The taxonomic status of the kukri snake *Oligodon arenarius* Vassilieva, 2015 with a redescription of *Oligodon macrurus* (Angel, 1927) (Squamata, Serpentes, Colubridae)

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Abstract

We investigated the taxonomic status of the recently described kukri snake *Oligodon arenarius* Vassilieva, 2015 and the morphologically similar *Oligodon macrurus* (Angel, 1927), two species endemic to the southern coast of Vietnam. Based on phylogenetic analyses using three mitochondrial genes (12S–16S rRNA, cytochrome *b*), we recovered *O. arenarius* and *O. macrurus* in a clade within the *O. cyclurus-taeniatus* species group, agreeing with previous intrageneric classifications. Genetic distances between *O. arenarius* and *O. macrurus* are extremely low (less than 0.5% based on 12S–16S) and render *O. arenarius* paraphyletic. All preserved specimens of *O. arenarius* and *O. macrurus* convey little to no differences in color pattern, hemipenial morphology and osteological features; the latter of which is based on three dimensional micro computer tomography (µCT) scans of one specimen per species. Contrasting these results, univariate and multivariate analyses revealed significant differences in relative tail length, and the number of ventral and subcaudal scales between both species. Although the molecular and morphological datasets present conflicting results, integrating the evidence leads us to synonymize *O. arenarius* with *O. macrurus*. We provide a formal redescription of *O. macrurus*, designate a neotype specimen to avoid future taxonomic confusion, and provide the first detailed osteological description of this species. *Oligodon macrurus* sensu stricto is endemic to coastal dunefields and adjacent forest habitats in southern Vietnam, where ongoing human development, tourism and road mortality pose significant threats to its conservation. Consequently, we suggest that *O. macrurus* should be listed as "Vulnerable" based on the assessment criteria of the International Union for Conservation of Nature (IUCN).

Keywords

Introduction

The kukri snakes of the genus *Oligodon* Fitzinger, 1826 are a species-rich group of colubrids comprised of 89 recognized species (Nguyen et al. 2022; Uetz et al. 2022; Yushchenko and Lee et al. 2023). Although the genus is taxonomically diverse, most members are infrequently collected in the field and are known from only a few specimens or their name-bearing types (Supsup and Carestia 2020; Lee et al. 2021). As a result, most lack information regarding their basic biology, morphological variation, phylogenetic position and conservation status. Roughly 24 species of *Oligodon* are known from Vietnam. Of these, eight are considered endemic, and ten have been described in the last decade (David et al. 2008a, 2008b, 2012; Vassilieva et al. 2013; Vassilieva 2015; Nguyen et al. 2016, 2017, 2022; Nguyen et al. 2020). Yushchenko and Lee et al. (2023) recently re-assessed the taxonomy of one newly described Vietnamese species, *Oligodon cattienensis* Vassilieva et al., 2013, resulting in its synonymziation with the more wide-ranging and morphologically variable *Oligodon cinereus* Günther, 1864. In addition, Nguyen et al. (2022) described another new species, *Oligodon tuani* Nguyen et al., 2022 from the Langbian Plateau of southern Vietnam. These studies indicate our knowledge of *Oligodon* in this country is far from complete, and taxonomic revisions are still needed to understand the species boundaries of many of its members. In this study, we re-assess the status of two poorly documented kukri snakes known only from the coastal dunefields of southern Vietnam: the Angel's kukri snake *Oligodon macrurus* Angel, 1927 and the recently described dune kukri snake *Oligodon arenarius* Vassilieva, 2015.

The first species, *O. macrurus*, was described as *Simotes violaceus macrurus* based on a single specimen collected in 1925 by M. Pierre Chevey from "Pointe Lagan", now the sand dunes surrounding Mui La Gan, Binh Thuan Province, Vietnam. The type specimen was deposited in the Museum Nationale d'Histoire Naturelle, Paris (MNHN), but according to Nguyen et al. (2009), it has not been traced in the collection and is thereby considered lost (Uetz et al. 2019, confirmed therein by I. Ineich March 2019). Smith (1943) elevated this taxon to species status as *Oligodon macrurus* and reported a second specimen collected 250 kilometers north of the type locality in what is now Khanh Hoa Province. Based on morphology, Smith (1943) included *O. macrurus* within the informally defined *Oligodon cyclurus* species-group specifically due to the presence of forked (bilobed, henceforth) hemipenes without obvious spines or "papillae" (lobular appendages found on the retracted hemipenes when in-situ). Roughly 70 years later, Geissler et al. (2011) rediscovered this species from Mui Ne, Binh Thuan Province, approximately 100 kilometers west of the type locality and presented additional morphological data on three specimens.

Vassilieva (2015) described the second species, *O. arenarius*, based on five specimens (two males and three females) from the coastal dunes surrounding Binh Chau–Phuoc Buu Nature Reserve in Ba Ria–Vung Tau Province. Although the type series of *O. arenarius* share similar color and head scalation features with *O. macrurus*, Vassilieva (2015) noted several differences between them. A key dissimilarity was the unusual structure of the hemipenes in the male holotype of *O. arenarius* (ZMMU Re-14503), which was unilobed without spines or obvious 'papillae'. The two species also had markedly different numbers of ventral scales, subcaudal scales and relative tail lengths, further supporting their differentiation as separate entities. The unique hemipenes of *O. arenarius* prevented Vassilieva (2015) from allocating it into any previous species grouping in *Oligodon*, but she surmised the *O. cinereus* and *O. dorsalis* species groups might be close relatives. Later, Nguyen et al. (2021) collected another male *O. arenarius* from the type locality and found that its hemipenial morphology was dramatically different from the description of Vassilieva (2015), bearing a long and deeply bilobed organ compared to the short and unilobed structure of the original male holotype. Therefore, these authors (Nguyen et al. 2021) recommended placing *O. arenarius* into the *O. cyclurus* species group, which shares the presence of a deeply bilobed hemipenes without spines or 'papillae'.

Over the past decade, some of us (PVY, NAP, HMP, PG) have collected additional kukri snake specimens from the dunefields of southern Vietnam that putatively resemble the original descriptions of *O. macrurus* and *O. arenarius*. Neither species has been sampled in a molecular phylogenetic assessment, and the descriptions of the *O. arenarius* hemipenes from Vassilieva (2015) and Nguyen et al. (2021) present two conflicting hypotheses. These circumstances prompted us to investigate the taxonomy of these snakes more carefully. We developed three core objectives for our study. First, we aimed to assess the phylogenetic position of both species to confirm whether their closest relatives are members of the morphologically defined *O. cyclurus* species group. Second, we wished to resolve the hemipenial morphology of *O. arenarius* to see if the results of Vassilieva (2015) or Nguyen et al. (2021) were correct. Third, we wished to assess the species boundaries between *O. arenarius* and *O. macrurus* under an integrative taxonomic approach to determine if they should be recognized as separate species. By examination of all available specimens of *O. arenarius* and *O. macrurus*, plus our newly collected material, and phylogenetic analyses of 16 samples using 3,033 bp of mtDNA, we recovered poor support for the species status of *O. arenarius* and relegate this taxon to the synonymy of *O. macrurus*.

