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A taxonomic re-assessment of *Oligodon cinereus* (Günther, 1864) (Squamata, Serpentes, Colubridae) populations from southern Indochina

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Abstract

The ashy kukri snake *Oligodon cinereus* (Günther, 1864) is a widely distributed and morphologically variable species found throughout mainland Southeast Asia. In this paper, we re-assessed the taxonomic status of *O. cinereus* populations found in southern Indochina (southern Vietnam, Cambodia, and southern Laos), including the recently described Cat Tien kukri snake *Oligodon cattienensis* Vassilieva et al., 2013, which was previously confused with this species. Phylogenetic analyses using mitochondrial DNA from the 12S–16S ribosomal subunit and cytochrome *b* gene revealed that *O. cattienensis* is embedded in a mixed clade containing samples of the subspecies *O. cinereus pallidocinctus*, which bears a dorsal color pattern with white crossbars and black edges. This clade forms a strongly supported sister group with a topotypic sample of *O. cinereus cinereus*, representing populations bearing a uniform dorsal color pattern and slight reticulate markings, however the genetic divergence between the two clades is very low. The morphological characters used to distinguish *O. cattienensis* from *O. cinereus* sensu lato broadly overlap and supposed differences in hemipenial morphology between the two taxa are due to outdated terminologies used to describe the organ. We relegate both *O. cattienensis* and *O. cinereus pallidocinctus* to the junior synonymy of *O. cinereus* and consider all color patterns of this species found near the type locality in Cambodia, southern Laos, and southern Vietnam to represent *O. cinereus* sensu stricto. Future integrative investigations across the range of *O. cinereus* sensu lato are needed to resolve the status of the remaining subspecies and synonyms associated with this taxon. Problems associated with hemipenial morphology and *Oligodon* systematics are also discussed.

Keywords

Biodiversity, morphology, *Oligodon cattienensis*, Reptilia, Southeast Asia, systematics

Introduction

Kukri snakes of the genus *Oligodon* Fitzinger, 1826 are a highly diverse group of colubrid snakes distributed across Asia presently containing 90 recognized species (Nguyen et al. 2022; Uetz et al. 2022), making it the second largest snake genus in the world, exceeded only by the neotropical earthsnake genus *Atractus* Wagner, 1828 (Arteaga et al. 2022; Passos et al. 2022; Uetz et al. 2022). Despite being one of the most species-rich snake clades in the world, most members are poorly studied because of their secretive behavior. In the past decade, several new species of *Oligodon* have been described, but most are based on a small number of specimens (David et al. 2012, 2022; David and Vogel 2012; Neang et al. 2012; Vassilieva et al. 2013; Vassilieva 2015; Nguyen et al. 2016, 2017, 2022; Pauwels et al. 2017; Sumontha et al. 2017; Nguyen et al. 2020; Amarasinghe et al. 2021; Mirza et al. 2021; Pauwels et al. 2021; Bandara et al. 2022). Moreover, a majority of recently described kukri snakes have been diagnosed based exclusively on morphology without the incorporation of tissue samples for molecular phylogenetic analyses. Since it is oftentimes difficult to obtain large sample sizes of specimens, the species boundaries of several *Oligodon* remain unclear, and some historically described taxa have been re-assessed and subsequently synonymized with other wide-ranging, morphologically variable species (e.g., Tillack 2008; Tillack and Günther 2009). In this paper, we provide a re-assessment of the widely distributed and phenotypically variable species, the ashy kukri snake *Oligodon cinereus* (Günther, 1864), focusing on southern Indochinese populations (herein defined as Cambodia, Laos, and southern Vietnam).

O. cinereus exhibits a wide distribution including northern and eastern India, Bhutan, Myanmar (Burma), southern China (including Hong Kong), Vietnam, Laos, Cambodia, before ending in Thailand and possibly Malaysia (Green 2010; Uetz et al. 2022). The species was first described based on an adult male specimen collected from "Gamboja" (= Cambodia), which displays a dorsal color pattern that is uniform brown and gray (Günther 1864). Since its description, additional names have been allocated to this species, and *O. cinereus* is currently considered to be a morphologically variable snake with several different color patterns known across its range. Some of these have been recognized as distinct subspecies, whereas others are currently considered junior synonyms (Smith 1943; Wagner 1975; Green 2010; David et al. 2011). Within southern Indochina, *O. cinereus* is thought to have two different color patterns. The first has

Figure 1. Members of *Oligodon cinereus* sensu stricto showing live coloration, labelled according to their OTUs. **A** *Oligodon cinereus cinereus*, CBC 02891, adult male from Kirirom National Park, Kreang, Kampong Speu Province, Cambodia; **B** *Oligodon cattienensis*, CBC 02954, adult male from Prey Lang Wildlife Sanctuary, Stung Treng Province, Cambodia; **C** *Oligodon cinereus pallidocinctus*, ZMMU Re-13586, adult male from Loc Bao, Lam Dong Province, Vietnam; and **D** *Oligodon cattienensis*, ZFMK 88921, subadult paratype of *Oligodon cattienensis* from Nam Cat Tien National Park, Dong Nai Province, Vietnam. Photos by Neang Thy (A–B), Eduard A. Galoyan (C), and Peter Geissler (D).

been recognized as nominotypical *O. cinereus*, which all bear a uniform brown or gray dorsum with small darker reticulated markings across the body (Fig. 1A). Specimens with this pattern are known throughout Cambodia (Günther 1864; Saint Girons 1972), and outside of southern Indochina in Myanmar, Thailand, central/north Laos, and northern Vietnam (Smith 1943; Taylor 1965; Deuve 1970; David et al. 2011). The second was described as *Simotes violaceus pallidocinctus* Bourret, 1934 and is occasionally recognized as a subspecies by some authors (Taylor 1965; David et al. 2022). For the sake of consistency, we shall use the subspecific combinations of both color patterns herein. Specimens referable to *Oligodon cinereus pallidocinctus* bear a color pattern with narrow white crossbars and dark brown/black edges across the dorsum (Fig. 1C). This name was first described from “Cochinchine” (= southern Vietnam) and appears to be restricted to southern Indochina, although specimens resembling this color pattern have also been found in Myanmar (Lee et al. unpublished data).

Additionally, the recently described Cat Tien kukri snake *Oligodon cattienensis* Vassilieva et al., 2013 was previously confused with *O. cinereus*. This taxon was first discovered in Cat Tien National Park, Dong Nai Province, Vietnam and was originally identified as *Oligodon* cf. *cinereus* based on similar scalation traits (Geissler et al. 2011) (Fig. 1B, D). After more specimens were collected from the same area, Vassilieva et al. (2013) determined that they represented a distinct species and described them as *O. cattienensis*. Based on hemipenial morphology, Vassilieva et al. (2013) placed *O. cattienensis* in the *O. cyclurus* species group due to the organ being “forked… lacking spines or papillae”, whereas *O. cinereus* and other members of the *O. cinereus* species group have unforked hemipenes with large “papillae”-like appendages visible on the organ when retracted in-situ. When directly compared to *O. cinereus*, the authors stated that *O. cattienensis* differs from this species by having “an entire nasal, by a head bearing prominent dark markings [temporal bars, chevron, interocular bar], and a red ventral coloration in juveniles [white to yellowish cream in *O. cinereus*].” Vassilieva et al. (2013) also compared *O. cattienensis* with specimens matching the color pattern of the subspecies *O. cinereus pallidocinctus*, which co-occurs in Cat Tien National Park. Although the differences in color pattern between *O. cattienensis* appear to be significant from adjacent populations of *O. cinereus*, Vassilieva et al. (2013) mostly relied on literature descriptions to obtain morphological data from other *Oligodon* and did not directly compare their new species with specimens of *O. cinereus* collected from areas outside of Cat Tien National Park. Furthermore, Vassilieva et al. (2013) did not perform molecular analyses on their new species, which could have clarified the status of the two sympatric *Oligodon* morphotypes co-occurring in the national park and adjacent regions.

Since 2013, we have discovered additional kukri snake specimens resembling the color patterns of *O. cattienensis*, *O. cinereus cinereus*, and *O. cinereus pallidocinctus* from southern Vietnam and adjacent Cambodia. Some of these specimens were discovered during recent field expeditions or were collected and deposited in natural history collections many years before the description of *O. cattienensis* was published. To shed light on the taxonomic status of these specimens, we carefully compared their morphology with the name-bearing types of *O. cattienensis*, *O. cinereus cinereus*, and *O. cinereus pallidocinctus*. We also sequenced mitochondrial DNA from recently collected specimens to determine their phylogenetic position amongst other members of the *O. cinereus* species group and the *O. cyclurus* species group. Our results recover substantial genetic and morphological overlap between *O. cattienensis*, *O. cinereus cinereus*, and *O. cinereus pallidocinctus*, suggesting that all three taxa are conspecific with one another. Consequently, we consider *O. cattienensis* and *O. cinereus pallidocinctus* to represent junior synonyms of *O. cinereus* herein.

Methods

Sampling and species delimitation

We examined preserved specimens of *O. cattienensis* and *O. cinereus* from natural history collections and sampled corresponding tissue samples for genomic DNA when available. For molecular analyses, we sequenced mitochondrial DNA from seven specimens resembling the color pattern of *O. cattienensis* (including the holotype), one specimen resembling the color pattern of topotypic *O. cinereus cinereus*, and six specimens of *O. cinereus pallidocinctus* preserved in different natural history collections (Appendix 1). In addition, we acquired two samples morphologically identified as *Oligodon joynsoni* (Smith, 1917) and *Oligodon inornatus* Boulenger, 1914, and 35 sequences of other *Oligodon* available on GenBank (see Table 1 for sources of each sequence). Geographic locations of the examined populations are shown in Fig. 2. We were not able to examine all GenBank samples of *Oligodon* for morphological data but re-identified one sample labeled as *O. cinereus* (HM591504, specimen voucher ROM 37092) reported by Green et al. (2010). These authors briefly described this specimen in their paper, and based on this information plus the collection locality, we are confident that this specimen matches the color pattern found in *O. cinereus pallidocinctus* and allocate the sample and specimen to this taxon. The phylogenetic position of *Oligodon* amongst other colubrid genera is poorly known (Green et al. 2010; Figueroa et al. 2016). We therefore chose one sequence each of *Oreocryptophis porphyraceus* (Cantor, 1839) (subfamily Colubrinae) and *Hebius vibakari* (Boie, 1826) (subfamily Natricinae) as outgroups because of their use in previous phylogenies (Nguyen et al. 2020).

We examined the morphology of 37 specimens of *O. cattienensis* and *O. cinereus* preserved in natural history collections (Appendix 1). We separated specimens into three different Operational Taxonomic Units (OTUs)

Table 1. List of sequences and corresponding voucher specimens of *Oligodon* and outgroup taxa used in this study. Note that the numbers (column one) included in this table do not match the numbers used in Appendix I and Fig. 2. Acronyms not described in the materials and methods include the following: CHS, unknown field tag series; RAP, field tags of R. Alexander Pyron; RS, field tags of Ruchira Somaweera; NP, National Park; NR, Nature Reserve.

