern end of Thailand (Pawangkhanant et al. 2021), by its uniform dorsum (vs. dark gray with a series of reddish-brown blotches), 8 supralabials (vs. 7) and two postoculars (vs. only one). Finally, *O. speleoserpens* **sp. nov.** differs from *Oligodon jintakunei* Pauwels et al., 2002, known from just one specimen allegedly from Krabi Province, by its uniform dorsum (vs. distinct black and

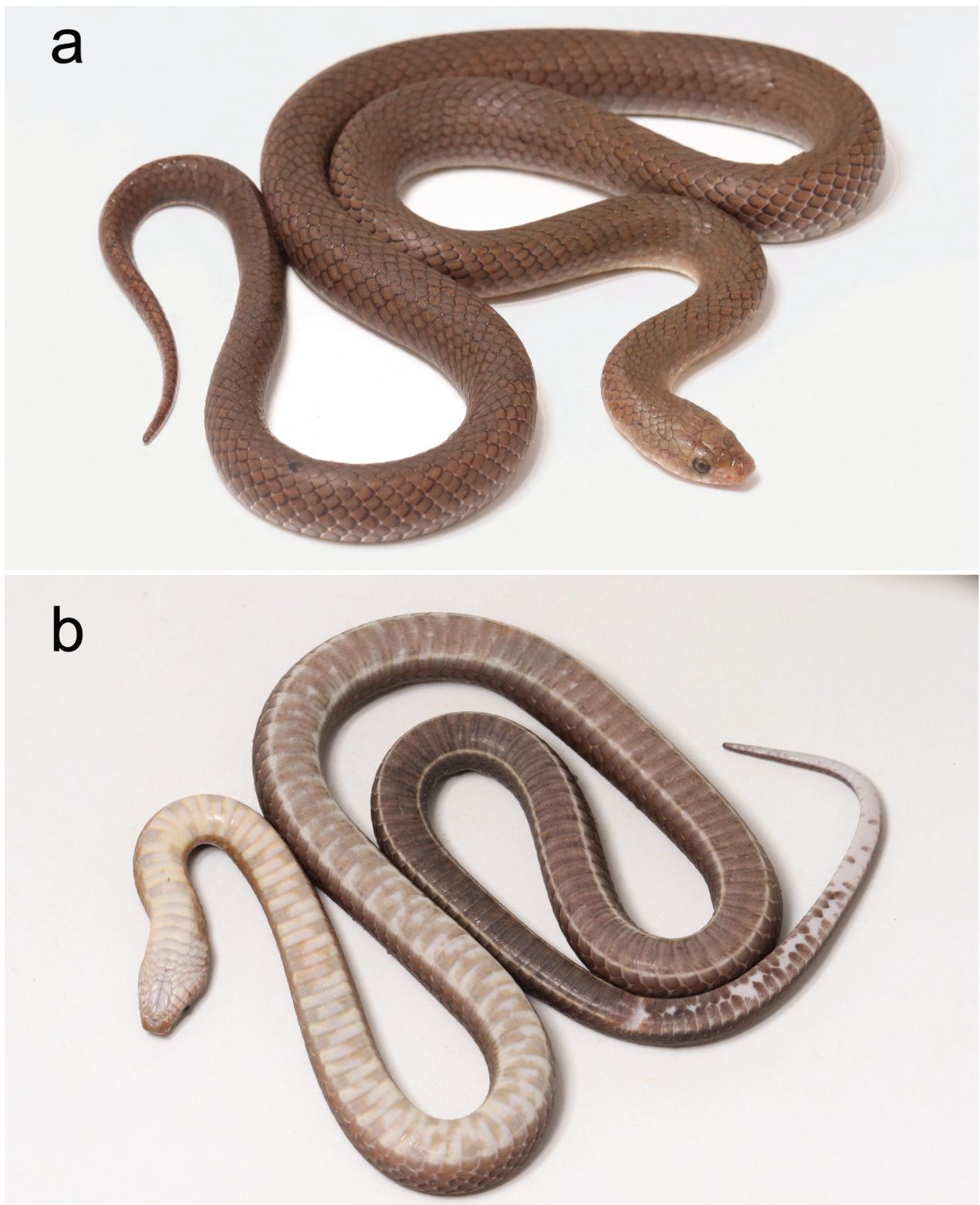


Figure 3. Photographs of the holotype of *Oligodon speleoserpens* sp. nov. (ZMMU Re-17696, adult male) (a) dorsal and (b) ventral views in life. Photographs taken by Parinya Pawangkhanant.

white crossbars) and by possessing an entire cloacal plate (vs. divided). Additional characters distinguishing each species can be found in Table S3.

Description of the holotype. Adult male specimen in excellent condition immediately after preservation (Fig. 3). Small ventral incisions at tail base and at midbody. SVL

601 mm, TailL 95 mm (TotalL 696 mm). HeadL 16.7 mm, HeadW 11.5 mm, HeadD 8.6 mm, SnoutL 5.3 mm, EyeD 2.7 mm, EyeLip 2.6, FrontalL 5.3 mm, FrontalW 4.3, IOD 6.5, IND 4.4 mm; RostralW 4.9. TailLR 0.136, HeadW/L 0.69, SnoutL/HeadL 0.32, EyeD/SnoutL 0.51, EyeD/HeadL 0.16, FrontalL/W 1.23. Body elongated and cylindrical in cross section; head oblong, only slightly