Material and Methods

Taxon sampling and species delimitation

This contribution is based on a study of 20 specimens of *O. arenarius* (n = 9) and *O. macrurus* (n = 11), including available museum specimens and new material collected
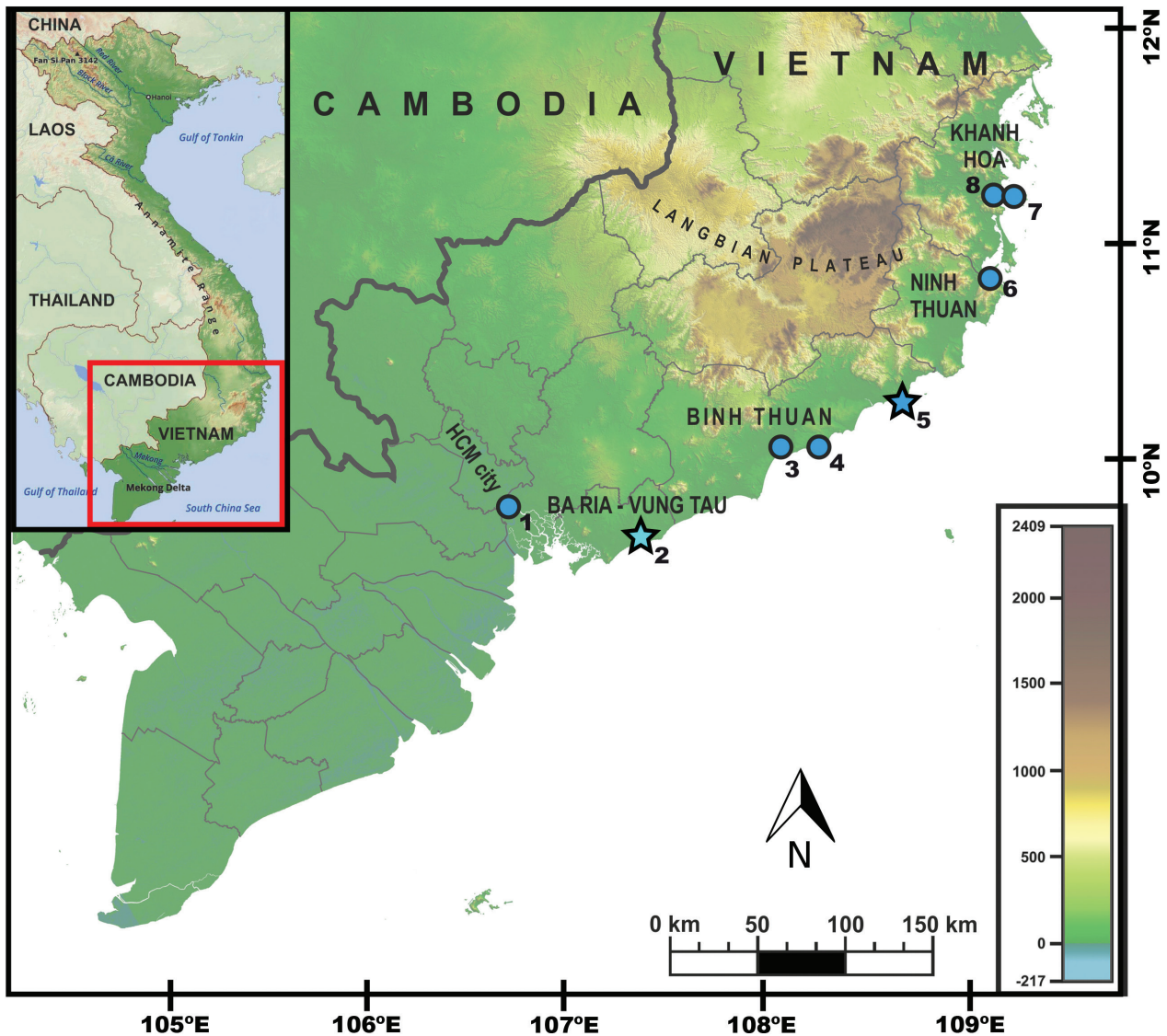
Figure 1. Known distribution of *Oligodon arenarius* (light blue) and *O. macrurus* (blue) in Vietnam. Stars denotes type locality. Localities: **1** Ho Chi Minh City; **2** Binh Chau–Phuoc Buu Nature Reserve, Ba Ria–Vung Tau Prov. (type locality of *O. arenarius*); **3** near Phan Thiet city, Binh Thuan Province; **4** Mui Ne, Binh Thuan Province; **5** Mui La Gan, Binh Thuan Province (type locality of *O. macrurus*); **6** Nui Chua National Park, Ninh Thuan Province; **7** Nha Trang, Khanh Hoa Province; **8** Hon Tre Island, Khanh Hoa Province.

by us. Data from an additional *O. arenarius* and four *O. macrurus* (including the lost holotype) originate from literature sources (Angel 1927; Geissler et al. 2011; Nguyen et al. 2021), increasing our dataset to a total of 24 specimens. One other specimen of *O. arenarius* (ZMMU NAP-10091) was excluded from the morphological dataset because it was discovered dead on road (DOR) in too poor of a condition to examine for morphological features. All *O. arenarius* are from the vicinity of the type locality in the Binh Chau–Phuoc Buu Nature Reserve, Ba Ria–Vung Tau Province (locality 2; Fig. 1). All examined *O. macrurus* originate from seven localities: vicinity of Ho Chi Minh City (locality 1; Fig. 1); near Phan Thiet city, Binh Thuan Province (locality 3; Fig. 1.); Mui Ne, Binh Thuan Province (locality 4; Fig. 1); type locality, Mui La Gan, Binh Thuan Province (locality 5; Fig. 1); Nui Chua National Park, Ninh Thuan Province (locality 6; Fig. 1); Nha Trang, Khanh Hoa Province (locality 7;

Fig. 1); Hon Tre Island, Khanh Hoa Provice (locality 8; Fig. 1). More details are provided in the redescription of *O. macrurus*. For molecular analyses, we sampled tissues from nine *O. arenarius* and seven *O. macrurus* (16 total samples). We also used 47 sequences of other *Oligodon* species publicly available from GenBank (see Table 2 for sources of each sequence), with the exception of *Oligodon melaneus* Wall, 1909 (Das et al. 2022). For outgroups, we chose one sequence each of the snake species *Oreocryptophis porphyraceus* (Cantor, 1839) (subfamily Colubrinae) and *Hebius vibakari* (Boie, 1826) (subfamily Natricinae) due to their use in previous phylogenies of *Oligodon* published in the literature (Nguyen et al. 2020).