No.	Sample ID	GenBank Accession No.	Species/OTU	Country	Locality	Reference
1	ZMMU Re-13815	OP752578, OP752593	*Oligodon cattienensis*	Vietnam	Dong Nai Prov., Cat Tien NP	this work
2	ZMMU Re-13866	OP752579, OP752594	*Oligodon cattienensis*	Vietnam	Dong Nai Prov., Cat Tien NP	this work
3	ZMMU Re-13865	OP752580, OP752595	*Oligodon cattienensis*	Vietnam	Dong Nai Prov., Cat Tien NP	this work
4	CBC02958	OP752581, OP752596	*Oligodon cattienensis*	Cambodia	Stung Treng Prov., Spong village	this work
5	SIEZC20209	OP752582, OP752597	*Oligodon cattienensis*	Vietnam	Dak Lak Prov., Yok Don NP	this work
6	FMNH262190	OP752583, OP752598	*Oligodon cattienensis*	Vietnam	Dong Nai Prov., Cat Tien NP	this work
7	ZMMU Re-13443	OP752589, OP752604	*Oligodon cinereus pallidocinctus*	Vietnam	Binh Phuok Prov., Bu Gia Map NP	this work
8	ZMMU Re-13946	OP752590, OP752605	*Oligodon cinereus pallidocinctus*	Vietnam	Lam Dong Prov., Loc Bao	this work
9	ZMMU Re-13586	OP752591, OP752606	*Oligodon cinereus pallidocinctus*	Vietnam	Dong Nai Prov., Cat Tien NP	this work
10	ZMMU Re-13271	OP752592, OP752607	*Oligodon cattienensis*	Vietnam	Lam Dong Prov., Bidoup–Nui Ba NP	this work
11	FMNH259201	OP752584, OP752599	*Oligodon cinereus pallidocinctus*	Cambodia	Mondolkiri Prov., Pichrada Dist.	this work
12	CBC02891	OP752585	*Oligodon cinereus cinereus*	Cambodia	Kampong Speu Prov., Kirirom NP	this work
13	DTU 500 (=BT.2019.3)	OP752586, OP752601	*Oligodon cinereus pallidocinctus*	Vietnam	Binh Thuan Prov., Phan Thiet, Ma Lam	this work
14	CBC01701	OP752587, OP752602	*Oligodon inornatus*	Cambodia	Pursat Prov., Samkos WS	this work
15	ZMMU Re-16480	OP752588, OP752603	*Oligodon joynsoni*	Thailand	Chiang Rai Prov., Doi Tung	this work
16	ROM37092	HM591504	*Oligodon cinereus pallidocinctus*	Vietnam	Dong Nai Prov., Cat Tien NP	Green et al. (2010)
17	CAS205028	HM591507	*Oligodon cinereus* sensu lato	Myanmar	Rakhine St., Rakhine Yoma Mts.	Green et al. (2010)
18	ROM32462	HM591501	*Oligodon cinereus* sensu lato	Vietnam	Hai Duong Prov., Chi Linh	Green et al. (2010)
19	ROM29552	HM591502	*Oligodon cinereus* sensu lato	Vietnam	Vinh Phuc Prov., Tam Dao NP	Green et al. (2010)
20	ROM30969	HM591503	*Oligodon cinereus* sensu lato	Vietnam	Nghe An Prov., Pu Mat NP	Green et al. (2010)
21	CAS215261	HM591508	*Oligodon cinereus* sensu lato	Myanmar	Shan St., Kalaw	Green et al. (2010)
22	UMMZ201913	HM591519	*Oligodon octolineatus*	Brunei	Tutong Dist., 3 km E of Tutong	Green et al. (2010)
23	ROM 35626	HM591526	*Oligodon chinensis*	Vietnam	Cao Bang Prov., Quang Thanh	Green et al. (2010)
24	ROM35629	HM591533	*Oligodon formosanus*	Vietnam	Cao Bang Prov., Quang Thanh	Green et al. (2010)
25	ROM32261	HM591534	*Oligodon ocellatus*	Vietnam	Dak Lak Prov., Yok Don NP	Green et al. (2010)
26	ROM32260	HM591521	*Oligodon taeniatus*	Vietnam	Dak Lak Prov., Yok Don NP	Green et al. (2010)
27	ROM32464	HM591523	*Oligodon barroni*	Vietnam	Gia Lai Prov., Krong Pa	Green et al. (2010)
28	CAS204963	HM591535	*Oligodon cyclurus*	Myanmar	Ayeyarwady Div., Mwe Hauk	Green et al. (2010)

No.	Sample ID	GenBank Accession No.	Species/OTU	Country	Locality	Reference
29	CAS204855	HM591509	*Oligodon splendidus*	Myanmar	Mandalay Div., Kyauk Se	Green et al. (2010)
30	CAS215976	HM591513	*Oligodon torquatus*	Myanmar	Mandalay Div., Min Gone Taung WS	Green et al. (2010)
31	CAS213822	HM591514	*Oligodon planiceps*	Myanmar	Magwe Div., Shwe Set Taw WS	Green et al. (2010)
32	CAS213896	HM591516	*Oligodon theobaldi*	Myanmar	Magwe Div., Shwe Set Taw WS	Green et al. (2010)
33	CAS213271	HM591517	*Oligodon cruentatus*	Myanmar	Yangon Div., Hlaw Ga NP	Green et al. (2010)
34	ROM27049	HM591518	*Oligodon eberhardti*	Vietnam	Cao Bang Prov., Quang Thanh	Green et al. (2010)
35	TNHC59846	HM591511	*Oligodon maculatus*	Philippines	Mindanao, Barangay Baracatan	Green et al. (2010)
36	SIEZC 20201	MN395604; MN396765	*Oligodon rostralis*	Vietnam	Lam Dong Prov., Bidoup – Nui Ba NP	Nguyen et al. (2020)
37	ZMMU Re-14304	MN395601; MN396762	*Oligodon annamensis*	Vietnam	Dak Lak Prov., Chu Yang Sin NP	Nguyen et al. (2020)
38	RS-OC	KC347328; KC347366	*Oligodon calamarius*	Sri Lanka	Kandy Dist.	Pyron et al. (2013)
39	RAP 504	KC347329; KC347367	*Oligodon sublineatus*	Sri Lanka	Kandy Dist.	Pyron et al. (2013)
40	RAP 483	KC347327; KC347365	*Oligodon arnensis*	Sri Lanka	Hambantota Dist.	Pyron et al. (2013)
41	RS 136	KC347330; KC347368	*Oligodon taeniolatus*	Sri Lanka	Polonnaruwa Dist.	Pyron et al. (2013)
42	NCBS NRC-AA-019	MZ675817	*Oligodon churahensis*	India	Himachal Pradesh Prov., Chamba distr.	Mirza et al. (2021)
43	KIZ014591	MW090140; MW133297	*Oligodon nagao*	China	Guangxi, Longzhou County, Nonggang National NR	Xu et al. (2021)
44	KIZ011002	MW090139; MW133296	*Oligodon lipipengi*	China	Tibet, Medok	Che et al. (2020)
45	CHS190	MK193970; MK201321; MK065403	*Oligodon* cf. *nagao*	China	Hainan Isl.	Li et al. (2020)
46	CHS850	MK194265; MK201568; MK065694	*Oligodon albocinctus*	China	Yunnan Prov., Gongshan	Li et al. (2020)
47	CHS668	MK194135; MK201461; MK065563	*Oligodon fasciolatus*	China	Yunnan Prov.	Li et al. (2020)
48	CHS304	MK194038; MK201386; MK065470	*Oligodon lacroixi*	China	Jiangxi Prov., Jinggangshan	Li et al. (2020)
49	CHS683	MK194147; MK065575	*Oligodon ornatus*	China	–	Li et al. (2020)
50	SYNU 1907027	MW489824	*Oligodon bivirgatus*	China	Hainan, Shangxi NR	Qian et al. (2021)
Outgroups						
51	—	KP684155	*Hebius vibakari*	—	—	—
52	—	GQ181130	*Oreocryptophis porphyraceus*	—	—	—

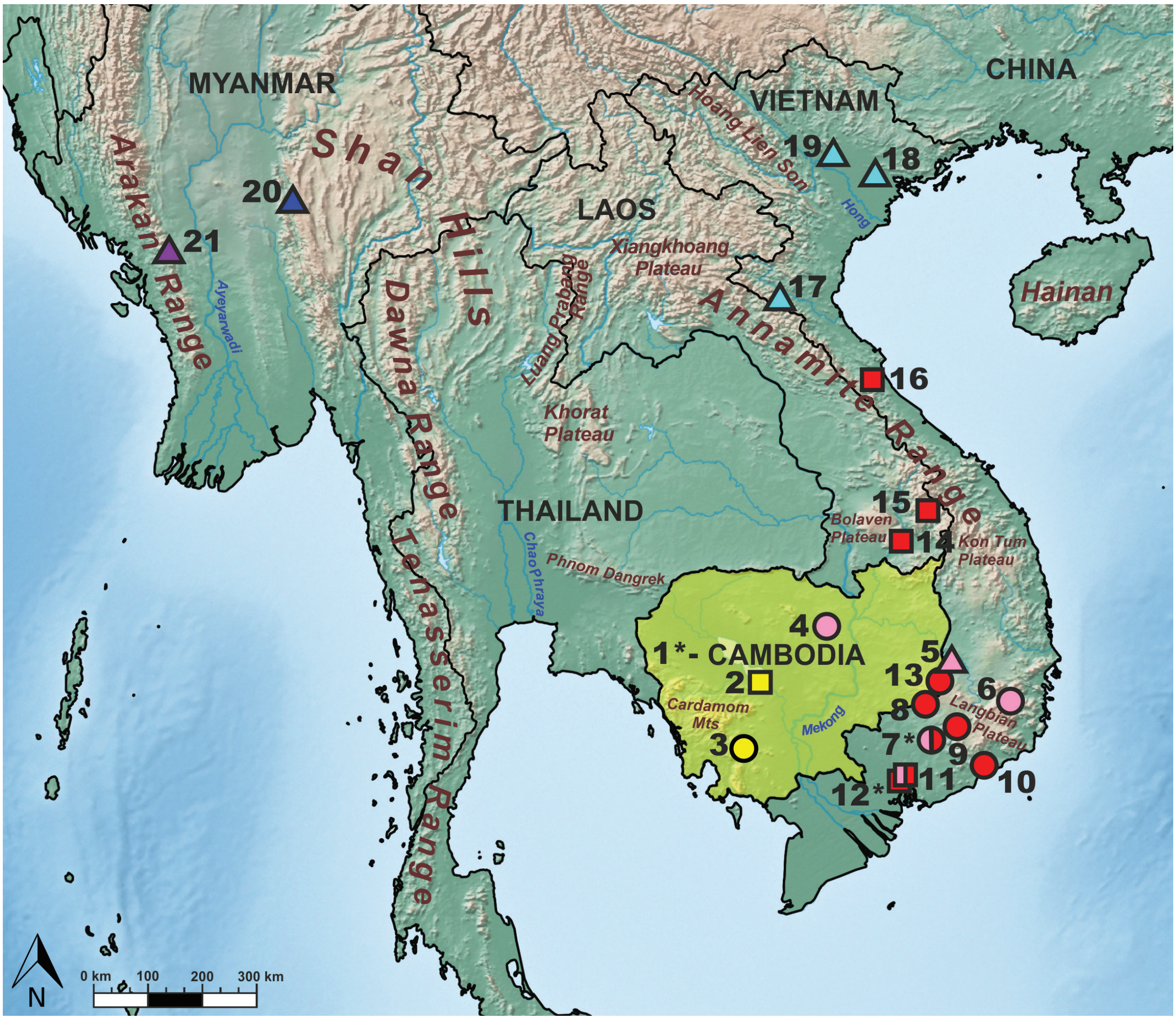

Figure 2. Known distribution of topotypic *Oligodon cinereus cinereus* (yellow), *Oligodon cattienensis* (pink), *Oligodon cinereus pallidocinctus* (red) and other lineages of *Oligodon cinereus* sensu lato (see color matching in Fig. 3) in Indochina. Triangle icons denote specimens with only molecular data; square icons denote specimens with only morphological data; and round icons denote specimens with both molecular and morphological data. Stars/asterisks next to numbers indicate type localities. Localities: **1** Cambodia (without further specification, type locality of *Oligodon cinereus*); **2** Trapeang Chan, Kampong Chhnang Prov., Cambodia; **3** Kirirom NP, Kreang, Kampong Speu Prov., Cambodia; **4** Prey Lang WS, Stung Treng Prov., Cambodia; **5** Yok Don NP, Dak Lak Prov., Vietnam; **6** Bidoup – Nui Ba NP, Lam Dong Prov., Vietnam; **7** Cat Tien NP, Dong Nai Prov., Vietnam (type locality of *Oligodon cattienensis*); **8** Bu Gia Map NP, Binh Phuoc Prov., Vietnam; **9** Loc Bao forest, Lam Dong Prov., Vietnam; **10** Ma Lam Phan Thiet, Binh Thuan Prov., Vietnam; **11** Bien Hoa, Dong Nai Prov., Vietnam; **12** Ho Chi Minh city, Vietnam (type locality of *Simotes violaceus pallidocinctus*); **13** Pichrada Distr., Mondolkiri Prov., Cambodia; **14** Attapu, Attapu Province, Laos; **15** Dak Cheung, Sekong Prov., Laos; **16** Phong Nha – Ke Bang NP, Quang Binh Prov., Vietnam; **17** 24 km W of Con Cuong, Nghe An Prov., Vietnam; **18** Chi Linh, Hai Duong, Vietnam; **19** Tam Dao NP, Vinh Phuc Prov., Vietnam; **20** Arakan Range (formerly 'Rakhine Yoma Mountain Range'), Rakhine State, Myanmar; **21** Kalaw township, Shan State, Myanmar.

a priori and classified specimens based on type status, matching color pattern descriptions, and geographic distribution. The OTUs include: 1) *Oligodon cattienensis* (n=11), including the type series, topotypic material and referred specimens bearing large dark-edged blotches and red ventral coloration in juveniles; 2) nominotypical *Oligodon cinereus cinereus* (n=7), including topotypic specimens found within Cambodia bearing a uniform or slightly reticulated dorsum; and 3) specimens referrable to the subspecies *Oligodon cinereus pallidocinctus* (n=19), which bear white crossbars with black or dark-brown edges across the dorsum (Tables 1, 5). We note that in our conclusion, we consider all three of these taxa as synonyms of *O. cinereus* sensu stricto by the end of this paper but continue to use their subspecific names throughout the text. Furthermore, because our focus was to compare southern Indochinese populations of *O. cinereus* and *O. cattienensis*, we refrained from including material found outside of Cambodia, southern Laos, and southern Vietnam in the morphological analyses. A complete taxonomic revision of *O. cinereus* is beyond the scope of this paper (see Discussion).