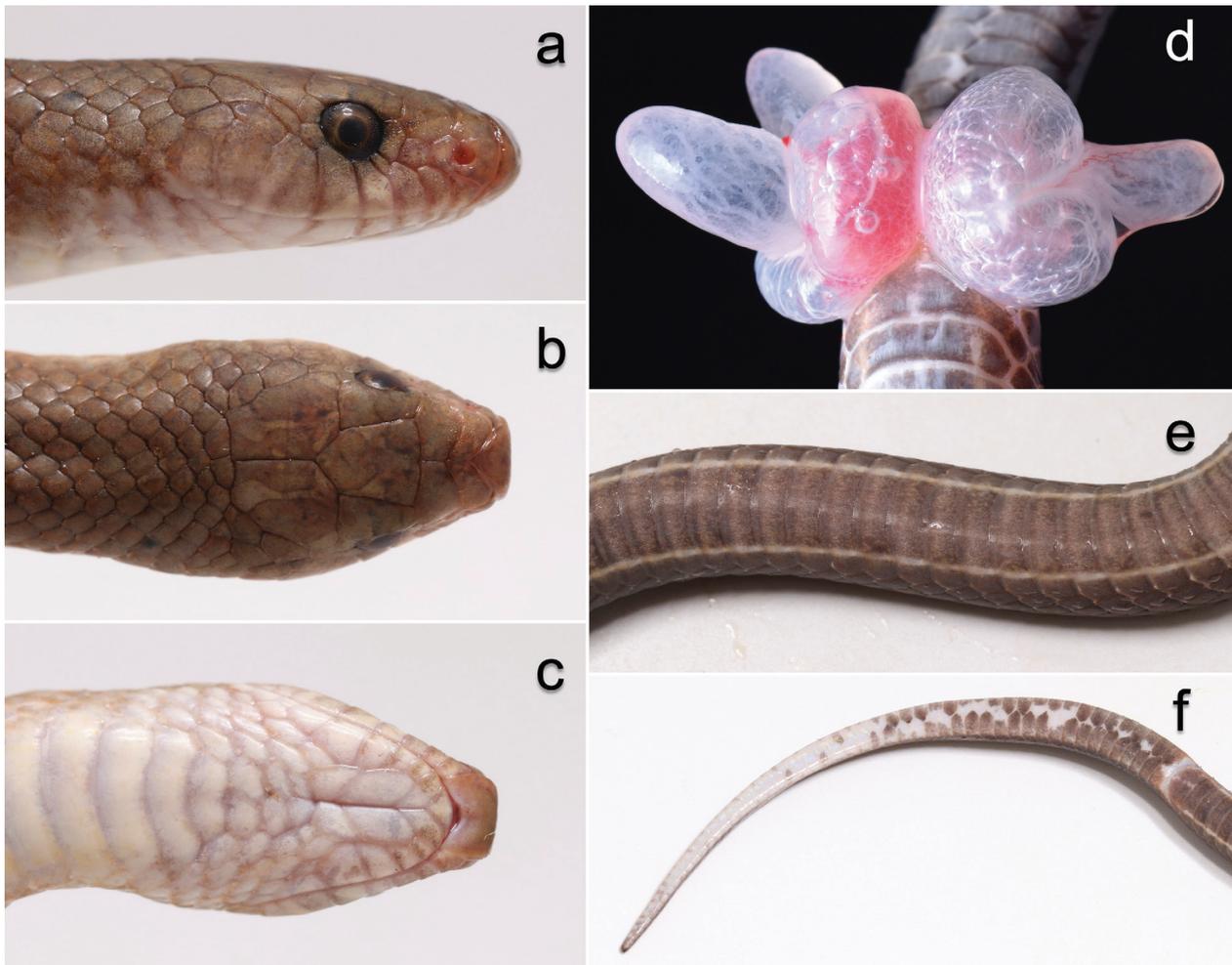


Figure 4. Photographs of the holotype of *Oligodon speleoserpens* sp. nov. (ZMMU Re-17696, adult male) (a) right lateral, (b) dorsal and (c) ventral views of the head in life; (d) partially everted hemipenes; (e) venter at midbody, note the distinctly keeled ventral scales; and (f) underside of tail depicting a dark gray and white color pattern. Photographs by Parinya Pawangkhanant (a–c and e–f), and Mali Naiduangchan (d).

distinct from neck (Fig. 4a, b); snout narrowing in dorsal view, in lateral view slightly truncate; snout tip subterminal near mouth; eyes moderately sized relative to head, pupil round; nostrils small and subelliptical, pointed laterally; lips curving upwards posteriorly along the last supralabial; tail broad at base, tapering gradually to a blunt terminal scute (Fig. 4f).

Rostral distinctly enlarged and inflated, wider than high, triangular in dorsal view, partially separating the anterior half of internasals (Fig. 4b); posterior rostral scale suture bordering the internasals “deep-V” shaped, creating a narrow obtuse angle ($\sim 100^\circ$); internasals subrectangular, $1.7\times$ wider than long, anterior suture of each scale rounded and concave, both scales oriented obliquely and posteromedially in dorsal profile; prefrontals subpentagonal, $1.5\times$ wider than long, $1.4\times$ longer than suture dividing both internasals, $1.2\times$ wider than internasals, anterior suture bordering each internasal slightly rounded, concave; frontal pentagonal and shield shaped, longer than wide, anterior suture bordering prefrontals straightened; frontal $2.3\times$ longer than prefrontals; eyes placed posterior to anterior edge of frontal; angle formed by sutures producing the posterior vertex of frontal a narrow obtuse

angle ($\sim 99^\circ$); supraoculars subrectangular, $1.8\times$ longer than wide, $0.7\times$ as long as frontal; parietals subpentagonal, $1.3\times$ longer than wide, width of each scale $1.1\times$ longer than parietal suture; posterior suture of parietals straightened; frontal and parietal approximately equal in length; frontal $1.4\times$ longer than parietal suture; anterior angle formed by the sutures between the parietal/frontal and the supraocular/parietal a broad obtuse angle ($\sim 130^\circ$) with the lateral ray oriented slightly posterolaterally. Nasal scale rectangular, longer than wide, fully divided (Fig. 4a); loreal 1/1, small, squared, slightly higher than long, less than half the size of nasal; supralabials 8/8; with 4th and 5th supralabials in contact with orbit; 6th supralabial largest, 1st supralabial smallest; all supralabials in broad contact; preoculars 1/1, wider than long; presubocular 1/1, less than half the size of preocular; postoculars 2/2, uppermost postocular slightly larger; anterior temporal 1/1; posterior temporals 2/2, all scales longer than wide; infralabials 9/9 in all specimens, first pair contacting each other, 4/4 infralabials in contact with anterior chin shields; 5th infralabial largest, 2nd and 9th infralabials smallest; mental subtriangular, wider than long; small, indistinct mental groove present, starting from border of

1st pair of infralabials and terminating past posterior pair of chin shields; both pairs of chin shields subrectangular, anterior pair 1.4× longer than posterior pair.