For all aspects of species concepts and delimitation, we follow the General Lineage Concept (De Queiroz 2007), where a species represents a single evolutionarily independent lineage following a separate trajectory compared

to its congeners. Specifically, our definition of evolutionary independence is measured by substantial differentiation in genetic divergence, discrete or statistical differences in morphological features, and evidence of monophyly from basic genetic markers, satisfying the criteria of an integrative taxonomic approach (Padial et al. 2010). The concept of the subspecies rank, and its potential applicability towards the taxa studied here, is addressed later (see Discussion). Lastly, we note that we shall eventually consider *O. arenarius* to be a synonym of *O. macrurus*, however we will refer to it by its full species combination until the results and subsequent sections. Museum and other natural history collection acronyms are provided as follows: **DTU:** Duy Tan University, Da Nang City, Vietnam; **ITBCZ:** Zoology Collection of the Institute of Tropical Biology, Ho Chi Minh City, Vietnam; **MNHN:** Muséum National d'Histoire Naturelle, Paris, France; **NHMUK:** Natural History Museum, London, UK (formerly BMNH); **SIEZC:** Herpetological Collection of the Department of Zoology, Southern Institute of Ecology, Ho Chi Minh City, Vietnam; **UNS:** University of Ho Chi Minh City, Vietnam; **VMNN:** Vietnam National Museum of Nature, Hanoi, Vietnam; **ZFMK:** Zoologisches Forschungsmuseum Alexander Koenig, Bonn, Germany; **ZMMU:** Zoological Museum of Lomonosov Moscow State University, Moscow, Russia.

Molecular analyses

Total genomic DNA was extracted from muscle tissue samples preserved in 95% ethanol using a Qiagen DNAeasy Blood and Tissue Kit following manufacture protocols. We performed polymerase chain reactions (PCRs) to amplify two fragments of mitochondrial DNA (mtDNA): the first fragment including partial sequences of 12S ribosomal RNA (rRNA), transfer RNA (tRNA)–Valine and 16S rRNA genes (total length 1942 bp), and the second fragment including complete sequences of the cytochrome *b* (cyt *b*) gene (1091 bp). Primers used for both PCRs and sequencing are summarized in Table 1. PCR protocol for 12S–16S rRNA roughly follows Green et al. (2010). For both primer pairs of 12S–16S rRNA, we used the following PCR protocol: (1) initial denaturation step at 94°C for 5 min; (2) 35 cycles of denaturation at 94°C for 1 min, annealing at 55°C for 1 min and extension at 72°C for 1 min; (3) final extension at 72°C for 10 min; and (4) cooling step at 4°C for storage. For cyt *b* sequences, we used a modified PCR protocol from Chen et al. (2014) with touchdown: (1) initial denaturation step at 94°C for 5 min; (2) 10 cycles of denaturation at 94°C for 1 min, annealing for 1 min with temperature decreasing from 50°C to 45°C (with cool-down at 0.5 °C per each cycle) and extension at 72°C for 1 min; (3) 24 cycles of denaturation at 94°C for 1 min, annealing at 45°C for 1 min and extension at 72°C for 1 min; (4) final extension at 72°C for 10 min; and (5) cooling step at 4°C for storage. All PCR products were sequenced in both directions by the "Evrogen" company at the Institute of Bioorganic Chemistry, Russian Academy of Science (Moscow, Rus-

sia). Obtained sequences were deposited in GenBank under accession numbers OP752557–OP752577 and OP764580–OP764588 (Table 2).

To examine the position of *O. macrurus* and *O. arenarius* in a mtDNA phylogeny of *Oligodon*, we aligned our newly obtained sequences with other available *Oligodon* sequences from GenBank (summarized in Table 2). The final sequence alignment contained 65 specimens, including 63 samples of 28 *Oligodon* species and two outgroup sequences of *O. porphyraceus* and *H. vibakari*, which were used to root the tree. Nucleotide sequences were initially aligned in MAFFT v.7 (Katoh and Standley 2013) with default parameters, and subsequently checked by eye in BioEdit 7.0.5.2 (Hall 1999) and slightly adjusted for translation when appropriate. We used the IQ-TREE web server (http://iqtree.cibiv.univie.ac.at; Trifinopoulos et al. 2016) to estimate optimal evolutionary models for our phylogenetic analyses. 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 7.0 (Kumar et al. 2016). Bayesian inference (BI) and Maximum Likelihood (ML) approaches were used to generate phylogenetic trees. The best-fitting model based on the AIC for both BI and ML analyses for 12S–16S rRNA fragments and the second codon partition of cyt *b* was the GTR+G+I model of DNA evolution. For the remaining partitions of cyt *b*, the AIC suggested the GTR+G model for the first codon partition, and the HKY+G+I model for the third codon partition. ML analyses were conducted using the IQ-TREE web server. Confidence in nodal topology was estimated by non-parametric bootstrapping (ML BS) with 100 pseudoreplicates (Felsenstein 1985). BI analyses were conducted in MrBayes 3.2.2 (Ronquist et al. 2012), and ran with Metropolis-coupled Markov chain Monte Carlo (MCMCMC) analyses with one cold chain and three heated chains for one million generations sampled every 1000 generations; two independent MCMCMC run iterations were performed, and 100 trees were discarded as burn-in. The convergence of the runs was checked by examining likelihood plots in TRACER v1.6 (Rambaut et al. 2020) and the effective sample sizes (ESS) were all above 200. Nodal support was assessed by calculating posterior probabilities (BI PP). Low ML BS and BI PP values (les than 50% and less than 0.90, respectively) were regarded as unresolved nodes (fide Huelsenbeck and Hillis 1993).

Morphological analysis

We included all examined *O. arenarius* ($n = 9$) and *O. macrurus* ($n = 11$), along with literature data from four specimens in our morphological dataset ($n = 24$). In all examined specimens, sex was determined by a ventral insertion near the tail base to detect the presence or absence of hemipenes. Color characters and patterns were recorded during examination of specimens in preservation. For some specimens these data were taken from digital im-

Table 1. A list of mitochondrial DNA primers used in this study.

Gene	Primer name	Sequence (5'–3')	Reference
12S–16S	Oligo12S2LM	A C A C A C C G C C C G T C A C C C T	Green et al. (2010)
12S–16S	Oligo16S5H	C T A C C T T T G C A C G G T T A G G A T A C C G C G G C	Green et al. (2010)
16S	Oligo16S1LM	C C G A C T G T T G A C C A A A A A C A T	Green et al. (2010)
16S	16S–H–1	C T C C G G T C T G A A C T C A G A T C A C G T A G G	Hedges (1994)
cytochrome b	H14910	G A C C T G T G A T M T G A A A A A C C A Y C G T T	Chen et al. (2014)
cytochrome b	THRSN2	C T T T G G T T T A C A A G A A C A A T G C T T T A	Chen et al. (2014)