Table 2. Primers for PCR and sequencing used in this study.

Gene	Primer name	Reference	Sequence
12S-rRNA	12S2LM	Green et al. (2010)	`5′ -ACACACCGCCCGTCACCCT-3′`
	16S5H	Green et al. (2010)	`5′ -CTACCTTTGCACGGTTAGGATACCGCGGC-3′`
16S-rRNA	16S1LM	Green et al. (2010)	`5′ -CCGACTGTTGACCAAAAACAT-3′`
	16SH1	Green et al. (2010)	`5′ -CTCCGGTCTGAACTCAGATCACGTAGG-3′`
cyt *b*	H14910	Dahn et al. (2018)	`5′ -GACCTGTGATMTGAAAAACCAYCGTT-3′`
	THRSN2	Dahn et al. (2018)	`5′ -CTTTGGTTTACAAGAACAATGCTTTA-3′`

For all aspects of species concepts and delimitation, we follow the General Lineage Concept (sensu De Queiroz 2007), where a species represents a single evolutionarily independent lineage following a separate trajectory compared to its relatives. We specifically delimit evolutionary independence when lineages are reciprocally monophyletic, exhibit substantial genetic divergence, and are morphologically diagnosable. Museum and other natural history collection acronyms are provided as follows: CAS: California Academy of Sciences, San Francisco, USA; CBC: Centre for Biodiversity Conservation of the Royal University of Phnom Penh, Phnom Penh, Cambodia; DTU: Duy Tan University, Da Nang City, Vietnam; FMNH: The Field Museum, Chicago, USA; IEBR: Institute of Ecology and Biological Research, Hanoi, Vietnam; KIZ: Kunming Institute of Zoology, Chinese Academy of Sciences, Kunming, Yunnan, China; MNHL: Muséum d'Histoire naturelle de Lyon, Lyon, France; MNHN: Muséum National d'Histoire Naturelle, Paris, France; NCBS: National Center for Biological Sciences, Bangalore, India; NHMUK: Natural History Museum, London, UK (formerly BMNH); ROM: Royal Ontario Museum, Toronto, Canada; SIEZC: Southern Institute of Ecology, Ho Chi Minh City, Vietnam; SYNU: Shenyang Normal University, Shenyang, China; TNHC: Texas Natural History Collections, Austin, USA; UMMZ: University of Michigan Museum of Zoology, Ann Arbor, USA; T.Ziegler: personal collection of Thomas Ziegler, Cologne, Germany; USNM: National Museum of Natural History, Smithsonian Institution, Washington, USA; ZFMK: Zoologisches Forschungsmuseum Alexander Koenig, Bonn, Germany; ZMA: Zoölogisch Museum Amsterdam, Amsterdam, The Netherlands (now included in the Naturalis Biodiversity Center, Leiden, Netherlands; RMNH); ZMMU: Zoological Museum of Lomonosov Moscow State University, Moscow, Russia.

Molecular analyses

We extracted total genomic DNA from muscle tissue preserved in 95% ethanol using a Qiagen DNAeasy Blood and Tissue Kit following manufacturer's protocol. We performed polymerase chain reactions (PCR) to amplify two fragments of mitochondrial DNA (hereafter mtDNA): the first fragment including partial sequences of 12S ribosomal RNA (rRNA), tRNA-Valine and 16 rRNA genes (12S–16S rRNA) (total length up to 1941 bp) and a complete sequence of the cytochrome *b* gene (cyt *b*) (1,091 bp). Primers used for both PCR and sequencing are summarized in Table 2. PCR protocols for amplifying the 12S–16S rRNA mtDNA fragment roughly follow Green et al. (2010). For both primer pairs of 12S and 16S rRNA, we used the following PCR protocol: (1) initial denaturation step at 94ºC for 5 min; (2) 35 cycles of denaturation at 94ºC for 1 min, annealing at 55ºC for 1 min and extension at 72ºC for 1 min; (3) final extension at 72ºC for 10 min; and (4) cooling step at 4ºC for storage. For cyt *b* sequences (fragment up to 1,096 bp) we used a modified PCR protocol of Dahn et al. (2018) with touchdown: (1) initial denaturation step at 94ºC for 5 min; (2) 10 cycles of denaturation at 94ºC for 1 min, annealing for 1 min with temperature decreasing from 50ºC to 45ºC (with cool-down at 0.5ºC per each cycle) and extension at 72ºC for 1 min; (3) 24 cycles of denaturation at 94ºC for 1 min, annealing at 45ºC for 1 min and extension at 72ºC for 1 min; (4) final extension at 72ºC for 10 min; and (5) cooling step at 4ºC for storage. Successful targeted PCR products were outsourced to Evrogen® (Moscow, Russia) for PCR purification and sequencing. The obtained sequences are deposited in GenBank under the accession numbers OP752578–OP752607 (Table 1).

Our newly obtained sequences of mtDNA and other *Oligodon* sequences available in GenBank were used to examine the position of *O. cattienensis* in a matrilineal genealogy of the genus (summarized in Fig. 3). In total, we analyzed mtDNA sequence data for 52 specimens, including 50 samples of approximately 32 species of *Oligodon*, and outgroup sequences of *O. porphyraceus* and *H. vibakari*. Nucleotide sequences were initially aligned in MAFFT v.6 (Katoh et al. 2002) with default parameters, then subsequently checked by eye in BioEdit 7.0.5.2 (Hall 1999) and slightly adjusted for translation when appropriate. MODELTEST v.3.6 (Posada and Crandall 1998) was applied to the alignment to estimate optimal evolutionary models for the dataset analyses under the Akaike Information Criterion (AIC). Mean uncorrected genetic distances (p-distances) were calculated in MEGA 6.0 (Tamura et al. 2013). The matrilineal genealogy was inferred using Bayesian inference (BI) and Maximum Likelihood (ML) approaches. ML was conducted using the IQ-TREE 1.6.10 (Nguyen et al. 2015). Confidence in nodal topology was estimated by non-parametric bootstrapping (ML BS) with 1000 pseudoreplicates (Felsenstein 1985). BI was conducted in MrBayes 3.1.2 (Ronquist and Huelsenbeck 2003); Metropolis-coupled Markov chain Monte Carlo (MCMCMC) analyses were performed run with one cold chain and three heated chains for one million generations and sampled every 1000 generations. Five independent MCMCMC run iterations were performed and 1000 trees were discarded as burn-in. The convergence of the runs was checked by examining the likelihood plots in TRACER v1.6 (Rambaut et al. 2014); the effective sample sizes (ESS) were all above 200. Nodal support was assessed by calculating posterior probabilities (BI PP). The best-fitting model for both BI and ML analyses of the 12S–16S rRNA fragments suggested by the AIC was the GTR+G+I model. For cyt *b*, following the AIC, the GTR+G model was used for the first codon partition, the GTR+G+I for the second codon partition and the HKY+G+I for the third codon partition. We a priori regarded tree nodes with BI PP values over 0.95 and ML BS values 75% or greater as sufficiently resolved, while BI PP values between 0.95 and 0.90 and ML BS values between 75% and 50% were regarded as tendencies. Lower values were regarded as indicating unresolved nodes (Huelsenbeck and Hillis 1993)**.**

Morphological analyses

Sex was determined by a ventral insertion near the tail base to look for the presence or absence of hemipenes. Body measurements such as Snout-Vent-Length (SVL), Tail Length (TailL) and Total Length (TotalL) were taken by straightening preserved specimens along a flexible ruler. Dorsal scales were counted anteriorly at one head length behind the head, at midbody, namely halfway between the terminus of the head and the vent, and posteriorly at one head length anterior to the cloacal plate (given as anterior–midbody–posterior in the description); ventral scales were counted according to Dowling (1951); the tail tip was not included in the number of subcaudal scales; counts for head scales are given in left/right order. The number of total body scales is the sum of the number of ventral scales, the cloacal plate (considered a single scale regardless of whether it is single or divided), and the number of subcaudal scales. When male specimens had their hemipenes everted or partially everted during preservation, their organs were examined and described in detail. Hemipenial terminology follows Dowling and Savage (1960) unless otherwise noted.

We adapted a data analysis workflow popularized by Chan and Grismer (2021) to determine whether significant differences in morphology exist between the three OTUs. All statistical analyses were conducted in R version 4.1.2 (R Core Team 2022). We used Shapiro-Wilks Tests and Levene's Tests to evaluate whether morphological characters in the dataset follow assumptions of normality and homoscedasticity, respectively. Because most of the characters used in the dataset failed these assumptions, we elected to use non-parametric tests for the remaining data analyses. These tests offer a more conserved approach for discerning morphological differentiation between taxa. First, we used a Kruskal-Wallis Test (the non-parametric alternative to ANOVA) to evaluate whether morphological characters in the dataset contained significant differences. In addition, we performed Mann-Whitney U tests between males and females to evaluate whether any characters exhibited sexual dimorphism in our entire dataset. Sample sizes were too low to test for dimorphism in morphological characters within each OTU. In all univariate tests, differences between characters were determined to be statistically significant when $p < 0.05$. After univariate analysis, we log-transformed the dataset and conducted a Principal Components Analysis (PCA) using the *prcomp*() command in R on the remaining residuals to determine whether there was visible structure in the morphological variation observed in each OTU. All data used in the PCA were scaled to standard deviation to help eliminate the effects of covariance and ensure the data was distributed normally. The following ten morphological characters were used for univariate and multivariate statistical analyses (abbreviations in parentheses): TailL/TotalL ratio (TAILR), midbody dorsal scale rows (MSR), ventrals (VEN), subcaudals (SC), total body scales (TOTAL), subcaudal ratio (SCR), supralabials (SL), number of supralabials in contact with the eye (SLE), infralabials (IL), number of infralabials in contact with the anterior chin shields (ILCS), and the number of anterior temporal scales (AT).

Results

Molecular analyses

The final concatenated alignment containing both the 12S–16S rRNA fragment and cyt *b* gene sequences contained 3032 base pairs, of which, 1759 sites were conserved, 1242 sites were variable, and 858 were found to be parsimony informative. The transition-transversion bias I was estimated as 1.3. Nucleotide frequencies were 37.4% (A), 23.0% (T), 25.1% (C), and 14.5% (G)**.** The uncorrected p-distances for the 12S–16S rRNA fragment among examined *Oligodon* species is presented in Table 3. The interspecific genetic distances within examined *Oligodon* varied significantly and ranged from p=0.2% between *O.* cf. *cinereus* clade 4 (sensu Li et al. 2020) and *Oligodon nagao* David et al., 2012, to p=9.0% between *Oligodon barroni* (Smith, 1916) and *O. inornatus* (Table 3). The dramatic degree of genetic differentiation (very high and very low genetic distances) between some species could reflect incomplete taxonomic sampling of *Oligodon* within the phylogeny (Green et al. 2010; David et al. 2011, 2012).