Dorsal scale rows 19–17–15, smooth throughout, without apical pits; dorsal scale reduction from 19 rows to 17 rows occurring at 30th ventral scale on either side of body; reduction from 17 rows to 15 rows occurring at 100th ventral scale on either side; precentrals 2 and ventral scales 189; lateral edges of each ventral scale with discrete lateral keeling; subcaudals 54, paired; total body scales 244; subcaudal ratio 0.221; cloacal plate entire. Maxillary teeth 8, posterior two teeth enlarged, laterally compressed, blade-like. The partially everted hemipenes is bilobed and weakly calyculate (Fig. 4d). The base of the organ and most of the capitulum is bulbous and covered with small smooth calyces. The sulcus spermaticus is simple, indistinct, extending from the base of the organ and terminating at the point of bifurcation. Both apical lobes are large, nude, and rounded distally, lacking any ornamentation.

Coloration in life and preservative. In life, dorsal ground color ashy gray, margins of most dorsal scales edged with black, but distinct reticulations absent (Figs 3a, 5a); scattered small reddish–orange mottling interspaced across dorsal surface of the tail and neck. Dorsal portion of head brown (Fig. 4b); a very indistinct temporal bar on each side of the head across the supraoculars, frontal, and me-

dial region of the parietals; a dark, hued, and indistinct nuchal chevron present at the medial region of each parietal, descending posterolaterally towards the neck; remainder of head plain, bottommost portion of supralabials light brown (Fig. 4a). Ventral surface of head white, dark brown hueing along lateralmost margins of first 5 infralabials; the anterior third of the venter is white, with long irregular gray blotches first visible along the seventh ventral scale; these blotches continue to merge until the venter is uniform and dark gray for the remaining two thirds of the body; discrete keeling present on the edges of each ventral scale light gray, forming a subtle longitudinal stripe along each side of the venter until the tail base. The underside of the tail is dark gray, with white pigment present midventrally until its posterior half, which is completely white until the last few subcaudals and the terminal scute. In preservative, coloration overall very similar, except the dorsum is darker gray.

Description of the paratype and variation. The adult female paratype (Fig. 5c) agrees in almost all scalation and mensural aspects of the holotype, with a few exceptions. The paratype has a small anterior portion of the dorsum with past injuries, and small ventral incisions at the tail base and midbody. Measurements of the paratype are as follows: SVL 681 mm, TailL 110 mm (TotalL 791 mm). HeadL 16.5 mm, HeadW 14.0 mm, HeadD 10.6 mm, SnoutL 7.6 mm, EyeD 2.7 mm, EyeLip 2.9,

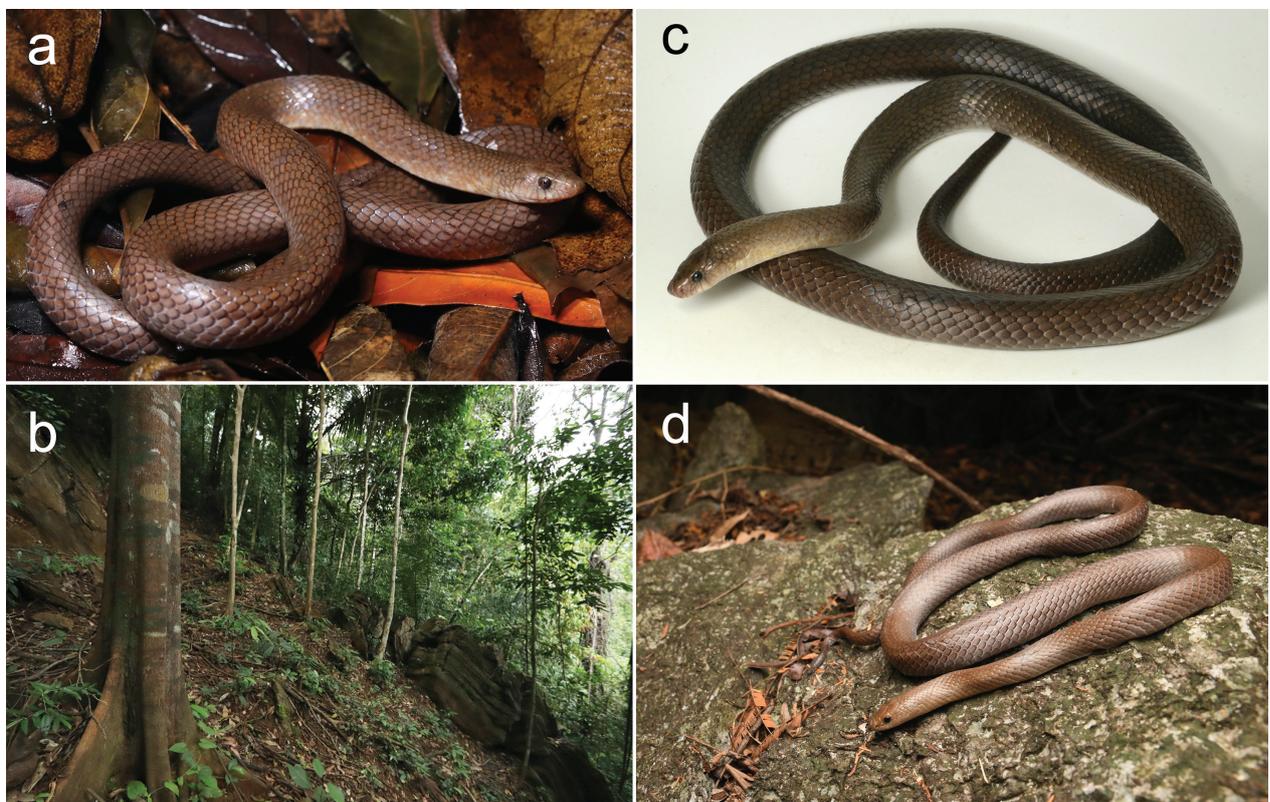


Figure 5. Photographs (a) of the holotype of *Oligodon speleoserpens* sp. nov. (ZMMU Re-17696, adult male) in life; (b) habitat at the type locality, Tham Le Stegodon cave, Satun Province, Thailand; (c) paratype of *Oligodon speleoserpens* sp. nov. (ZMMU Re-17697, adult female) in life from Tham Khao Ting cave, Trang Province, Thailand; and (d) uncollected adult male specimen of *Oligodon speleoserpens* sp. nov. from the same locality as the paratype. Photos by Parinya Pawangkhanant (a, b), Nikolay A. Poyarkov (c), and Harry Ward-Smith (d).