ages that depicted their coloration in life. Morphological characters and morphometric ratios considered to be of taxonomic importance in *Oligodon* were used for species descriptions and followed a number of recent taxonomic treatments (David et al. 2008a, 2008b, 2011, 2012; Vassilieva et al. 2013; Vassilieva 2015; Nguyen et al. 2016, 2017, 2022; Nguyen et al. 2020; Qian et al. 2021; Mirza et al. 2021; Amarasinghe et al. 2021; Bandara et al. 2022; Das et al. 2022). Body measurements such as Snout-vent-length (SVL), tail length (TailL) and total length (TotalL) were taken using a flexible ruler. All other measurements were taken under a Leica dissecting microscope using Mitutoyo digital slide-calipers to the nearest 0.1 mm. Specimens were not examined by a single observer (JLL measured NHMUK specimens, Tan Van Nguyen measured DTU specimens, Morris Flecks and PG measured ZFMK specimens, PVY measured all other material). Dorsal scales were counted anteriorly at one head length behind the head, at midbody (halfway between the anterior 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 terminal scute 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. Head scale suture angle descriptions are adapted from Kaiser et al. (2019). When possible, hemipenes were everted from freshly preserved male specimens using the protocols outlined by Jiang (2010). Information about structure and size of the hemipenis was taken from preserved specimens both by examination of partially everted and in-situ organs, and from literature data. Terminology for hemipenial structures follows Dowling and Savage (1960). We use the term myoectases (coined from Wagner 1975) instead of the term "papillae" to describe appendages observed on the retracted hemipenes in-situ in some *Oligodon* species. These structures tend to transform into awn-shaped lobular protrusions when the organ is partially or fully everted.

The micro Computer Tomograph (µCT) scans of *O. arenarius* and *O. macrurus* were performed at the Paleontological Institute of the Russian Academy of Sciences (RAS) using a SkyScan 1172 Computer Tomography scanner (Bruker micro-CT, Kontich, Belgium). Scans were generated from one adult specimen of *O. arenarius*

(ZMMU Re-14502, paratype) and one adult specimen of *O. macrurus* (ZMMU Re-13857), both males. The heads of each specimen were scanned for 150 minutes at a voxel size of 5.3 µm and recorded data at every 0.2° rotation for 180° with an Aluminum 1.0 mm filter. The source voltage for the scan was 60 kV and the source current was 165 µA. For each specimen, a total of 1021 transmission images were reconstructed into a 1160 × 1160 matrix of 1000 TIFF slices using Nrecon 1.6.10.4 reconstruction software. Volume rendering and further processing was performed using Avizo 8.1. Cranial osteological descriptions were based on three dimensional (3D) volume renders of each specimen retrieved from Avizo. Terminology used in osteological descriptions are adapted from Cundall and Irish (2008).

The following linear measurements taken (all in mm), along with acronyms for morphological characters used in Tables 4–8 and statistical analyses are listed below: snout to vent length (SVL), measured from the tip of the snout to the vent; tail length (TailL), measured from the vent to the tip of the tail; total length (TotalL), sum of SVL and TailL; relative tail length to total length (TailLR) calculated as tail length to total length ratio; head length (HeadL) from the tip of the snout to the posterior margin of the rictus; head width (HeadW) measured at the widest part of the head immediately posterior to the eye; snout length (SnoutL), distance between the tip of the snout and anterior edge of eye; eye diameter (EyeD), maximal horizontal length of the eye; frontal scale length (FrontalL); frontal scale width (FrontalW); interorbital distance (IOD), the shortest distance between the eyes; and internarial distance (IND), distance between the nostrils. Additional morphological characters examined include the number of maxillary teeth (MT), counted based on examining the maxillary bone through µCT-scans or from examining the bone by pulling back the gum layer to count the teeth and its sockets; anterior scale rows (ASR), the number of scale rows at one head length behind the head; midbody scale rows (MSR), the number of scale rows at midbody (halfway between the posterior portion of the head and the vent); posterior scale rows (PSR), the number of dorsal scale rows at one head length prior to the vent; dorsal scale row formula (DSR), a given acronym summarizing the three dorsal scale row counts (i.e., ASR-MSR-PSR); ventral scales (VEN), the number of elongated belly scales starting at the first dorsal scale row to the vent, excluding the cloacal plate; subcaudal scales (SC), the number of paired subcaudal scales excluding the terminal scute; total body scales (TOTAL),

Table 2. 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 other tables or figures in the text. 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; WS, wildlife sanctuary.