The phylogenetic relationships within the genus *Oligodon* inferred by our mtDNA-based analyses (Fig. 3) are generally consistent with the results of previous authors (Green et al. 2010; Nguyen et al. 2020; Mirza et al. 2021). Both the ML and BI trees show five well supported clades, one of which resembles the morphologically defined *Oligodon cinereus* species group (*sensu* Smith 1943; Wagner 1975; Green et al. 2010; David et al. 2011). The specimens of *O. cattienensis* were recovered within the *Oligodon cinereus* species group and all clustered

Table 3. Mean uncorrected genetic p-distances (percentage) of 12S–16S rRNA sequences between (below diagonal) and within (diagonal, bold font) the species and lineages of the *Oligodon cinereus* species group and other *Oligodon* taxa included in this study. *Oligodon cinereus* s. s. includes samples from *O. cattienensis*, *O. c. cinereus* and *O. c. pallidocinctus* OTUs.

	Species	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**	**25**	**26**	**27**	**28**	**29**	**30**	**31**	**32**	**33**	**34**
1	*O. cinereus* s.s.	**0.3**																																	
2	*O. inornatus*	2.0	—																																
3	*O. joynsoni*	2.6	2.9	—																															
4	*O. arnensis*	5.9	7.2	7.2	—																														
5	*O. taeniolatus*	4.6	5.5	6.2	5.5	—																													
6	*O. chinensis*	6.2	7.5	7.8	5.8	6.4	—																												
7	*O. formosanus*	5.4	7.0	6.9	4.8	5.5	1.3	—																											
8	*O. annamensis*	4.4	6.2	6.2	5.3	5.9	5.3	4.4	—																										
9	*O. rostralis*	6.3	7.7	7.8	6.2	6.2	4.6	4.2	3.7	—																									
10	*O. cyclurus*	4.8	6.8	6.5	7.9	7.1	6.4	6.0	5.5	6.0	—																								
11	*O. calamarius*	7.1	6.8	6.9	6.5	4.4	7.0	6.2	6.2	7.0	7.5	—																							
12	*O. sublineatus*	5.1	6.1	6.3	5.5	3.6	6.7	5.8	5.4	6.7	7.2	3.1	—																						
13	*O. eberhardti*	5.4	6.0	6.7	6.0	6.2	6.4	6.0	5.7	6.8	7.7	6.6	5.4	—																					
14	*O. splendidus*	3.6	4.4	4.7	6.5	4.8	5.9	5.9	6.4	7.0	6.2	5.7	4.9	6.2	—																				
15	*O. cinereus* 1	3.5	3.2	3.4	7.3	5.6	6.9	6.5	6.1	7.6	6.3	6.7	6.2	5.8	4.2	—																			
16	*O. cinereus* 2	2.4	2.2	2.4	6.2	4.6	6.2	5.7	5.1	6.6	5.5	5.5	4.9	4.9	2.9	1.7	—																		
17	*O. cinereus* 3	3.4	2.9	3.6	7.2	5.5	6.9	6.4	5.8	7.1	6.4	6.0	5.4	5.5	4.4	3.1	1.5	—																	
18	*O. torquatus*	4.4	5.9	5.6	6.5	6.4	7.3	6.4	5.1	7.0	6.6	7.3	7.0	6.4	5.7	5.6	4.4	5.5	—																
19	*O. planiceps*	4.6	6.2	5.6	7.2	5.9	7.3	6.4	5.9	7.0	7.3	6.2	6.5	7.3	5.3	5.9	4.6	5.3	3.3	—															
20	*O. theobaldi*	3.4	5.1	4.2	5.5	4.2	5.9	5.1	4.2	5.7	5.5	5.9	5.8	5.5	4.0	4.3	3.1	4.6	2.2	2.6	—														
21	*O. cruentatus*	4.0	5.7	4.9	6.2	4.8	6.6	5.7	4.8	6.4	5.7	6.6	6.5	6.2	4.6	4.9	3.7	5.3	2.9	3.3	0.7	—													
22	*O. octolineatus*	7.7	8.8	8.9	8.1	7.7	6.8	5.9	4.6	4.6	8.2	7.5	7.4	7.7	8.4	8.2	7.3	7.1	8.6	8.6	7.0	7.7	—												
23	*O. maculatus*	3.6	3.8	4.7	5.3	4.2	5.7	5.3	6.0	7.3	6.4	5.7	4.3	4.9	3.1	4.2	3.3	4.0	5.5	5.5	4.0	4.6	8.4	—											
24	*O. lipipengi*	4.5	4.4	5.3	6.7	5.3	6.2	5.7	5.3	5.9	5.7	5.9	5.6	6.2	4.6	4.6	3.7	4.4	6.6	6.2	5.1	5.3	6.2	4.4	—										
25	*O. nagao*	2.2	1.8	1.6	6.5	5.5	6.2	5.7	5.5	7.0	5.7	6.6	6.1	5.5	4.0	2.1	1.5	2.7	4.8	5.3	3.5	4.2	8.1	3.5	4.2	—									
26	*O. bivirgatus*	4.8	5.9	6.4	6.0	5.1	6.8	6.4	5.1	7.0	7.1	5.7	4.5	4.9	5.7	5.8	5.1	6.4	6.8	6.8	5.3	5.9	8.4	4.6	6.2	5.7	—								
27	*O. ornatus*	5.2	6.4	6.9	5.5	4.8	6.2	5.3	4.8	6.6	6.8	5.1	4.3	4.4	5.9	6.3	5.5	6.4	6.2	6.4	4.8	5.5	7.7	4.6	6.4	6.2	2.2	—							
28	*O. albocinctus*	4.5	4.8	5.8	6.2	5.3	5.5	5.5	5.1	5.3	6.2	5.7	5.2	6.2	4.2	4.8	3.7	4.9	6.8	6.4	5.1	5.7	5.7	4.4	2.0	4.6	5.7	6.4	—						
29	*O. cinereus* 4	2.3	2.0	1.8	6.2	5.5	5.9	5.5	5.7	6.8	6.0	6.8	6.1	5.5	4.2	2.3	1.8	2.9	5.1	5.5	3.7	4.4	8.1	3.5	4.0	0.2	5.9	6.4	4.4	—					
30	*O. fasciolatus*	5.4	7.5	7.3	6.2	5.7	3.7	3.3	4.2	4.6	4.4	6.4	6.3	7.1	6.2	7.1	6.2	7.1	5.9	6.8	5.1	5.7	6.2	6.4	6.2	6.6	6.4	5.3	5.9	6.8	—				
31	*O. lacroixi*	4.4	5.5	6.0	5.1	4.6	5.9	5.1	4.6	5.5	6.8	5.1	5.2	3.5	5.5	5.2	4.2	5.5	5.7	6.2	4.2	4.8	6.4	5.1	5.1	5.1	3.7	3.5	4.8	5.3	4.6	—			
32	*O. taeniatus*	5.8	7.9	7.6	6.5	6.4	4.0	3.5	4.2	4.2	3.8	7.0	7.0	7.3	6.4	7.4	6.4	6.9	6.2	6.8	4.8	5.5	5.9	6.6	6.6	6.8	7.0	5.9	6.4	7.0	2.0	5.7	—		
33	*O. barroni*	7.0	9.0	8.7	7.9	7.7	5.1	4.6	5.5	5.3	5.3	8.1	8.1	8.6	7.5	8.5	7.5	8.0	7.0	7.9	6.2	6.8	6.6	7.9	7.3	7.9	8.4	7.3	7.0	8.1	3.1	6.6	2.4	—	
34	*O. ocellatus*	5.4	7.0	7.3	6.7	7.0	4.2	3.7	4.6	4.4	4.0	7.7	7.2	7.5	6.6	6.9	6.2	6.6	7.7	7.3	6.2	6.8	5.9	6.6	5.5	6.2	6.4	6.6	5.7	6.4	3.7	5.5	3.3	4.4	—

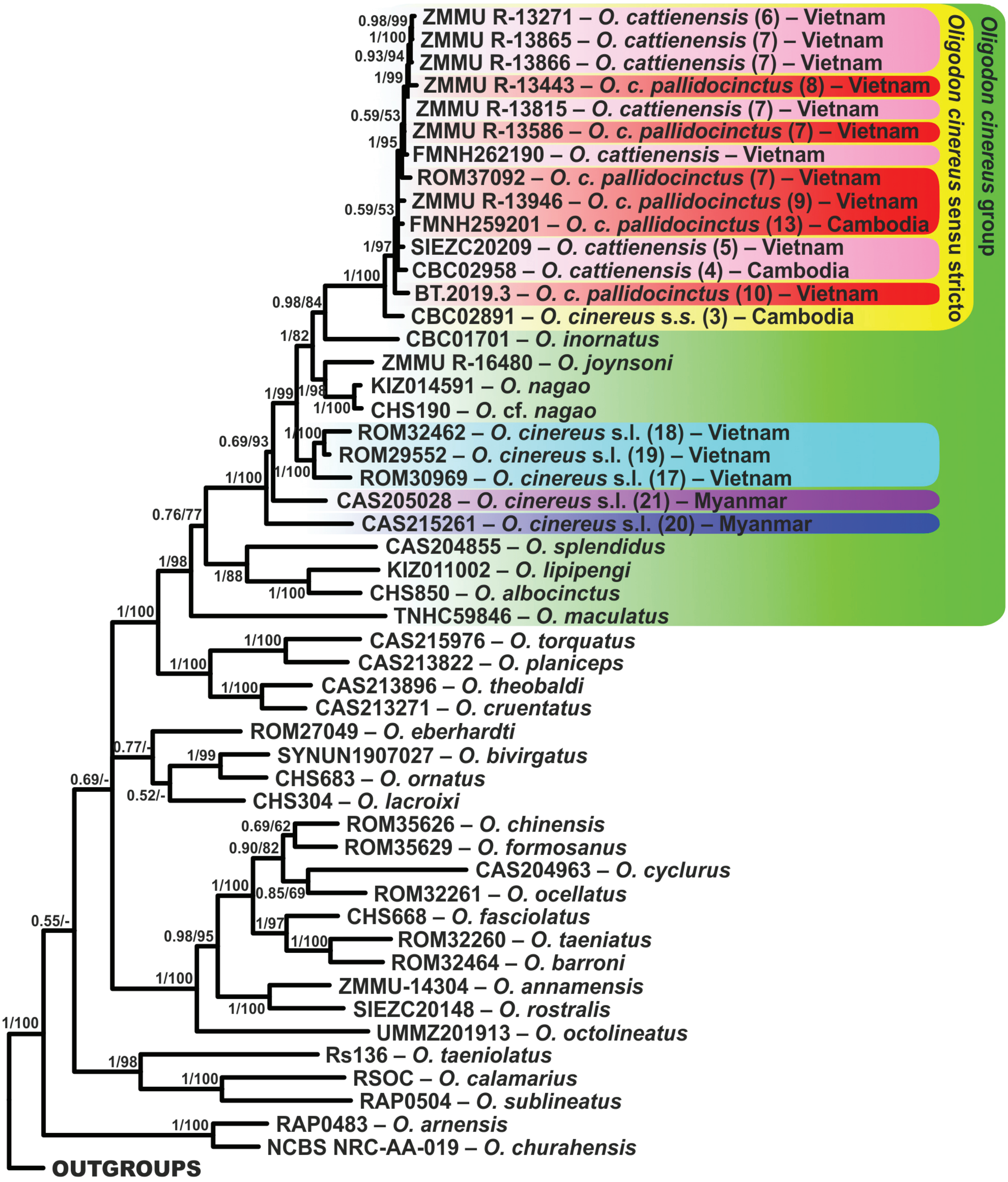

Figure 3. Molecular phylogeny based on mtDNA sequences (12S–16S rRNA and cyt *b* genes) of *Oligodon cattienensis*, *Oligodon cinereus* and congeners showing the non-monophyly of both species. The low genetic divergence between *O. cattienensis* and *O. cinereus* populations from southern Indochina suggests the two taxa are conspecific.

with samples of *O. cinereus* from Cambodia and southern Vietnam (BI 1.00/ML 100), including those whose specimen vouchers were morphologically identified as *O. cinereus cinereus* and *O. cinereus pallidocinctus*. Intraspecific distances were counted only for the members of this clade and amounted to 0.3%. This divergence value is significantly lower than the genetic differentiation between most of other recognized *Oligodon* species (Table 3). Samples of *O. cinereus* and *O. cattienensis* from southern Vietnam and Cambodia were recovered paraphyletic, suggesting very weak support for evolutionary independence between the two taxa. Moreover, the sequences of *O. cinereus* from Myanmar, China, and northern Vietnam were found to be paraphyletic respective to other members of the *O. cinereus* group, such as *O. inornatus*, *O. joynsoni* and *O. nagao*.