Table 1. Selected morphological counts of all three specimens of *Oligodon speleoserpens* sp. nov. All linear measurements are in millimeters, with abbreviations matching those listed in the materials and methods section.

Character	<i>Oligodon speleoserpens</i>		
	ZMMU Re-17697	ZMMU Re-17696	No voucher
Catalog number			
Sex	F	M	M
SVL	681	601	612
TailL	110	95	97
TailLR	0.139	0.136	0.137
HeadL	16.5	16.7	–
HeadW	14.0	11.5	–
HeadW/L	0.85	0.69	–
HeadD	10.6	8.6	–
RostralW	4.91	4.9	–
FrontalL	5.6	5.3	–
FrontalW	4.7	4.3	–
SnoutL	7.3	5.3	–
EyeD	2.7	2.7	–
EyeLip	2.9	2.6	–
DSR	19-17-15	19-17-15	17-17-15
Preventrals + VEN	2+193	2+189	2+190
CP	Entire	Entire	Entire
SC	48	54	47
SL	8/8	8/8	8/8
SL-eye	4+5/4+5	4+5/4+5	4+5/4+5
IL	9/9	9/9	9/9
IL-CS	4/4	4/4	4/4
LOR	1/1	1/1	1/1
PrO	1/1	2/1	1/1
PrsO	1/1	1/1	1/1
PtO	2/2	2/2	2/2
Temporals (Ate + Pte)	1+2 / 1+2	1+2 / 1+2	1+2 / 1+2
MT	8	8	–

FrontalL 5.6 mm, FrontalW 4.7, IOD 8.0, IND 5.7 mm; RostralW 4.9. TailLR 0.139, HeadW/L 0.85, SnoutL/HeadL 0.46, EyeD/SnoutL 0.36, EyeD/HeadL 0.16, FrontalL/W 1.19. Body elongated, cylindrical in cross section. Head oblong, only slightly distinct from neck. Snout more elongate in lateral view than the holotype; snout tip subterminal near mouth; eyes moderately sized relative to head, pupil round; nostrils small, subelliptical, pointed in lateral view; mouth with lips curving upwards posteriorly across the last supralabial; tail gradually tapering to a blunt terminal scute.

Rostral wider than high, triangular in dorsal view; posterior scale suture of rostral bordering internasals “deep-V” shaped, creating a narrow obtuse angle (~100°, same as holotype); internasals subrectangular, 2.3× wider than long, anterior sutures rounded, concave; prefrontals subpentagonal, 2.4× wider than long, 1.3× longer than internasals, anterior sutures bordering each internasal also rounded; prefrontals 1.3× wider than internasals; frontal pentagonal, shield shaped, 1.2× longer than wide, anterior suture bordering each prefrontal straightened; frontal 1.4× longer than prefrontals; eyes placed posterior relative to the anterior edge of frontal; angle formed by suture producing the posterior vertex of frontal a narrow obtuse angle (~96°); supraoculars subrectangular, 1.4×

longer than wide, 1.3× shorter than frontal; parietals sub-pentagonal, 1.2× longer than wide, width of each scale 1.2× longer than parietal suture, posterior suture of parietals straightened; length of parietals approximately 1.1× longer than frontal; frontal 1.1× longer than parietal suture; anterior angle formed by the sutures between the parietal/frontal and supraocular/parietal a broad obtuse angle (~131°) with its lateral ray pointing somewhat posterolaterally. Nasal scale rectangular, longer than wide, fully divided; loreal 1/1, small and square shaped, 1.2× longer than high, less than half the size of nasal; supra-labials 8/8; with 4th and 5th supralabial in contact with orbit; 6th supralabial largest, 1st supralabial smallest; all supra-labials in broad contact; preoculars 1/1, wider than long; presubocular 1/1, less than half the size of preocular; postoculars 2/2, uppermost postocular slightly larger in size; anterior temporal 1/1; posterior temporals 2/2; infralabials 9/9 in all specimens, first pair in contact, 4/4 infralabials in contact with anterior chin shields; 5th infralabial largest, both 2nd and 9th infralabials smallest; mental subtriangular, wider than long; small, indistinct mental groove present, condition identical to holotype; chin shields subrectangular, anterior pair 1.2× longer than posterior pair.