No.	Sample ID	Genbank AN	Species	Country	Locality	Reference
1	ZMMU Re-13857	OP752557; OP752571	*Oligodon macrurus*	Vietnam	Khanh Hoa Prov., Hon Tre island	this work
2	ZMMU Re-11561	OP752565; OP752576	*Oligodon macrurus*	Vietnam	Ninh Thuan Prov., Nui Chua NP	this work
3	ZMMU Re-16807	OP752561; OP764583	*Oligodon macrurus*	Vietnam	Binh Thuan Prov., Phan Thiet	this work
4	ZMMU Re-16808	OP752562; OP764584	*Oligodon macrurus*	Vietnam	Binh Thuan Prov., Phan Thiet	this work
5	ZMMU Re-16809	OP752563; OP764585	*Oligodon macrurus*	Vietnam	Binh Thuan Prov., Phan Thiet	this work
6	ZFMK 88884	OP764587	*Oligodon macrurus*	Vietnam	Binh Thuan Prov., Mui Ne	this work
7	ZFMK 88885	OP764588	*Oligodon macrurus*	Vietnam	Binh Thuan Prov., Mui Ne	this work
8	ZMMU Re-14502	OP752568; OP752573	*Oligodon arenarius*	Vietnam	Ba Ria–Vung Tau Prov., Binh Chau–Phuoc Buu NR	this work
9	ZMMU Re-15136	OP752569; OP752574	*Oligodon arenarius*	Vietnam	Ba Ria–Vung Tau Prov., Binh Chau–Phuoc Buu NR	this work
10	ZMMU Re-14503	OP752566; OP752577	*Oligodon arenarius*	Vietnam	Ba Ria–Vung Tau Prov., Binh Chau–Phuoc Buu NR	this work
11	ZMMU Re-14504	OP752567; OP752572	*Oligodon arenarius*	Vietnam	Ba Ria–Vung Tau Prov., Binh Chau–Phuoc Buu NR	this work
12	VNMN 04724	OP752570; OP752575	*Oligodon arenarius*	Vietnam	Ba Ria–Vung Tau Prov., Binh Chau–Phuoc Buu NR	this work
13	ZMMU Re-16804	OP752558; OP764580	*Oligodon arenarius*	Vietnam	Ba Ria–Vung Tau Prov., Binh Chau–Phuoc Buu NR	this work
14	ZMMU Re-16805	OP752559; OP764581	*Oligodon arenarius*	Vietnam	Ba Ria–Vung Tau Prov., Binh Chau–Phuoc Buu NR	this work
15	ZMMU Re-16806	OP752560; OP764582	*Oligodon arenarius*	Vietnam	Ba Ria–Vung Tau Prov., Binh Chau–Phuoc Buu NR	this work
16	ZMMU NAP-10091	OP752564; OP764586	*Oligodon arenarius*	Vietnam	Ba Ria–Vung Tau Prov., Binh Chau–Phuoc Buu NR	this work
17	SIEZC 20201	MN395604; MN396765	*Oligodon rostralis*	Vietnam	Lam Dong Prov., Bidoup–Nui Ba NP	Nguyen et al. (2020)
18	ZMMU Re-14304	MN395601; MN396762	*Oligodon annamensis*	Vietnam	Dak Lak Prov., Chu Yang Sin NP	Nguyen et al. (2020)
19	CBC 01899	MN395602; MN396763	*Oligodon annamensis*	Cambodia	Pursat Prov., Veal Veng, Samkos WS	Nguyen et al. (2020)
20	UMMZ201913	HM591519	*Oligodon octolineatus*	Brunei	Tutong Dist., 3 km E of Tutong	Green et al. (2010)
21	ROM 35626	HM591526	*Oligodon chinensis*	Vietnam	Cao Bang Prov., Quang Thanh	Green et al. (2010)
22	ROM 30970	HM591528	*Oligodon chinensis*	Vietnam	Nghe An Prov., 24 km W of Con Cuong	Green et al. (2010)
23	ROM 34540	HM591527	*Oligodon chinensis*	Vietnam	Hai Duong Prov., Chi Linh	Green et al. (2010)
24	ROM 31032	HM591524	*Oligodon chinensis*	Vietnam	Vinh Phuc Prov., Tam Dao NP	Green et al. (2010)
25	ROM 30824	HM591525	*Oligodon chinensis*	Vietnam	Tuyen Quang Prov., Pac Ban	Green et al. (2010)
26	ROM 30823	HM591529	*Oligodon formosanus*	Vietnam	Tuyen Quang Prov., Pac Ban	Green et al. (2010)
27	ROM30826	HM591530	*Oligodon formosanus*	Vietnam	Vinh Phuc Prov., Tam Dao NP	Green et al. (2010)
28	ROM30939	HM591531	*Oligodon formosanus*	Vietnam	Cao Bang Prov., Ba Be NP	Green et al. (2010)
29	ROM35629	HM591533	*Oligodon formosanus*	Vietnam	Cao Bang Prov., Quang Thanh	Green et al. (2010)
30	ROM35806	HM591532	*Oligodon formosanus*	Vietnam	Hai Duong Prov., Chi Linh	Green et al. (2010)
31	ROM32261	HM591534	*Oligodon ocellatus*	Vietnam	Dak Lak Prov., Yok Don NP	Green et al. (2010)
32	ROM32260	HM591521	*Oligodon taeniatus*	Vietnam	Dak Lak Prov., Yok Don NP	Green et al. (2010)
33	ROM37091	HM591522	*Oligodon taeniatus*	Vietnam	Dong Nai Prov., Cat Tien NP	Green et al. (2010)
34	ROM32464	HM591523	*Oligodon barroni*	Vietnam	Gai Lai Prov., Krong Pa	Green et al. (2010)

No.	Sample ID	Genbank AN	Species	Country	Locality	Reference
35	USNM520625	HM591520	*Oligodon cf. taeniatus*	Myanmar	Chatthin, 2 km WNW Chatthin WS	Green et al. (2010)
36	CAS204963	HM591535	*Oligodon cyclurus*	Myanmar	Ayeyarwady Reg., Mwe Hauk	Green et al. (2010)
37	CAS215636	HM591536	*Oligodon cyclurus*	Myanmar	Sagaing Reg., Alaungdaw Kathapa NP	Green et al. (2010)
38	ROM37092	HM591504	*Oligodon cinereus*	Vietnam	Dong Nai Prov., Cat Tien NP	Green et al. (2010)
39	CAS213379	HM591506	*Oligodon cinereus*	Myanmar	Yangon Reg., Hlaw Ga NP	Green et al. (2010)
40	CAS205028	HM591507	*Oligodon cinereus*	Myanmar	Rakhine St., Rakhine Yoma Mts.	Green et al. (2010)
41	ROM32462	HM591501	*Oligodon cinereus*	Vietnam	Hai Duong Prov., Chi Linh	Green et al. (2010)
42	ROM29552	HM591502	*Oligodon cinereus*	Vietnam	Vinh Phuc Prov., Tam Dao NP	Green et al. (2010)
43	ROM30969	HM591503	*Oligodon cinereus*	Vietnam	Nghe An Prov., 24 km W of Con Cuong	Green et al. (2010)
44	CAS215261	HM591508	*Oligodon cinereus*	Myanmar	Shan St., Kalaw	Green et al. (2010)
45	CAS204855	HM591509	*Oligodon splendidus*	Myanmar	Mandalay Reg., Kyauk Se	Green et al. (2010)
46	USNM520626	HM591510	*Oligodon splendidus*	Myanmar	Chatthin, 2 km WNW Chatthin WS	Green et al. (2010)
47	CAS210693	HM591512	*Oligodon torquatus*	Myanmar	Magwe Reg., Pakokku	Green et al. (2010)
48	CAS215976	HM591513	*Oligodon torquatus*	Myanmar	Mandalay Reg., Min Gone Taung WS	Green et al. (2010)
49	CAS213822	HM591514	*Oligodon planiceps*	Myanmar	Magwe Reg., Shwe Set Taw WS	Green et al. (2010)
50	CAS210710	HM591515	*Oligodon theobaldi*	Myanmar	Mandalay Reg., Naung U	Green et al. (2010)
51	CAS213896	HM591516	*Oligodon theobaldi*	Myanmar	Magwe Reg., Shwe Set Taw WS	Green et al. (2010)
52	CAS213271	HM591517	*Oligodon cruentatus*	Myanmar	Yangon Reg., Hlaw Ga NP	Green et al. (2010)
53	ROM27049	HM591518	*Oligodon eberhardti*	Vietnam	Cao Bang Prov., Quang Thanh	Green et al. (2010)
54	TNHC59846	HM591511	*Oligodon maculatus*	Philippines	Mindanao, Barangay Baracatan	Green et al. (2010)
55	RS-OC	KC347328; KC347366	*Oligodon calamarius*	Sri Lanka	Kandy Dist.	Pyron et al. (2013)
56	RAP 504	KC347329; KC347367	*Oligodon sublineatus*	Sri Lanka	Kandy Dist.	Pyron et al. (2013)
57	RAP 483	KC347327; KC347365	*Oligodon arnensis*	Sri Lanka	Hambantota Dist.	Pyron et al. (2013)
58	RS 136	KC347330; KC347368	*Oligodon taeniolatus*	Sri Lanka	Polonnaruwa Dist.	Pyron et al. (2013)
59	CHS 683	MK194147; MK065575	*Oligodon ornatus*	China	—	Li et al. (Unpublished)
60	SYNU 1808001	MW489823	*Oligodon bivirgatus*	China	Hainan	Qian et al. (2021)
61	CHS 703	MK194159; MK201481	*Oligodon catenatus*	China		Li et al. (Unpublished)
62	CHS 187	MK193967; MK201318	*Oligodon lacroixi*	China		Li et al. (Unpublished)
63	CHS 850	MK194265; MK201568	*Oligodon albocinctus*	China		Li et al. (Unpublished)
Outgroups						
64	—	KP684155	*Hebius vibakari*	—	—	—
65	—	GQ181130	*Oreocryptophis poryphyraceus*	—	—	—