Table 4. Summary statistics and PCA scores for the *O. cattienensis* and *O. cinereus* OTUs studied. Abbreviations are listed in the materials and methods.

Dataset		**Both Sexes**			**Males**			**Females**	
Character	**PC1**	**PC2**	**PC3**	**PC1**	**PC2**	**PC3**	**PC1**	**PC2**	**PC3**
Standard deviation	1.850557	1.508423	1.278185	1.940926	1.633927	1.342585	1.916619	1.343130	1.043076
Proportion of Variance	0.311320	0.206850	0.148520	0.342470	0.242700	0.163870	0.459180	0.225500	0.136000
Cumulative Proportion	0.311320	0.518170	0.666700	0.342470	0.585170	0.749040	0.459180	0.684680	0.820680
Eigenvalues	3.424560	2.275340	1.633757	3.767196	2.669717	1.802536	3.673427	1.803998	1.088008
TailLR	0.503256	–0.006110	0.200619	0.457408	–0.118357	–0.227457	0.482489	–0.162017	0.149240
MSR	0.144185	0.023893	–0.178296	0.176297	–0.110583	0.161378	—	—	—
VEN	–0.158522	0.555766	–0.099219	–0.182414	–0.483959	0.101803	0.498420	–0.166028	–0.084618
SC	0.502171	0.168735	0.182013	0.419963	–0.305378	–0.192145	0.018229	–0.732140	–0.011911
TOTAL	0.166733	0.580147	0.020919	0.090520	–0.562103	–0.023934	0.512555	0.002566	–0.084913
SCR	0.513058	0.012518	0.198012	0.459296	–0.161628	–0.216211	0.154397	–0.028541	–0.877349
SL	0.004413	0.332873	0.080875	–0.251949	–0.386279	0.055124	–0.298365	–0.594549	0.051445
SLE	–0.043070	0.362023	–0.385916	–0.156117	–0.326579	0.436096	—	—	—
IL	–0.176045	0.183687	0.419863	–0.304766	–0.181974	–0.348231	0.056616	–0.233668	0.035099
ILCS	–0.292082	0.217417	0.373393	–0.328878	–0.121088	–0.393823	–0.373727	–0.035311	–0.435425
AT	0.198575	0.049395	–0.611689	0.204971	–0.023776	0.598362	—	—	—

Morphological analyses

Within our sample of 37 specimens, all but two characters (SC and SCR) in this study rejected the assumptions of normality and homoscedasticity. We note that the name-bearing type specimen of *O. cinereus* (NHMUK 1946.1.1.25) has a broken tail and was thus excluded from the multivariate analyses but kept for univariate comparisons. No morphological characters exhibited significant differences between sexes within the entire dataset, except for the number of anterior temporal scales (AT), which was weakly dimorphic (p=0.041). We did not have an adequate sample size to test for sexual dimorphism between individual OTUs. Kruskal-Wallis Tests on combined male and female datasets showed no statistically significant differences between OTUs (p=0.08403–0.69470). P-values for males ranged from 0.04105 (VEN) to 0.59240 (IL), and 0.08606 (SCR) to 0.67780 (SL and ILCS) for females. The number of ventrals between males was the only character determined to be significant based on the Kruskal-Wallis Test results (p=0.04105), although this likely reflects the small sample size of male *O. c. cinereus* (n=3). When a pairwise Mann-Whitney U Test was performed on male VEN between the OTUs *cinereus*/*cattienensis* and *cinereus*/*pallidocinctus* with the Holm-Bonferroni correction applied, none of the values were significant (p=0.06900 and p=0.06300, respectively). Furthermore, two of the *O. c. cinereus* specimens have 164 and 165 ventrals respectively, overlapping with the other two OTUs. Summary statistics of all OTUs can be found in Tables 4 and 5.

The PCA plot shows broad overlap between OTUs for *O. cattienensis*, topotypic *O. cinereus cinereus* and *O. cinereus pallidocinctus* (Fig. 4). For the dataset containing both sexes, PC1 accounted for 31.1% of the total variance and loaded most heavily for SCR, TailLR and SC. PC2 accounted for 20.8% of the total variance and loaded most heavily for VEN and TOTAL. PC3 accounted for 14.9% of the total variance and loaded most heavily for AT, SLE, IL and ILCS. We therefore interpret PC1 to represent variation in tail length and subcaudal scales, PC2 for the number of body scales and PC3 for labial and other cephalic scales. The three principal components represent 66.7% of the total cumulative variance in the analysis. For males, PC1 accounted for 34.2% of the total variance and loaded most heavily for SCR, TAILR, and SC. PC2 accounted for 24.3% of the total variance and loaded most heavily for TOTAL and VEN. PC3 accounted for 16.4% of the total variance and loaded most heavily for AT and SLE. We interpret PC1 to represent variation in tail length and subcaudal scales, PC2 for number of body scales and PC3 for labial scales and temporal scales, with the three principal components representing 74.9% of the cumulative variance in the analysis. For females, PC1 accounted for 45.9% of the total variance and loaded most heavily for SL, TOTAL, and TAILR. PC2 accounted for 22.6% of the total variance and loaded most heavily for SCR and SC. PC3 accounted for 13.6% of the total variance and loaded most heavily for SLE and ILCS. We interpret PC1 to represent variation in tail length, body scales and labial scales, PC2 for the number of subcaudal scales and PC3 for labial scales, with the three principal components representing 82.1% of the cumulative variance in the analysis. The combined univariate and multivariate analyses indicate that *O. cattienensis* and its sympatric congener *O. cinereus pallidocinctus* occupy the same morphospace. Furthermore, the analyses show that topotypic *O. cinereus* bearing a uniform/reticulated color pattern are not morphologically differentiated from these two taxa.

Table 5. Summary statistics for OTUs studied: *Oligodon cattienensis*, *Oligodon cinereus cinereus* (topotypic material), and *Oligodon cinereus pallidocinctus*. Means and standard deviations are given in parentheses when appropriate. Data for males are marked with an (M), and data for females are marked with an (F). Abbreviations are listed in the Materials and Methods section.

Character	***Oligodon cattienensis***	***Oligodon cinereus cinereus* [topotypic]**	***Oligodon cinereus pallidocinctus***
No. of specimens	11 (8 M, 3 F)	7 (3 M, 4 F)	19 (11 M, 8 F)
TailLR	10.1–13.3 (11.95 ± 0.96)	12.8–14.1 (13.29 ± 0.54)	9.4–15.0 (12.30 ± 1.45)
TailLR (M)	10.1–13.3 (12.11 ± 1.02)	13.9–14.1 (14.00 ± 0.56)	10.1–15.0 (12.74 ± 1.55)
TailLR (F)	10.7–12.1 (11.50 ± 0.73)	12.8–13.1 (12.94 ± 0.12)	9.4–13.9 (11.81 ± 1.33)
DSR	17–17–15	17–17–15	17–17–15
VEN	164–179 (171.6 ± 4.2)	159–171 (167.3 ± 5.8)	164–177 (170.9 ± 4.0)
VEN (M)	164–179 (171.3 ± 4.5)	159–165 (162.0 ± 4.2)	165–177 (171.4 ± 4.1)
VEN (F)	166–176 (171.0 ± 4.4)	166–176 (170.0 ± 4.5)	164–176 (170.4 ± 4.0)
SC	30–37 (33.3 ± 2.2)	33–37 (35.5 ± 1.5)	27–41 (34.0 ± 3.7)
SC (M)	30–37 (33.8 ± 2.4)	35–37 (36.0 ± 1.4)	27–41 (35.1 ± 4.3)
SC (F)	31–33 (32.0 ± 1.0)	33–37 (35.3 ± 1.7)	28–36 (32.6 ± 2.7)
TOTAL	197–213 (205.9 ± 5.2)	197–211 (203.7 ± 4.7)	196–214 (205.8 ± 5.4)
TOTAL (M)	197–213 (206.0 ± 5.9)	197–201 (199.0 ± 2.8)	196–214 (207.4 ± 6.2)
TOTAL (F)	202–210 (205.7 ± 3.6)	203–211 (206.0 ± 3.5)	197–210 (204.0 ± 3.8)
SCR	14.9–17.6 (16.15 ± 0.85)	16.1–18.8 (17.44 ± 0.98)	13.7–19.3 (16.47 ± 1.55)
SCR (M)	14.9–17.6 (16.37 ± 0.88)	17.4–18.8 (18.10 ± 0.97)	13.8–19.32 (16.89 ± 1.76)
SCR (F)	15.1–15.8 (15.56 ± 0.38)	16.1–18.1 (17.12 ± 0.93)	13.7–17.6 (15.96 ± 1.28)
LOREAL	Present	Present	Present
SL	8/8–8/9	8/8	7/7–8/8
SLE	4+5, 5+5	4+5	4+5
IL	7/7–8/8	7/8–8/8	7/7–9/9
ILCS	4/4–5/5	4/4	3/3–5/5
AT	1–2	1	1–2

The remaining traits Vassilieva et al. (2013) used to distinguish *O. cattienensis* from its congener *O. cinereus* include an entire nasal scale, the head bearing prominent dark markings, red ventral coloration in juveniles, and the presence of a "forked" hemipenis. After a re-examination of all the name-bearing type specimens and our additional material, we found that most of these characters overlap with *O. cinereus*. First, the nasal scale in *O. cattienensis* is said to be entire in the species diagnosis, but in the description of the holotype (ZMMU Re-13865) by Vassilieva et al. (2013), it is stated that the scale is subdivided at the bottom half by a suture running below the nostril. We also found that one of the paratypes (ZMMU Re-11473), clearly had a divided nasal and possessed a suture above and below the nostril on either side of the head. The prominent dark markings on the head found across *O. cattienensis* also appear to have little diagnostic value when compared to *O. cinereus*. All specimens we examined consistently bear a dark-edged orbital bar stretching from the margins of the lip up to the prefrontal and frontal scales, a temporal bar stretching from the parietals down towards the nape, and an arrow-shaped chevron stretching from the anterior edge of the parietals to the nape. In larger specimens, the color of the head markings may vary from light gray to darker brown, but the composition of the head pattern is consistent amongst all OTUs. Ventral coloration is also variable in *O. cinereus* and becomes unreliable when examining large series of preserved specimens, because red pigment quickly fades away in preservative fluids and turns cream or yellow in old specimens (Figs 5–6). Finally, Vassilieva et al. (2013) state that *O. cinereus* referrable to *O. cinereus pallidocinctus* can be distinguished by having white, black-edged crossbars, and unspotted ventrals. However, the type specimen of *Simotes violaceus pallidocinctus* (MNHN-RA-1938.0135) has spots on its ventral scales, and 13 of the 16 *O. cinereus pallidocinctus* specimens in our sample have small dark spots on the margins of the ventral surface (Fig. 6).

The biggest difference between *O. cattienensis* and *O. cinereus* is the shape of the hemipenes (forked vs. unforked, respectively). The difference presented by this character, however, is due to inaccurate terminologies used to describe the organ. In the case of *O. cinereus* sensu lato, the retracted hemipenis of male specimens is unilobed (= unforked) with "papillae"-like appendages *in-situ*, but our examination of organs that are partially everted shows that the hemipenis is bilobed (= forked) with the lobes bifurcating medially along the capitulum before extending apically as large tapering awns (Fig. 7). Two bifurcating awn-shaped lobes are clearly seen on the hemipenis in ZMMU Re-13866 of *O. cattienensis* in Vassilleva et al. (2013) and in specimen FMNH 262190 examined by us (Fig. 7A–B). By correctly interpretating the retracted and everted hemipenial morphology according to standard terminologies (Dowling and Savage 1960), it is clear *O. cattienensis* falls within the variation of *O. cinereus*, and thereby the *O. cinereus* species group.