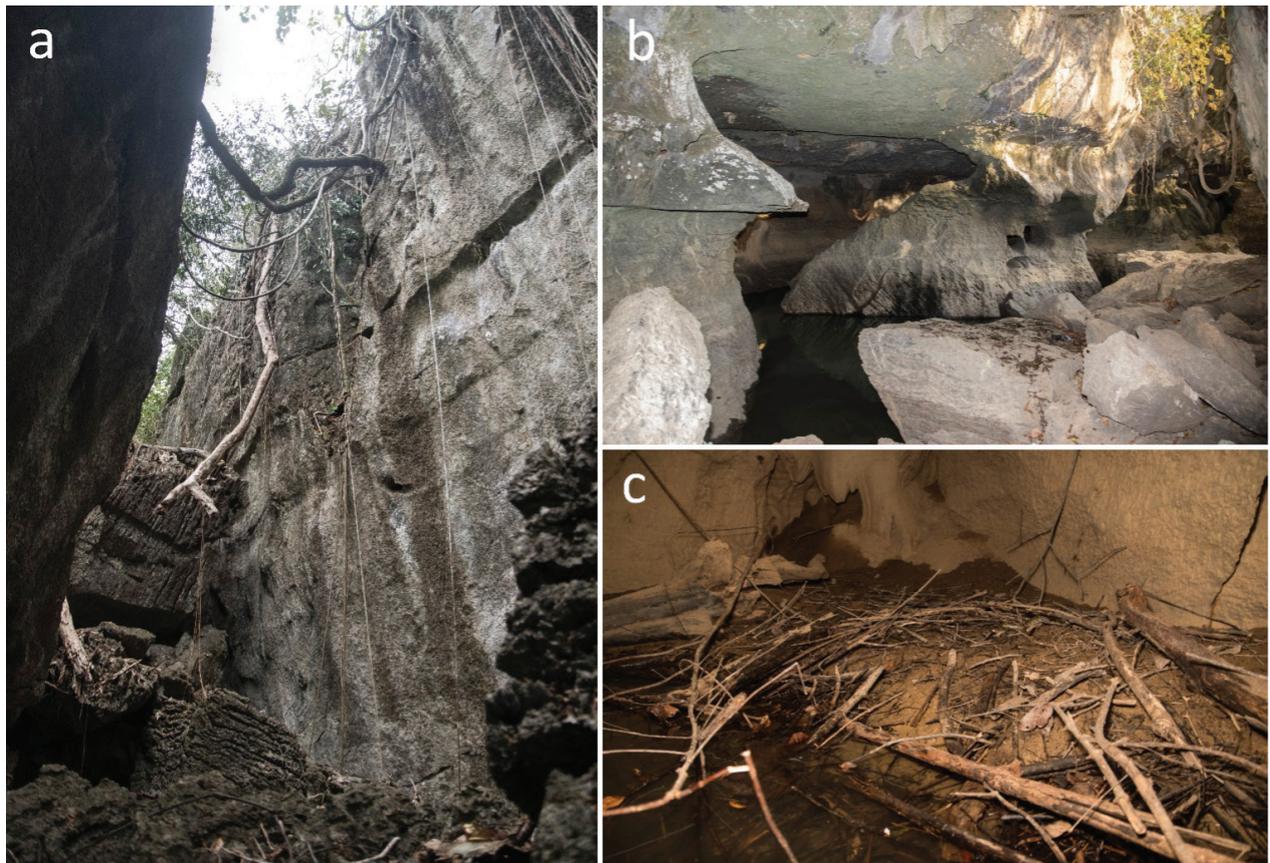


Figure 6. Habitat photographs (a) of the karst wall above an entrance to Tham Khao Ting Cave, Trang Province, Thailand that the uncollected specimen of *Oligodon speleoserpens* sp. nov. was found ~12–15 m high; (b) flooded exit of the Tham Khao Ting cave; and (c) flooded habitat 50 m past the entrance of Tham Le Stegodon cave, Satun Province, Thailand. Photographs by Harry Ward–Smith.

Dorsal scale rows 19–17–15, scale ornamentation like holotype; dorsal scale reduction from 19 rows to 17 rows occurring at the 28th ventral scale; reduction from 17 rows to 15 rows occurring at the 113th ventral scale; pre-ventrals 2, ventral scales 193, distinctly keeled; subcaudals 48, paired; total body scales 242; subcaudal ratio 0.198; cloacal plate entire. Maxillary teeth 8, posterior two teeth enlarged and blade-like.

In life, dorsal ground color dark olive–gray (Fig. 5c), plain, edges of each dorsal scale slightly darker, distinct reticulations absent; a very indistinct pair of vertebral stripes present from nape to vent; scattered, small reddish–orange mottling interspaced across dorsal surface of tail; tail tip dark gray. Dorsal portion of head olive–brown; indistinct ocular and temporal bar present on each side of head, both subdued, dark brown, present across the supraoculars, frontal and medial portion of the parietals; remainder of head plain olive–brown, bottommost portion of supralabials light gray. Ventral surface of head also light gray, darker hueing along lateralmost margins of the first four infralabials; anterior third of ventral surface white with small irregularly-shaped olive–gray mottling; posterior two thirds of the venter plain dark gray; keel along ventral scales forming a narrow light-gray stripe present until the vent. Ventral surface of tail dark gray, less white pigment than holotype, anterior half similar to ventral surface of body, posterior half with small

white spotting at midline until tail tip. After preservation, coloration very similar but head markings completely subdued and dorsal coloration darker gray, matching the coloration of the ventral surface.

Morphological data of another male individual from the same locality as the paratype were collected by two of us (HWS and RGL; Fig. 5d) shortly after capture (see Table 1 for more information). The uncollected specimen from Tham Khao Ting cave agrees with the paratype in most features except it has 17 anterior dorsal scale rows compared to the 19 rows found in both type specimens (total dorsal scale row formula: 17–17–15). The dorsum is ashy gray with dark edges on each dorsal scale, as observed in the type series. The indistinct temporal bar and nuchal chevron present in the holotype are extremely subdued and essentially absent. The venter is white anteriorly with small gray and irregularly shaped markings along the anterior third of the body before becoming plain and dark gray along its remaining posterior two thirds. The ventral underside of the tail resembles the paratype and is entirely dark gray except for a few subdued white spots present near the posterior end of the tail.

Etymology. The species epithet “*speleoserpens*” is a compound name combining the Latinized Greek noun “*spelēum*”, meaning “cave” and the Latin noun “*serpens* [= *serpentis*]”, the present active participle of “*ser-*

pō” meaning “to crawl or creep”, often used in reference to snakes. This roughly translates to “cave crawler” or “cave serpent”, an allusion to both the type locality and the discovery of the paratype. We recommend the English common name “Cave Kukri Snake” and the Thai common name “ปีแก้วควานหิน” (Ngu Pi Kaew Kuan Hin) for this species.

Distribution and natural history. *Oligodon speleoserpens* **sp. nov.** is currently known from only two localities in southeastern Peninsular Thailand: Tham Le Stegodon, Satun Province and Tham Khao Ting cave, Trang Province (see locality 1, Fig. 1). Both locations are cave formations that form part of a larger complex of limestone karst massifs along the border between Satun and Trang provinces. The holotype was discovered crawling along a vertical limestone wall just outside the entrance of Tham Le Stegodon (Fig. 5b) at 1950 hrs (local ITC time), whereas the paratype was discovered at 2200 hrs in-situ coiled within a crevice in Tham Khao Ting cave, approximately 10 meters past the entrance. The third, uncollected specimen from Tham Khao Ting cave was observed by two of us (HWS and RGL) on 19 March 2023 at 2100 hrs. It was first observed ~12–15 meters up a karst wall (Fig. 6a) with its head peeking into a small crack. It proceeded into this crack, emerging 5 minutes later with no signs of finding prey. Both of these specimens were adult males, whereas the paratype collected earlier in September 2022 was an adult female. Due to the proximity of Satun and Trang Provinces to the equator, sunset varies very little through the year, from 1810 hrs at the winter solstice to 1837 hrs at the summer solstice. All specimens were observed after sunset (1900–2300 hrs), but we assume this species is cathemeral (including both diurnal and nocturnal surface activity), as is consistent with other members of the *O. cinereus* species group.