the sum of ventral and subcaudal scales and the cloacal plate (included as one scale regardless of whether the plate is single or divided); subcaudal ratio (SCR), namely the ratio between the number of subcaudal scales and the number of total body scales given as a decimal value; cloacal plate (CP), the number of terminal ventral scales immediately anterior to vent (given as single for one scale, and divided for two scales); condition of nasal scale (NASAL), given as either vertically divided, entire, or partially divided; condition of loreal scale (LOREAL), given as present or absent; supralabials (SL), the number of scales on upper lip; number of supralabials in contact with the eye (SL-Eye); infralabials (IL), the number of scales on lower lip; infralabials contacting each other (IL-contact), the number of pairs of infralabial scales in contact; infralabials contacting the anterior chin shields (IL-CS), the number of infralabial scales contacting the anterior chin shields; number of preocular scales (PrO); number of presubocular scales (PrsO); number of postocular scales (PtO); number of anterior temporals (Ate), the number of temporal scales in contact with the postocular scales; number of posterior temporals (Pte), the number of temporal scales immediately contacting the anterior temporal scales. Symmetric characters are given in left/right order. We quantified hemipenis shape into two character states: (1) unilobed, a single organ with no lobes at the apex; (2) bilobed, organ containing two lobes at its apex. Hemipenis length was quantified relative to the number of subcaudal scales when in-situ and when partially everted.

For statistical analyses, we made adaptations to a workflow popularized by Chan and Grismer (2021) to determine whether *O. arenarius* and *O. macrurus* differ morphologically from one another. All statistical analyses were conducted in R version 4.1.2 (R Core Team 2022). Univariate analyses were ran separately on males, females and on a pooled dataset with both sexes to reduce the effects of sexual dimorphism; however, we only ran multivariate statistics on the pooled datasets because we lacked sufficient sample sizes for males/females. We used Shapiro–Wilks Tests and Levene's Tests to test for normality and heteroscedasticity, respectively. We used Mann–Whitney U Tests (also known as Wilcoxon signed-rank tests) using the *pairwise.wilcox.test*() command and Student's T-Tests using the *t.test*() command from the *stats* package to compare quantitative differences between species. Tests for sexual dimorphism within species were performed using Mann–Whitney U Tests. For all univariate statistics, differences between characters were determined to be statistically significant when p-values were less than 0.05. After univariate analyses, we log-transformed the pooled 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 between species. We ran Mann–Whitney U Tests on PC1 and PC2 factors using the same procedures described above to determine if the PC centroids of the two taxa were also significantly different. Following this, we ran the non-transformed portion of the dataset under a Discriminant Function Analysis (DFA; also known as a Linear Discriminant Analysis, LDA) using the *MASS* Package in R (Venables and Ripley 2002) to establish if the two species could be separated unambiguously based on the morphological data. The *predict*() command in *MASS* was used to calculate the posterior probability of *a priori* membership for each individual. All data in both the PCA and DFA were scaled to standard deviation prior to analysis to help eliminate the effects of covariance and ensure data was normally distributed. Results from multivariate analyses were visualized using the *ggplot2* package (Wickham 2016). The following morphological characters were used for univariate and multivariate 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), number of postocular scales (PtO), and number of posterior temporal scales (PT).

Results

Molecular analyses

The final concatenated alignment of 12S rRNA–16S rRNA and cyt *b* gene sequences contained 3033 base pairs, of which, 1889 sites were conserved and 1109 sites were variable, of which 782 were found to be parsimony informative. The transition-transversion bias for (I) was estimated as 2.31. Nucleotide frequencies were 37.2% (A), 22.4% (T), 25.3% (C), and 15.0% (G) (all data given for ingroups only). Our mtDNA-based genealogy for the genus *Oligodon* (Fig. 2) correlates well with the set of phylogenetic relationships obtained from previous phylogenies (Nguyen et al. 2020; Qian et al. 2021; Mirza et al. 2021; Das et al. 2022; Yushchenko and Lee et al. 2023) and confirms the inferring of five major clades within the genus, along with the suggested presence of one additional clade (see Fig. 2). The first clade is comprised of Indian and Sri Lankan species, including *Oligodon taeniolatus* (Jerdon, 1853), *Oligodon calamarius* (Linnaeus, 1758) and *Oligodon sublineatus* Duméril, Bibron & Duméril, 1854 (1.0/98; hereafter node support values are given for BI PP/ML BS, respectively). The species *Oligodon arnensis* (Shaw, 1802) was recovered in a more deeper position than in Nguyen et al. (2020), but its relationships compared to the first clade remains unclear; (1/–). The second clade includes species in the morphologically defined *Oligodon cinereus* and *O. torquatus* species groups (sensu Green et al. 2010; Vassilieva 2015), including *Oligodon splendidus* (Günther, 1875), *Oligodon theobaldi* (Günther, 1868), *Oligodon cruentatus* (Günther, 1868), *Oligodon torquatus* (Boulenger, 1888), *Oligodon planiceps* (Boulenger, 1888), *O. cinereus* and the Philippines endemic *Oligodon maculatus* (Taylor, 1918); (1.0/98).
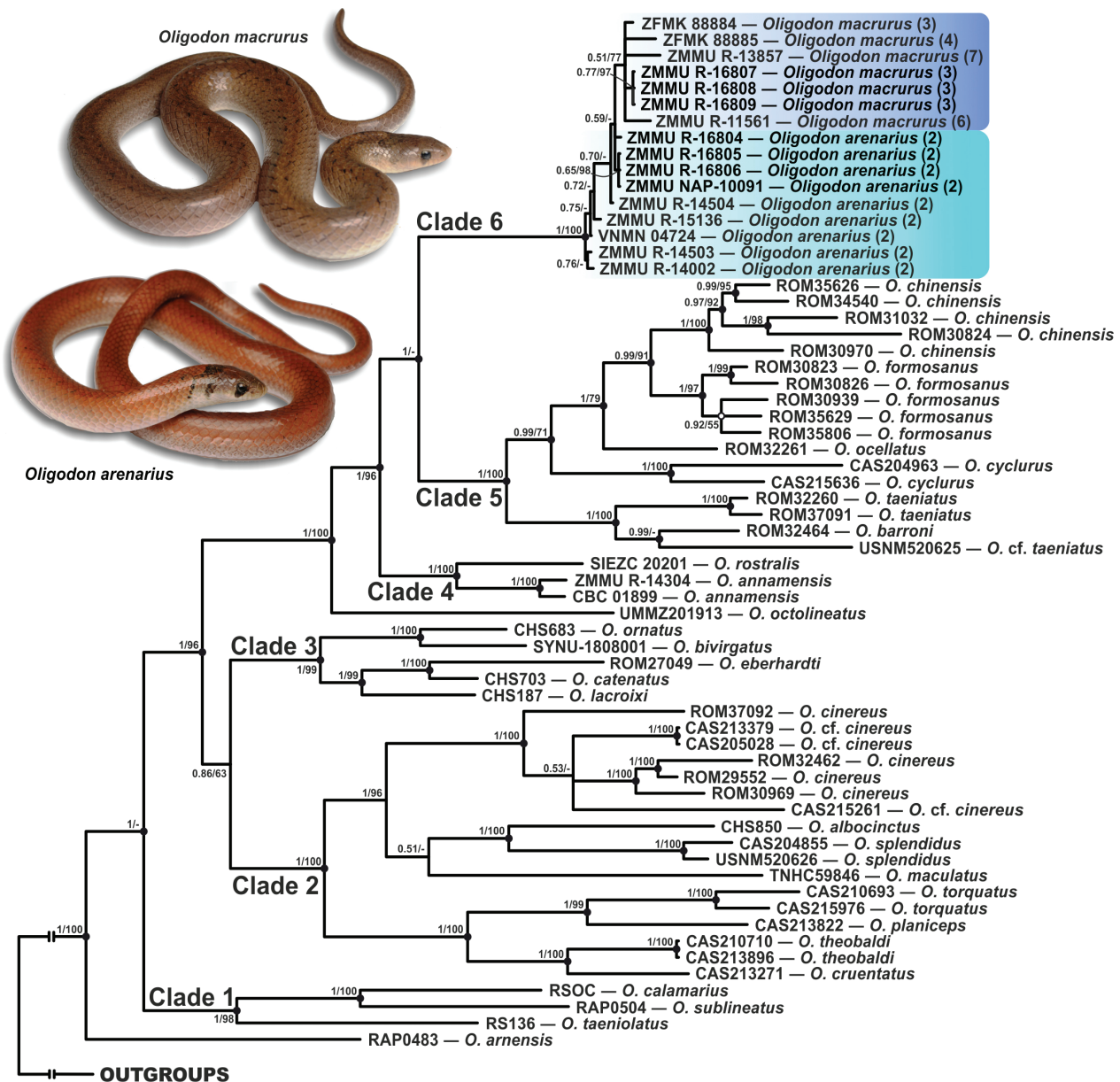
Figure 2. Bayesian inference tree of *Oligodon* derived from the analysis of 3,019 bp of 12S rRNA–16S rRNA and cyt *b* mitochondrial DNA gene sequences. For voucher specimen information and GenBank accession numbers see Table 1. Numbers at tree nodes correspond to BI PP/ML BS support values, respectively; an en-dash denotes no support. Outgroup taxa are not shown. Colors of clades and locality numbers correspond to those in Fig. 1. Photographs taken by Nikolay A. Poyarkov Jr.