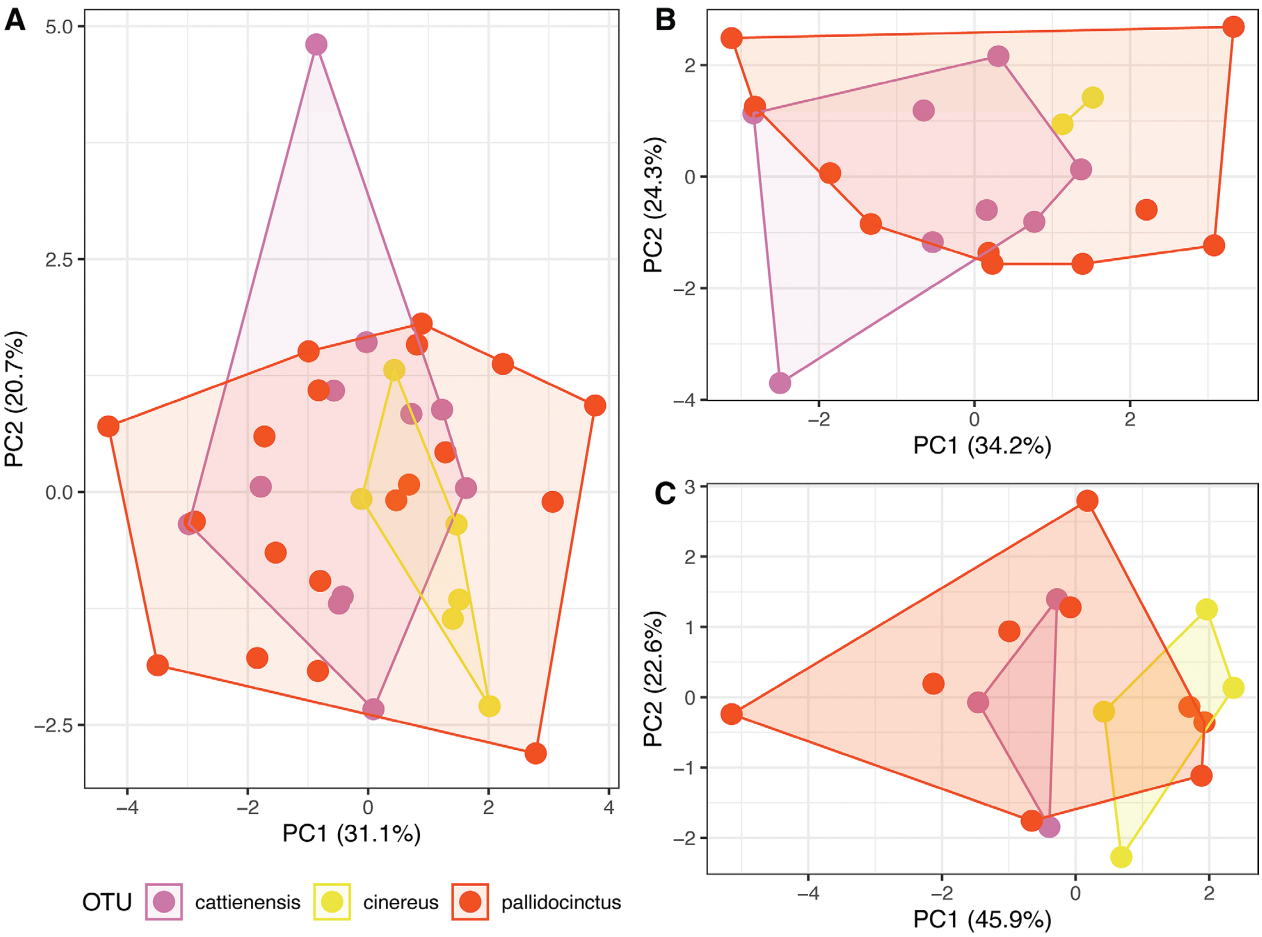

Figure 4. Principal Components Analyses (PCAs) conducted on both sexes (**A**), only males (**B**) and only females (**C**) for OTUs studied: *Oligodon cattienensis* (pink circles), *Oligodon cinereus cinereus* (yellow circles) and *Oligodon cinereus pallidocinctus* (red circles).

Discussion

Preliminary remarks on the Oligodon cinereus *species group*

Although it is not our goal to revise the entire *O. cinereus* species group, we discuss some preliminary taxonomic implications of our results in this section. The mtDNA phylogeny in this study revealed high levels of genetic divergence between sampled populations of *O. cinereus*. We lacked enough samples of cyt *b* to create a pairwise distance matrix, but it is likely that the genetic divergences would be higher than we observed in the 12S–16S rRNA matrix (Table 3) as it is a more rapidly evolving marker. Specimens identified as *O. inornatus*, *O. joynsoni*, and *O. nagao* were also recovered between different clades of *O. cinereus* sensu lato, rendering the species paraphyletic in our tree. This agrees with the conclusions of Green et al. (2010) and David et al. (2011), who state that there is unrecognized diversity within this taxon. Many authors acknowledge that *O. cinereus* exhibits considerable variation in morphology and coloration across its range. Several color morphs that are now associated with *O. cinereus* were described as separate species, subspecies and/or variants in the past (Günther 1864; Jan and Sordelli 1865; Bourret 1934, 1935, 1939, 1941). Most of these were reviewed by Smith (1943), who recognized a total of four morphs (also noted as "forms") analogous with previously described names. Some of these are now known as distinct subspecies (Taylor 1965; Saint Girons 1972; David et al. 2022), although there are also authors that prefer to retain these color patterns as synonyms (Deuve 1970; Wagner 1975). At least three different color morphs correspond with the mixed clade in our phylogeny containing samples of *O. cinereus* from southern Indochina. These include specimens with rectangular or butterfly-shaped blotches referrable to *O. cattienensis*, specimens with a uniform dorsum referrable to nominotypical *O. cinereus* (morphs I–II fide Smith 1943), and specimens with white and black-edged crossbars referrable to *O. cinereus pallidocinctus* (morph IV fide Smith 1943). Since there is little to no phylogenetic signal for color pattern and broad morphological overlap between different morphs in this clade, we feel it is most appropriate to consider all populations of *O. cinereus* in southern Indochina as a single taxon instead of several subspecies diagnosed only by color. Consequently, we relegate both *O. cattienensis* and *O. cinereus pallidocinctus* as junior synonyms of *O. cinereus*. Since the type specimen of *O. cinereus* originates from the study area (i.e., Cambodia), we assign *O. cinereus* sensu stricto to all uniform/reticu-

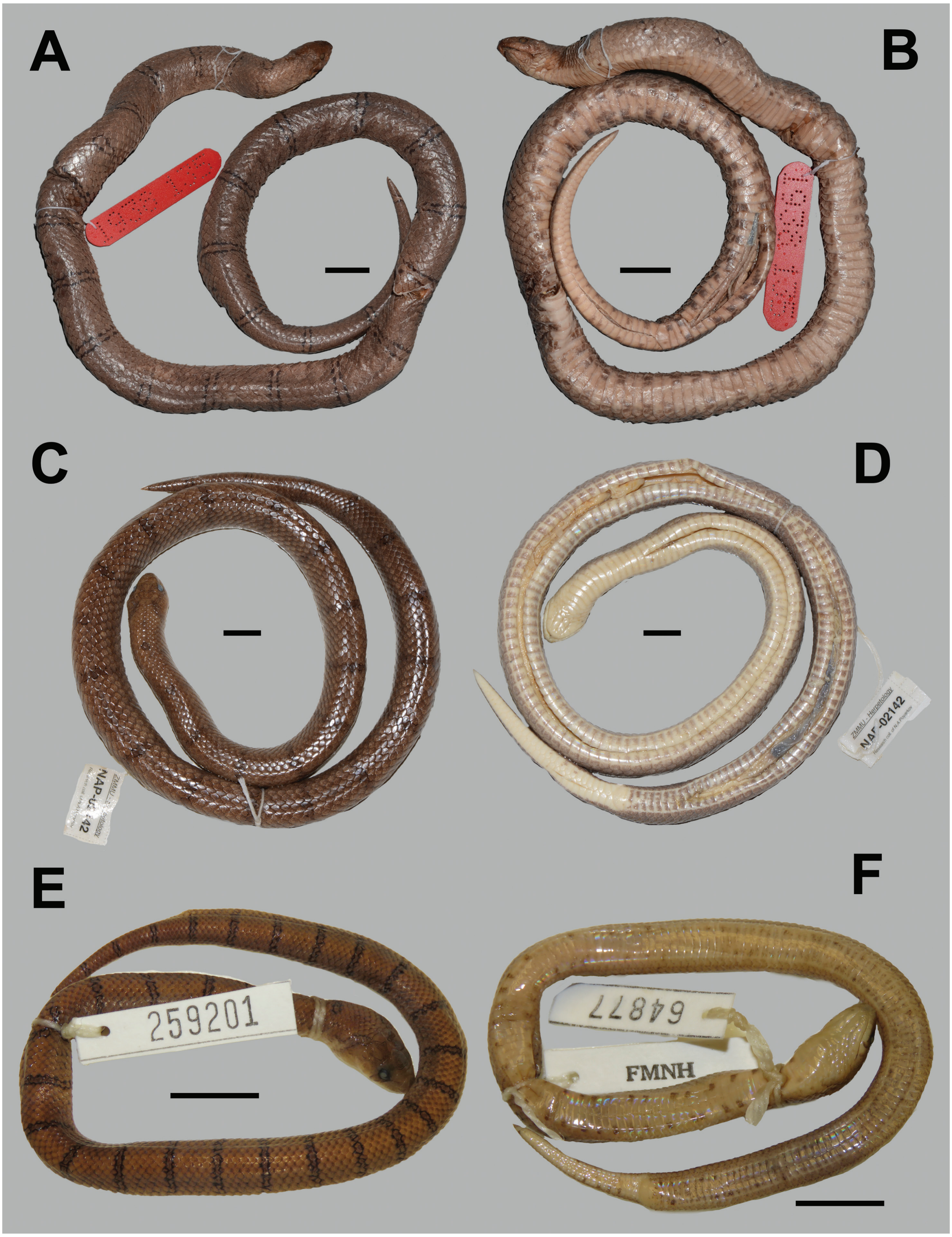

Figure 5. Preserved specimens bearing the color pattern referrable to *Oligodon cinereus pallidocinctus* showing overall variation between adults and juveniles. MNHN-RA-1938.0135, holotype of *Simotes violaceus pallidocinctus*, adult, dorsal (**A**) and ventral (**B**) views. ZMMU Re-13586, adult, dorsal (**C**) and ventral (**D**) views. FMNH 259201, juvenile, dorsal (**E**) and ventral (**F**) views. All scale bars equal 10 millimeters in length. Photos by Gernot Vogel (A, B), Platon V. Yushchenko (C, D), and Justin L. Lee (E, F).

lated, white with black-edged cross-barred and blotched patterned populations found in Cambodia, southern Laos, and southern Vietnam.