The diet of most *Oligodon* is presumed to consist primarily of reptile eggs and frogs (Wall 1923; Bringsøe et al. 2020; David et al. 2023), but Meggitt (1931) and Pope (1935) both recorded several arachnid and arthropod species in the stomachs of specimens in the *O. cinereus* species complex (Savitzky 1983; as *O. cinereus*). Whether *O. speleoserpens* **sp. nov.** has a similar reptile egg-rich diet remains an open question. We observed three highly abundant gecko species present in sympatry with *O. speleoserpens* **sp. nov.** including *Cnemaspis niyomwanae* Grismer et al., 2010, *Cyrtodactylus* cf. *lekaguli* Grismer et al., 2012 and *Gekko gekko* (Linnaeus, 1758). All three lizards occupy the same karstic surfaces and utilize crevices as egg laying sites. The exploratory behavior observed in the uncollected specimen could be related to foraging for these species and their eggs. We also observed five additional generalist and widespread gecko species at the same locality, including *Cyrtodactylus quadrivirgatus* Taylor, 1962, *Cyrtodactylus zebraicus* Taylor, 1962, *Gekko tokehos* (Grismer et al., 2019), *Gekko kuhli* (Stejneger, 1902) and *Hemidactylus frenatus* Duméril and Bibron, 1836. Other snake species found in sympatry with *O. speleoserpens* **sp. nov.** include *Ahaetulla mycterizans* (Linnaeus, 1758), *Ahaetulla prasina* (Boie, 1827), *Boiga*

melanota (Boulenger, 1896) (recognized at species-level fide Weinell et al. 2021), *Bungarus flaviceps* Reinhardt, 1843, *Elaphe taeniura ridleyi* (Butler, 1889), *Lycodon capucinus* Boie, 1827, *Lycodon (Dryocalamus) davisonii* (Blanford, 1878), *Malayopython reticulatus* (Schneider, 1801), *Pareas carinatus* Wagler, 1830, *Trimeresurus ciliaris* Idiitullina et al., 2023, *Tropidolaemus wagleri* (Boie, 1827), and *Xenochrophis trianguligerus* (Boie, 1827). The diversity and abundance of geckos and other squamate reptiles in this karstic habitat provides numerous potential prey items for *Oligodon speleoserpens* **sp. nov.**, especially in the form of eggs. No other information on its natural history or behavior is known.

Conservation status. Only three specimens of *Oligodon speleoserpens* **sp. nov.** have been documented so far, all within a span of six months. The surrounding limestone karst massif where the new species has been collected spans a total area of approximately 10.7 square kilometers. Both sites are offered protection from human development. Tham Le Stegodon is part of the Satun UNESCO Global Geopark and Tham Khao Ting is owned by the Liphang Subdistrict Administrative Organization of Trang Province. The underground river networks of both cave systems are popular tourist attractions for swimming and kayaking. We believe the current level of recreation poses minimal impact on the caves and surrounding karst habitat and is thus unlikely to threaten the conservation of *Oligodon speleoserpens* **sp. nov.** at these sites. However, future work on the ecology and behavior of this species is needed to understand whether any other human activities in this region might act as conservation threats. Owing to a lack of ecological information on this species, we suggest classifying *Oligodon speleoserpens* **sp. nov.** as “Data Deficient” based on the criteria adopted by the International Union for Conservation of Nature (IUCN) Red List of Threatened Species. This classification is based on the fact that little data exists for the new species, and that more information is needed to understand its distributional limits within southern Thailand.

Discussion

The discovery of *Oligodon speleoserpens* **sp. nov.** brings the total number of recognized *Oligodon* species to 88 or 91 (see Introduction) and the number of species known from Thailand to 21 (but see David and Pauwels 2005; Lee et al. 2023a; Poyarkov et al. 2023; and David et al. 2023 for discussion of some species records and their validity). The surrounding karst formations of southern Thailand and the broader Nakawan Range are home to several putatively endemic reptile species (Kiew 1985; Grismer et al. 2008; Grismer et al. 2010; Grismer et al. 2012; Termprayoon et al. 2023; Grismer et al. 2023; Idiitullina et al. 2023), including the gecko *Cnemaspis niyomwanae* and the newly described pit-viper *Trimeresurus ciliaris*. The type localities of these two species sit

on the same karst massif as the type locality of *O. speleoserpens* **sp. nov.**, and their precise location (Tham Khao Ting cave) is also the site where the paratype and one other specimen of *O. speleoserpens* **sp. nov.** were observed. Another endemic colubrid snake species, *Lycodon cavernicolus* Grismer et al., 2014, was discovered less than 64.0 km SE of the *O. speleoserpens* **sp. nov.** type locality in Gua Wang Burma cave, Perlis, Malaysia. The addition of *Oligodon speleoserpens* **sp. nov.** reinforces the importance of karst habitats as local hotspots of herpetofaunal endemism in Peninsular Thailand and suggests that many more undescribed species of reptiles restricted to these ecosystems await discovery.