The third clade mostly contains species from northern Vietnam and southern China, including *Oligodon lacroixi* Angel & Bourret, 1933, *Oligodon eberhardti* Pellegrin, 1910, *Oligodon ornatus* Van Denburgh, 1909, and *Oligodon bivirgatus* Qian et al., 2021; (1.0/99). The fourth clade includes species from southern Vietnam, including *Oligodon annamensis* Leviton, 1953 and the recently described *Oligodon rostralis* Nguyen et al., 2020 (1.0/100). The fifth major clade includes other species of *Oligodon* from Indochina and southern China largely assigned to the *Oligodon cyclurus–taeniatus* species group sensu Green et al. (2010); (1.0/98). Our data suggest that this clade can be divided into two more specific subclades, contrasting some of the phylogenetic results presented by Nguyen et al. (2020). The first cluster, includes *Oligodon taeniatus* (Günther, 1861) and *Oligodon barroni* (Smith,

1916), joint with *Oligodon cyclurus* (Cantor, 1839) and one specimen of *Oligodon* cf. *taeniatus* with unclear species status (1.0/76). The second cluster includes the remaining three species, namely *Oligodon formosanus* (Günther, 1872), *Oligodon chinensis* (Günther, 1888) and *Oligodon ocellatus* (Morice, 1875); (1.0/77). Finally, the sixth clade includes our samples of *O. macrurus* and *O. arenarius* (1.0/100), which tend to group with the fifth clade, but with no certain node support (1/–). The species *Oligodon octolineatus* (Schneider, 1801) from Sundaland is recovered sister to Clades 4–6 with strong support (1.0/100) (see Fig. 2).

The uncorrected p-distances for the 16S rRNA gene fragment among and within examined *Oligodon* species are presented in Table 3. Intraspecific distances varied significantly and ranged from p = 0% in a number of ex-

Table 3. Genetic differentiation of *Oligodon*. Uncorrected p-distances (given as percentages) between sequences of 12S–16S rRNA (below diagonal) and intraspecific genetic p-distances of *Oligodon* species (on diagonal) included in phylogenetic analyses.