We have insufficient evidence to properly assess the relationships between the remaining deeply divergent clades of *O. cinereus*, their color morphs, and corre-

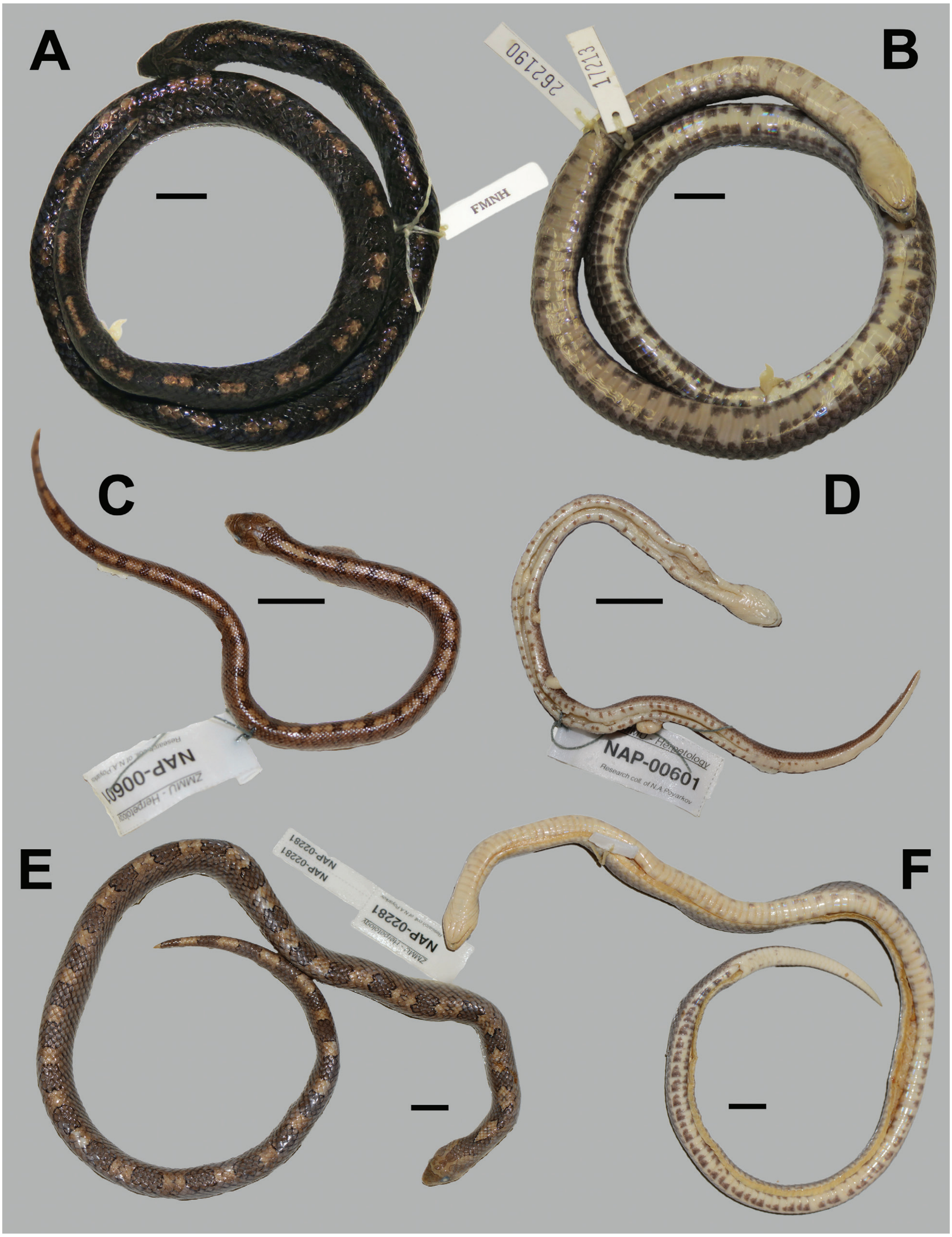

Figure 6. Preserved specimens bearing the color pattern referrable to *Oligodon cattienensis* showing overall variation between adults and juveniles. FMNH 262190, adult, dorsal (**A**) and ventral (**B**) views. ZMMU Re-13271, adult, dorsal (**C**) and ventral (**D**) views. ZMMU Re-13865, adult and holotype of *O. cattienensis*, dorsal (**E**) and ventral (**F**) views. All scale bars equal 10 millimeters in length. Photos by Justin L. Lee (A, B) and Platon V. Yushchenko (C–F).

sponding subspecies and synonyms described in the literature. David et al. (2011) showed that there are significant differences in scalation and head shape between *O. cinereus* resembling the immaculate/reticulated morphs I+II and those resembling the dark cross-barred morph III diagnosed by Smith (1943). These authors specifical-

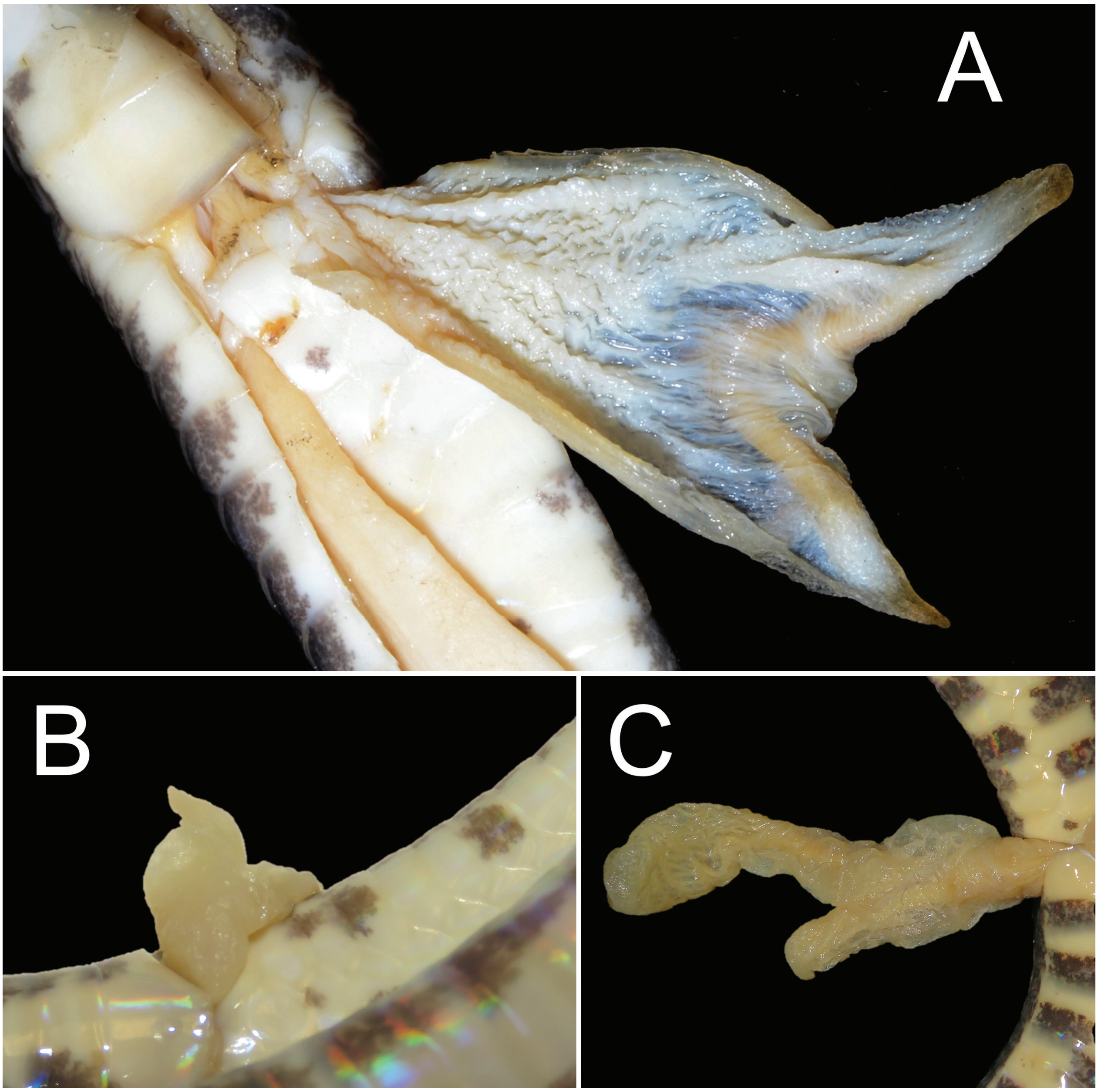

Figure 7. Partially everted hemipenes from preserved specimens of *Oligodon cinereus*, including (**A**) paratype of *Oligodon cattienensis* (ZMMU Re-13866) with the right organ partially dissected revealing a bilobed condition with awn-shaped lobes, and (**B**) awn-shaped lobes visible on the partially everted organ of another specimen of *O. cattienensis* (FMNH 262190); (**C**) everted hemipenis of *Oligodon cinereus* sensu lato (CAS 240006) from Rakhine State, Myanmar demonstrating a bilobed condition, with the bottommost lobe still partially everted. Photo A by Anna B. Vassilieva and Vitaly L. Trounov, copyright Magnolia Press, reproduced with permission from the copyright holder. Photos B–C by Justin L. Lee.

ly associated Smith's "Form III" (= morph III) with the name *Simotes multifasciatus* Jan & Sordelli, 1865, which would be the oldest available name if this color morph represents a distinct species. Additional investigations are needed to determine if this morph corresponds with any of the lineages identified in this study. In the meantime, we recommend conserving the name *O. cinereus* sensu lato for populations outside of southern Indochina, including the clades revealed by our mtDNA phylogeny. While this leaves the species paraphyletic, we refrain from recommending any more taxonomic changes, as we lack genetic samples from other regions where *O. cinereus* sensu lato occurs — specifically southern China, eastern India, Laos, Myanmar, and Thailand. Separating the remaining lineages as undescribed species, or as *conferatur* populations, would cause additional destabilization.

Outside of southern Indochina, two other synonyms of *O. cinereus* deserve discussion, namely *Holarchus violaceus poilani* Bourret, 1939 and *Holarchus violaceus plurimaculatus* Bourret, 1941. Both were collected in the same region of Quang Tri Province, central Vietnam and have only been mentioned a few times in the literature. Smith (1943) included *H. v. poilani* in his account for *O. cinereus* but did not examine the type specimen or consider it amongst other color morphs. Deuve (1970) considered *H. violaceus plurimaculatus* to be a color va-

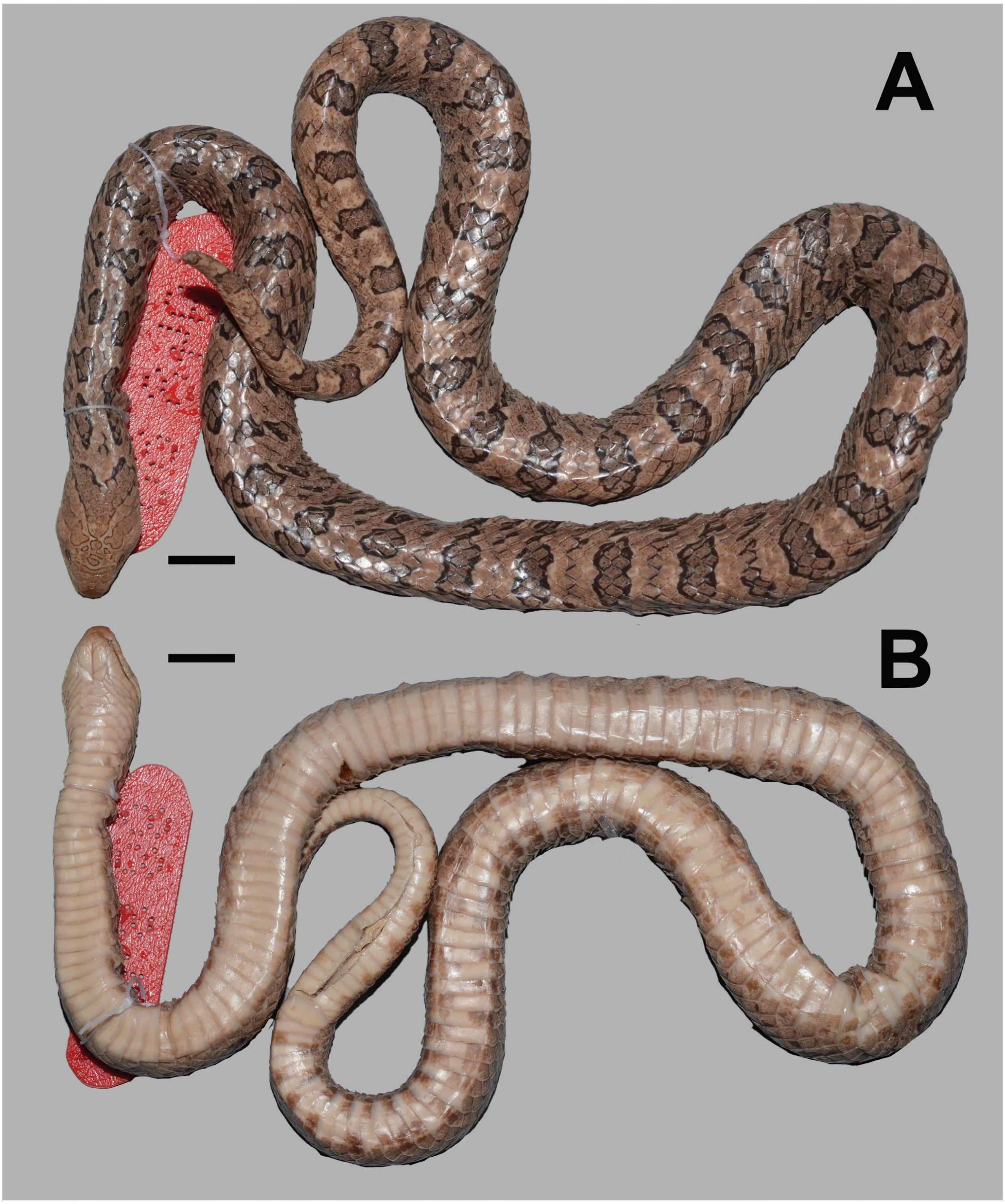

Figure 8. Preserved specimen of *Holarchus violaceus plurimaculatus*, MNHN-RA-1948.0088, dorsal (**A**) and ventral (**B**) views, currently considered a junior synonym of *Oligodon cinereus* sensu lato. This taxon along with *Holarchus violaceus poilani* are similar in color pattern to specimens previously recognized as *Oligodon cattienensis* from southern Vietnam and Cambodia. All scale bars equal 10 millimeters in length. Photos by Gernot Vogel.