Limestone karsts and their caves are well-known for supporting high levels of range-restricted herpetofauna (Clements et al. 2006; Quah et al. 2021), especially species with low-dispersal capabilities such as geckos (Ellis and Pauwels 2012; Grismer et al. 2018; Davis et al. 2019), frogs (Köhler et al. 2010; Brown et al. 2015; Grismer et al. 2017; Suwannapoom et al. 2018) and snakes (Vogel et al. 2012; Teynié et al. 2014; Grismer et al. 2014; Ruane et al. 2016; Sumontha et al. 2017; Luu et al. 2020; Sumontha et al. 2021). Before this study, three species of *Oligodon* were considered limestone karst specialists: *O. nagao*, *O. promsombuti* (Ian Dugdale pers. obs., February 2023) and *O. saiyok* (David et al. 2012; Sumontha et al. 2017; Pauwels et al. 2021). In addition, Grismer et al. (2006) and Quah et al. (2021) reported a fourth species, *O. fasciolatus*, from limestone caves in Thailand and Peninsular Malaysia (on the island of Pulau Langkawi). We confirm this behavior and supplement these reports with observations of *O. fasciolatus* in karstic landscapes in Kanchanaburi Province and Prachuap Khiri Khan Province, Thailand (HWS, pers. obs., 2022). Additionally, we add *O. huahin* as a species known from karst habitats, based on a single specimen (USNM 94932) collected from Sam Roi Yot, Prachuap Khiri Khan Province, Thailand, a locality that is completely comprised of limestone karst massifs. This specimen was originally identified as *O. cinereus*, but subsequent examination by one of us (HWS) confirms that it can be referred to *O. huahin* (Appendix S1). We have also observed another species, *O. purpurascens*, active along the edges of limestone karst formations in Phatthalung Province, Thailand. However, we do not consider *O. fasciolatus*, *O. huahin* or *O. purpurascens* to be limestone karst specialists, as these species are also found in mixed forests and agricultural landscapes (Tillack and Günther 2009; Das 2010; Pauwels et al. 2017). *Oligodon speleoserpens* **sp. nov.** is thus the seventh *Oligodon* recorded from karstic formations, and based on our observations, it appears restricted to these habitats. With the level of diversity and local endemism of geckos found in the Nakawan Range, it is not surprising that an endemic snake from a genus that normally preys on reptile eggs is also present. This discovery remains consistent with other karst dwelling *Oligodon*, including *O. saiyok*, which is sympatric with five species of endemic geckos (Bauer et al. 2003; Bauer et al. 2004; Bauer et al. 2008; Grismer et al. 2010; Panitvong et al. 2014; Sumontha et al. 2017) found in karst habitats

surrounding Sai Yok, Kanchanaburi Province, Thailand. This example, and our current study, suggest both the high detectability of lizards and the beta diversity of karst endemic gecko species could be used as indicators for targeting novel *Oligodon* populations across peninsular Thailand, allowing researchers to refine future surveying efforts.

It is difficult to make any biogeographic assessments of *O. speleoserpens* **sp. nov.** because the broader evolutionary relationships of *Oligodon* remain poorly understood. Nevertheless, it is instructive to note that *O. speleoserpens* **sp. nov.**, differs from most of its congeners in the *O. cinereus* species complex by its placement south of the Isthmus of Kra, a location that is known for its high-levels of species endemism and its function as an area of faunal turnover between Indochina and Peninsular Malaysia (Pauwels et al. 2003; de Bruyn et al. 2014; Mulcahy et al. 2018; Poyarkov et al. 2023). Although it is possible that *O. speleoserpens* **sp. nov.** represents a site-specific endemic, the continuity of similar limestone karst habitats adjacent to the type locality suggests it probably occurs at other neighboring localities. Similarly sized karst formations are found immediately east of the type locality of the new species along the leeward foothills of the broader Nakawan Range. This series of mountains extends from the Thai–Malay border near Perlis, Peninsular Malaysia to the northern edge of Trang Province, where it continues to the Gulf of Thailand as the Nakhon Si Thammarat Range. If *O. speleoserpens* **sp. nov.** is not a site-specific endemic to the karst surrounding Tham Le Stegodon and Tham Khao Ting caves, it likely inhabits adjacent habitats throughout Satun and Trang Provinces. Likewise, we also expect that additional new *Oligodon* in the *O. cinereus* species complex await discovery in southern Thailand, as has been the case for other karst-endemic geckos and pit vipers in this region (Termprayoon et al. 2023; Idiattullina et al. 2023). Already, we are aware of two *Oligodon* specimens that were found in more northerly limestone karst localities on the citizen scientist website iNaturalist (www.inaturalist.org), the first from Chumphon Province (obs. 147890899) and Krabi Province (obs. 151275183). The specimen photographed from Krabi Province (see locality 2, Fig. 1) shares some features that resemble the coloration observed in *O. speleoserpens* **sp. nov.**, specifically a plain, dark olive dorsum, however the remaining photos do not provide enough information to confidently identify it. Future taxonomic research and fieldwork is necessary to determine the status of these two populations. Outside of Thailand, we encountered a few sources (Green 2010; Stuart 2010; Yushchenko et al. 2023a; Uetz et al. 2023) that note the occurrence of *O. cinereus* in neighboring Peninsular Malaysia. However, we could not find any evidence supporting the occurrence of *O. cinereus* in the country (L. Lee Grismer, pers. comm. April 2023). Possibly, the statements from other authors were the result of confusion with de Rooij (1917), who reported the taxon as *Oligodon violaceus* (a name now synonymized with *O. cyclurus*, but historically confused with *O. cinereus*) from the island of Borneo, although that record is now considered doubtful (Stuebing et al. 2014).

Until further evidence is presented, we suggest removing *O. cinereus* from the snake fauna of Malaysia, but do not rule out the possibility that *Oligodon speleoserpens* **sp. nov.** might eventually be detected within its geographic boundaries, as has been the case with the pitviper species *T. ciliaris* (Idiattullina et al. 2023) and the re-confirmation of *Cyrtodactylus zebraicus* (Quah et al. 2023).

While only three specimens of *O. speleoserpens* **sp. nov.** have been observed so far, a few aspects of its natural history can be hypothesized. One feature found in all individuals of the new species is the presence of keeled ventral scales. This scalational feature has been observed in other *Oligodon*, including members of the *O. cinereus* species group (Tillack and Günther 2009), but its presence across other genus members is poorly documented. In snakes, keeled ventral scales are generally associated with arboreal and scansorial behaviors since they help maintain traction on rough, vertical surfaces. The habitats surrounding the type locality of *O. speleoserpens* **sp. nov.** contain large rock outcrops that pose as significant navigational challenges for many snakes. It seems reasonable to hypothesize that the distinctly keeled ventral scales found in this species might assist with climbing across these terranes, as evidenced by the discovery of one specimen found active high up a vertical karst wall, and the discovery of the paratype active along the chamber of Tham Thao King cave (Fig. 6a). The apparent restriction of *O. speleoserpens* **sp. nov.** to limestone karst massifs with accompanying underground caves may also suggest it is troglomorphic, a behavior that is common in other snake species that utilize these types of habitats, such as *E. taeniura riddlei* (Monroe, 1970; Quah et al. 2021). Nonetheless, all of these speculations can only be confirmed if additional observations of *O. speleoserpens* **sp. nov.** are made in the future.