riety of *O. cinereus* (as *Holarchus violaceus*) but did not address *H. violaceus poilani*. Wagner (1975) examined both names and considered them to represent "blotched" morphs of *O. cinereus*. More recently, David et al. (2022) recognized *H. violaceus plurimaculatus* as a subspecies of *O. cinereus* and referred an additional specimen from Laos to this taxon. Based on their original descriptions (Bourret 1939, 1941), *H. violaceus poilani* and *H. violaceus plurimaculatus* share a strong resemblance to *O. cattienensis* (see Fig. 8). Although these two names were available as synonyms of *O. cinereus* in the literature, Vassilieva et al. (2013) did not address either taxon when they described *O. cattienensis*, despite the notable similarities in morphology. In all three taxa, the dorsum contains brown or dark-brown rectangular-shaped blotches with black edges. The number of body blotches in *H. violaceus poilani* and *H. violaceus plurimaculatus* (28 and 38, respectively), also overlap with the number of blotches found in our sample of *O. cattienensis* (24–38). However, *O. cattienensis* (and thereby *O. cinereus* sensu stricto) differs from *H. violaceus poilani* and *H. violaceus plurimaculatus* in relative tail length and the number of ventral and subcaudal scales (40 subcaudals in *poilani*, 43 in *plurimaculatus*; SCR 19.4 in *poilani*, 20.7 in *plurimaculatus*). These values are at the higher end of subcaudals and subcaudal ratios found in *O. cinereus* OTUs examined from southern Indochina (subcaudals 27–41 and SCR 13.7–19.3 in both sexes, including *O. cattienensis*). Whether these two names represent an artifact of geographic variation or a separate taxonomic unit can be tested with additional specimens and molecular data. Until then, we agree with Wagner (1975) and recommend retaining these two names within the synonymy of *O. cinereus* sensu lato.

Finally, our phylogenetic results tentatively support the validity of *O. inornatus*, *O. joynsoni*, and *O. nagao*, but further sampling of these species and *O. cinereus* from adjacent regions are needed to demarcate species boundaries between taxa. All three species were historically confused with *O. cinereus*, and their placement amongst lineages of this species confirms a close relationship. One sample from GenBank (CHS190) identified as *O.* cf. *cinereus* was recovered sister to a sample morphologically verified as *O. nagao* (KIZ 014591) by only 0.4% in 12S–16S rRNA. This GenBank sample originating from Li et al. (2020) is part of a larger phylogenetic dataset on Chinese snakes, with locality data given as "Hainan, China". Since the locality information provided for the sample is not specific and we cannot examine the specimen voucher, we are unsure if it represents a variant of *O. cinereus* or a range extension of *O. nagao* (Jiang et al. 2012). Tentatively, we recommend identifying this sample as *Oligodon* cf. *nagao* until this specimen and/or additional material from Hainan Island can be examined. The mislabeling of GenBank samples from studies such as Li et al. (2020) has been criticized by other authors (David et al. 2021; Smart et al. 2021; Mulcahy et al. 2022). It should also be noted that the name *Holarchus dolleyanus* Cope, 1895 presently considered as a junior synonym of *O. cinereus* (Smith 1943), was described based on a specimen collected from "China, Hainan" and could be applicable to populations from the island. If the type specimen is found to be conspecific with populations of *O. nagao*, it is available as a senior synonym for this species.

Problems with hemipenial morphology and Oligodon

Hemipenial morphology has been used as an important morphological character in earlier works on kukri snake systematics (Wall 1923; Smith 1943; Leviton 1962; Wagner 1975). Despite the taxonomic significance of the hemipenis in many snakes, much of the terminology used by researchers to describe the hemipenial morphology of *Oligodon* appears to be outdated. In fact, most of the terms used to describe the hemipenes of Southeast Asian snake species are based on the works of 19th and 20th century authors, mainly Cope (1893), Pope (1935) and Smith (1943). These earlier authors used the terms "forked" and "unforked" to describe the lobes on the hemipenis, and "papillae" to describe appendages on the lower portion of the hemipenis near its contact with the *m. retractor penis magnus*. Dowling and Savage (1960) standardized the terminology for snake hemipenes and used "papillae" to describe the ornamental calyces on the organ instead of appendages bordering the retractor muscle. The terms forked and unforked were used to describe the condition of the *sulcus spermaticus*, rather than the entire shape of the organ (the terms "simple" to describe unforked sulci and "bifurcated" for forked sulci were also used). A forked hemipenis with two lobes sensu Smith (1943) would be referred to as a bilobed organ under Dowling and Savage (1960), whereas an unforked hemipenis would be a unilobed organ. The failure to update standard hemipenial terminology in *Oligodon* has led to several problems in the recent literature and may be the reason why *O. cattienensis* was mistakenly described as a distinct species in the *O. cyclurus* species group, rather than as a blotched color form of *O. cinereus*. In his unpublished thesis, Wagner (1975) recognized that the retracted hemipenis of *O. cinereus* appears unilobed (unforked) with distinct "papillae" seen when *in-situ*, but during the examination of fully everted hemipenes, showed that the organ is clearly bilobed (forked) with large awn-shaped lobes. To correct the use of "papillae", he coined the word "myoectases" as an alternative term to describe the unusual appendages on the retracted hemipenis. Because the *sulcus spermaticus* in *Oligodon cinereus* sensu lato is unforked (simple) and does not expand onto the lobes, it is likely that the "papillae" appendages described by Smith (1943) and earlier authors represent the extended awn-shaped lobes that form when the organ becomes everted. While many contemporary studies on *Oligodon* have agreed with Wagner's taxonomic conclusions, they continue to use the hemipenial terminology coined by earlier authors (i.e., Smith 1943). To rectify this issue, we recommend future authors follow the terminology utilized by Dowling and Savage (1960) in future descriptions of the hemipenis. At the very least, the terminology used to describe the hemipenis should be explicitly stated in the methods section of any taxonomic paper.

The case of *O. cattienensis* exemplifies the need to follow a consistent and standard terminology used to describe the hemipenes of Southeast Asian snakes. The case also underlies the importance of an integrative taxonomic approach when dealing with variable and polymorphic snake taxa such as *Oligodon cinereus*. Errors associated with interpreting morphological characters, such as the shape and ornamentation of hemipenes, can lead to inaccurate taxonomic conclusions at the interspecific and intrageneric level, as evidenced here in this study. While the case of *O. cattienensis* is just one example of this problem, it is possible that many other kukri snakes described recently may also suffer from mistakes related to hemipenial morphology. We hope that the concerns we have raised help clarify future taxonomic work on *Oligodon* and facilitate more integrative approaches when treating species within this genus.

Conclusions

In this paper, we provided additional morphological and molecular data to reassess the taxonomic status of the kukri snake species *Oligodon cattienensis* and *O. cinereus* within southern Indochina. Based on the mtDNA dataset consisting of the 12S–16S rRNA fragments and cyt *b*, phylogenetic analyses renders both *O. cattienensis* and *O. cinereus* sensu lato paraphyletic, and minimal intraspecific genetic divergences exist between the two taxa (~0.3%). Relationships within the phylogeny agree with past studies conducted on *Oligodon* (Green et al. 2010; Pyron et al. 2013; Figueroa et al. 2016; Nguyen et al. 2020; Li et al. 2020; Mirza et al. 2021), however our analyses are the first to include the species *O. inornatus* and *O. joynsoni* in a molecular dataset. Vassilieva et al. (2013) originally diagnosed *O. cattienensis* from *O. cinereus* based largely on color pattern characters, the condition of the nasal scale, and hemipenial morphology. By re-examining the type series and including new specimens, we show that most of these characteristics fall well within the variation observed in *O. cinereus*, particularly populations found at the vicinity or in sympatry with *O. cattienensis* in southern Vietnam and Cambodia. In addition, our molecular analyses show that there is little to no phylogenetic signal between the color patterns associated with *O. cattienensis*, or the white and black-edged crossbarred specimens previously known as *O. cinereus pallidocinctus*. By considering *O. cattienensis* and *O. cinereus pallidocinctus* as junior synonyms of *O. cinereus* sensu stricto, we lower the total number of species of *Oligodon* to 89, and the number of species found within Vietnam to 24. This includes the recently described *Oligodon tuani* Nguyen et al., 2022 discovered in the Langbian Plateau, Dat Lat Province, Vietnam. While the species was not sampled for molecular data, its morphology places it within the *O. cyclurus* species group and it is not closely related to *O. cinereus*, however additional sampling is recommended to confirm this. The results in this paper help set the stage for future integrative taxonomic revisions in the *O. cinereus* species group, which shall hopefully address issues that are beyond the scope of this study.

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Appendix I

A list of specimens examined for morphological analyses, organized by operational taxonomic unit (OTU). Numbers found in this appendix follow the numbered list of mapped locations provided in Fig. 2, but not for Table 1.

Oligodon cattienensis (n = 11)

CAMBODIA: CBC 02958, CBC 02954 Stung Treng Province, Prey Lang Wildlife Sanctuary, Spong Village (13°26'N, 105°32'E) (4).

VIETNAM: USNM 90011 Dong Nai Province, Bien Hoa (11); ZMMU Re-13865 (holotype of *O. cattienensis*), ZMMU Re-11473, ZMMU Re-13866, ZMMU Re-13815 (paratypes of *O. cattienensis*), FMNH 262190, ZMMU Re-15699–700 Dong Nai Province, Cat Tien National Park, Nam Cat Tien sector (11°25’30'N, 107°20’25'E) (7); ZMMU Re-13271 Lam Dong Province, Bidoup-Nui Ba National Park, Long Lanh environs, Da Nhim River valley (12°10'N, 108°40'E) (6).

Oligodon cinereus cinereus (n = 7)

CAMBODIA: NHMUK 1946.1.1.25 “Gamboja” [= Cambodia] (1); MNHN-RA-1892.0264 Cambodia, no specified locality (1); MNHN-RA-1970.0437–0.440 Kampong Chhnang Province, Trapaeng Chang, no specified locality (2); CBC 02891 Kampong Speu Province, Kirirom National Park (11°18'N 104°04'E) (3).

Oligodon cinereus pallidocinctus (n = 16)

CAMBODIA: FMNH 259201 Mondolkiri Province, Pichrada District (13).

LAOS: MNHN-RA-1897.0425 Attapu Province, Attapeu [= perhaps the city of Attapu] (14); ZMA 19170 Xékong Province, Dakchung District (15).

VIETNAM: ZMMU Re-13443 Binh Phuoc Province, Bu Gia Map National Park (12°11'N, 107°13'E) (8); MNHN-RA-1937.0022, USNM 90009–90010 Dong Nai Province, Bien Hoa (11); ZMMU Re-13586 Dong Nai Province, Cat Tien National Park, Lagerstroemia Forest, road near the meteorological tower (11°26'N, 107°24'E) (7); NHMUK 1938.8.7.33–34 Saigon [= now Ho Chi Minh City] (12); USNM 73850 Gia Dinh [= now included in Ho Chi Minh City] (12); ZMMU Re-13946 Lam Dong Province, Loc Bao Forest, campground at disturbed forest near river (11°44'N, 107°42'E) (9); IEBR 94, S 0154 (T. Ziegler’s personal collection) Quang Binh Province, Phong Nha-Ke Bang National Park, no specified locality (16); MNHL 42 00 0348 (1575) Cochinchine, Tay Ninh [= now Tay Ninh Province]; MNHN-RA-1899.0278 Annam (Indochine) [= central Vietnam]; MNHN-RA-1938.0135 (holotype of *Simotes violaceus pallidocinctus* Bourret, 1934) “Cochinchine” [= extreme southern Vietnam], Ho Chi Minh City (12).