A significant hurdle preventing a broader understanding of *Oligodon* systematics has been their low detectability during field surveys, which makes assessments based on large series of specimens difficult. Characters that have traditionally been used to classify *Oligodon* species include the shape and ornamentation of the hemipenis, number of maxillary teeth, number of dorsal scale rows, and number of body scales (ventrals and subcaudals) (Wall 1923; Smith 1943; Leviton 1963; Wagner 1975; David et al. 2008a, 2008b). These features normally diagnose taxa efficiently; however, recent studies have pointed out errors promulgated in several hemipenial descriptions of *Oligodon*, resulting in taxonomic confusion (Yushchenko et al. 2023a, 2023b). In this study, samples of the four recently described Thai *Oligodon* we included in our phylogeny (*O. huahin*, *O. phangan*, *O. promsombuti* and *O. sai yok*) were all recovered in the *O. cinereus* species complex, even though three were originally classified in a separate species group (Pauwels et al. 2017, 2021). The fact that these species (*O. huahin* and *O. promsombuti*) were incorrectly classified exemplify the issues related to the hemipenis raised by Yushchenko et al. (2023a, 2023b). After a re-examination of the hemipenes of *O. huahin* and *O. promsombuti*, we found that their organs are bilobed with large broad lobes, no distinct flounced

calyces and an unforked sulcus spermaticus (Pauwels et al. 2017, 2021). All of these characteristics resemble the hemipenial morphology observed in *O. cinereus* (Yushchenko et al. 2023a). Since the molecular and morphological evidence both point to the same conclusion, we formally assign *O. huahin*, *O. phangan*, *O. promsombuti* and *O. sai yok* to the *O. cinereus* species group.

Outside of these taxonomic decisions, we are unable to sort out the identities of the many lineages recovered in the *O. cinereus* species complex, and our results raise several issues that await further study. The most glaring is the non-monophyly between *O. joysoni* and *O. promsombuti*, and between *O. nagao* and *O. cinereus* clade 3. Both specimens of *O. joysoni* sampled for genetic data agree with the morphological diagnosis of that species by having a large number of ventral scales (>190) and a color pattern consisting of dark reticulations and narrow crossbars, with one specimen (KIZ 09128) described in detail by Jiang et al. (2012). It is puzzling that such a close relationship exists between the two species, since *O. joysoni* and *O. promsombuti* have significantly different color and scalational features and are separated from one another by a distance of ~650 km (see Table S3 and Fig. 1). However, the genetic samples obtained from the holotype of *O. promsombuti* consist of two short reads of 16S rRNA and *cyt b* respectively, and the internal node connecting the sample to the other two *O. joysoni* sequences could easily be overturned if longer DNA fragments, or additional topotypic material are obtained. Similarly, *O. nagao* also has several color and scale characteristics that differentiate it from populations assignable to *O. cinereus* clade 3, specifically a higher number of ventral scales and a distinct dorsal pattern consisting of large butterfly-shaped blotches (David et al. 2012; Jiang et al. 2012). Consequently, we are hesitant to adjust the taxonomic status of *O. joysoni*, *O. nagao*, and *O. promsombuti* until additional sampling and revisionary work on the *O. cinereus* species complex can be conducted.

Our study also supports the existence of a paraphyletic *O. “cinereus”*, with more than six species nested within or between each of its lineages. The inclusion of *O. huahin* and *O. phangan* within the *O. cinereus* species complex significantly affects each species’ morphological diagnosis because many of their scalation features now overlap with *O. “cinereus”* sensu lato (Table S3). We included two topotypic samples of *O. phangan* from Pha Ngan Island and two specimens (AUP TS2605 and CAS 213379) from Krabi Province, Thailand and Yangon, Myanmar, respectively, that cluster within the same clade. While these latter samples would seemingly extend the distribution of *O. phangan*, their morphologies do not precisely match the original description of the type specimens. For example, CAS 213379 is part of a series of *Oligodon* collected from Yangon Region, Myanmar, and all of these specimens have a faint reticulated dorsum with dark spots along the posterior portion of the venter. As a result, we conservatively identify the two non-topotypic samples as *O. cf. phangan* for the time being. At a minimum, our results indicate the morphological diagnoses that would normally distinguish *Oligodon* from one another fail to

accurately describe the lineage diversity found within *O. "cinereus"*. A clearer understanding of the species boundaries of the *O. cinereus* species complex will have to await denser sampling of genetic and morphological material.

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Supplementary Material 1

Appendices S1, S2

Authors: Pawangkhanant P, Poyarkov NA, Ward-Smith H, Grassby-Lewis R, Sumontha M, Kliukin NS, Idiiatullina SS, Trofimets AV, Suwannapoom C, Lee JL (2024)

Data type: .pdf

Explanation notes: **Appendix S1.** List of referred *Oligodon* specimens examined for comparative morphological analysis. — **Appendix S2.** Expanded phylogeny of *Oligodon* excluding outgroup genera showing relationships of species outside of the *O. cinereus* species complex.

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Supplementary Material 2

Tables S1–S4

Authors: Pawangkhanant P, Poyarkov NA, Ward-Smith H, Grassby-Lewis R, Sumontha M, Kliukin NS, Idiiatullina SS, Trofimets AV, Suwannapoom C, Lee JL (2024)

Data type: .pdf

Explanation notes: **Table S1.** List of sequences and corresponding voucher specimens of *Oligodon* and outgroup taxa used in this study. — **Table S2.** Primers for PCR and sequencing used in this study. — **Table S3.** Morphological comparisons between *Oligodon speleoserpens* **sp. nov.** and other species of *Oligodon* native to Thailand. — **Table S4.** Genetic differentiation of *Oligodon* within the *O. cinereus* species complex.

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