No.	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
1	O. macrurus	0.6																											
2	O. arenarius	0.5	0.4																										
3	O. annamensis	5.2	4.9	1.0																									
4	O. rostralis	6.1	5.6	4.1	—																								
5	O. arnensis	6.2	5.9	5.5	6.1	—																							
6	O. calamarius	7.0	6.5	6.3	6.6	6.6	—																						
7	O. sublineatus	7.7	7.2	6.4	7.3	5.9	3.1	—																					
8	O. taeniolatus	6.7	6.3	7.1	6.9	5.4	3.8	3.3	—																				
9	O. octolineatus	6.8	6.5	5.0	4.5	7.9	6.9	7.9	8.3	—																			
10	O. chinensis	6.3	6.1	5.5	4.9	5.6	6.5	7.2	7.0	7.1	0.8																		
11	O. ornatus	6.8	6.6	5.3	6.9	5.7	4.7	5.0	5.2	7.9	6.3	—																	
12	O. cinereus	7.8	7.4	7.1	8.1	7.1	6.3	6.6	6.1	8.7	7.5	6.9	3.7																
13	O. eberhardti	8.4	8.1	6.9	7.9	6.9	6.9	6.7	7.2	8.7	7.4	5.5	6.9	—															
14	O. bivirgatus	8.0	7.8	5.5	7.3	6.1	5.4	5.2	5.4	8.6	7.3	2.4	6.5	6.0	—														
15	O. albocinctus	7.4	7.0	6.0	5.9	6.1	5.4	5.4	5.7	6.2	6.3	6.9	5.5	7.4	6.1	—													
16	O. lacroixi	6.0	5.6	5.0	5.7	5.0	4.5	5.7	5.0	6.4	6.1	3.5	5.9	4.3	3.8	5.2	—												
17	O. catenatus	7.1	6.8	5.2	6.1	5.2	5.9	5.7	6.1	7.4	6.1	4.3	6.3	2.2	4.7	6.6	3.1	—											
18	O. formosanus	5.5	5.3	4.7	4.3	4.9	5.7	6.4	6.2	6.0	1.7	5.5	7.3	7.3	6.7	6.1	5.2	5.5	0.6										
19	O. ocellatus	6.3	6.1	4.6	4.5	5.9	6.6	7.1	7.1	6.0	3.7	6.1	6.9	7.9	5.9	5.7	5.0	6.1	3.3	—									
20	O. taeniatus	4.8	4.6	4.5	4.6	6.1	6.3	7.2	6.8	6.3	3.9	5.8	7.4	7.8	7.0	6.8	5.6	6.3	3.6	3.9	0.2								
21	O. barroni	5.1	5.0	5.8	5.7	7.3	7.3	8.3	8.0	6.9	4.9	7.1	8.5	9.1	8.3	7.3	6.4	7.6	4.6	5.0	2.8	—							
22	O. cyclurus	6.6	6.5	5.4	6.0	6.9	6.5	7.3	7.2	7.5	5.7	6.4	7.0	8.1	6.9	6.6	6.0	6.6	5.4	4.0	3.4	5.1	3.1						
23	O. splendidus	7.2	6.8	7.2	7.3	7.2	5.2	5.4	5.0	8.3	6.2	6.6	4.7	7.4	6.4	4.5	5.9	6.9	6.5	6.4	6.5	7.6	6.7	0.5					
24	O. torquatus	8.3	8.0	8.3	9.9	8.4	8.4	8.6	8.3	11.1	10.0	8.6	7.4	9.7	9.1	9.7	8.6	8.4	9.2	9.7	7.8	9.1	8.6	7.6	1.4				
25	O. planiceps	7.4	7.1	7.2	7.8	7.3	5.9	7.1	6.2	9.3	7.8	7.3	6.3	8.9	7.8	7.1	6.9	7.6	6.9	7.3	7.1	8.3	7.7	5.9	5.1	—			
26	O. theobaldi	7.0	6.6	7.5	8.5	7.3	6.9	7.6	5.9	9.3	8.7	7.3	6.1	8.6	7.8	7.8	6.6	7.3	7.9	8.3	6.5	8.0	7.5	6.1	2.5	4.3	0.0		
27	O. cruentatus	7.7	7.3	8.2	9.2	8.0	7.6	8.3	6.6	10.0	9.4	8.0	6.8	9.3	8.5	8.5	7.3	8.0	8.7	9.0	7.2	8.7	7.9	6.9	3.2	5.0	0.7	—	
28	O. maculatus	7.5	7.3	7.1	8.3	6.1	5.7	5.2	4.7	9.3	6.5	5.7	5.2	5.5	5.7	5.4	5.9	5.9	6.3	6.9	7.0	8.3	7.5	3.8	8.0	6.6	6.6	7.3	—

Table 4. Resulting P-values from univariate morphological analyses of sexual dimorphism in *Oligodon arenarius* and *Oligodon macrurus* specimens. Characters in bold are considered statistically significant. Cells denoted with a "—" symbol were not examined. All characters were examined using Mann–Whitney U Tests. Abbreviations include "n" standing for number of specimens; "(m)" standing for males, and "(f)" standing for females.

Character	*Oligodon arenarius*	*Oligodon macrurus*	Combined (both species)
n	6 (m) 3 (f)	9 (m) 6 (f)	15 (m) 9 (f)
TailLR	**0.023810**	**0.000400**	**1.53E-06**
MSR	—	0.447500	0.350200
VEN	**0.026880**	**0.000799**	**0.002337**
SC	**0.026880**	**0.001723**	**0.000063**
TOTAL	**0.027530**	**0.001598**	0.083700
SCR	**0.023810**	**0.000400**	**1.53E-06**
SL	0.637400	0.313400	0.236100
SLE	0.637400	0.286400	0.222500
IL	0.637400	0.735700	0.519500
ILCS	0.776200	0.539200	0.857500
PtO	—	0.819500	0.678800
PT	—	0.496200	0.491100

Table 5. Resulting P-values from univariate morphological analyses comparing *Oligodon arenarius* and *Oligodon macrurus* specimens. Characters in bold are considered statistically significant. Cells denoted with a "/" symbol were not examined. All characters were examined using Mann–Whitney U Tests, except for those denoted with an asterisk, which were performed using Student's T-Tests. Abbreviations include "n" standing for number of specimens; "(ar)" standing for *O. arenarius*, and "(ma)" standing for *O. macrurus*.

Character	Males	Females	Pooled (Both sexes)
n	6 (ar) 9 (ma)	3 (ar) 6 (ma)	9 (ar) 15 (ma)
TailLR	**1.38E-06***	**0.010790***	0.083780
MSR	0.496200	0.373000	0.177200
VEN	**0.002607**	**0.000723***	**0.001270***
SC	**7.02E-07***	**0.001027***	**0.006939***
TOTAL	**4.71E-06***	**0.000014***	**1.25E-07***
SCR	**7.77E-08***	0.057290*	0.106900*
SL	0.477300	0.637400	0.380100
SLE	0.437300	0.637400	0.325200
IL	0.865200	0.637400	0.645500
ILCS	0.590600	0.721600	0.857500
PtO	0.273200	—	0.107400
PT	0.496200	—	0.491100

amined species to p = 3.7% in the *O. cinereus* complex and p = 3.1% in the *O. cyclurus* complex, which is most likely explained by the incomplete taxonomy of these groups (David et al. 2008a; Green et al. 2010; David et al. 2011). A more detailed study including topotypic materials on these species complexes is desired. The interspecific genetic distances within examined *Oligodon* varied from p = 2.2% (*O. catenatus* / *O. eberhardti*) to p = 11.1% (*O. octolineatus* / *O. torquatus*) (Table 3). The *O. macrurus–arenarius* clade is highly divergent from other congeners, however the sequence divergence in 16S rRNA gene between *O. macrurus* and *O. arenarius* reached only 0.5%, which is notably lower than the genetic differentiation between many other *Oligodon* species (see Table 3). Moreover, samples of *O. arenarius* in the phylogeny are recovered paraphyletic with respect to the samples of *O. macrurus* (see Fig. 2).

Morphological analyses

Four characters (VEN, SC, TOTAL, SCR) exhibited normal distributions in all datasets. Relative tail length (TAILR) was the only normally distributed character in the male and female datasets. All characters were heteroscedastic, except for VEN, which exhibited a non-heteroscedastic distribution in the male and combined datasets. Univariate analyses for both male, female and combined datasets showed significant differentiation in the number of body scales and relative tail length between *O. arenarius* and *O. macrurus* (Table 4). Strong sexual dimorphism in body scales and relative tail length were also noted within each species, and when both species were pooled together into one dataset to increase sampling size (Table 5). PCA plots revealed that the two species are modestly separated in morphospace, although consider-

Table 6. Summary of PC scores and statistics for the Principal Components Analysis (PCA) consisting of *Oligodon arenarius* and *Oligodon macrurus* specimens. Abbreviations are listed in the materials and methods. Cells denoted with a "——" symbol were unavailable or not examined.

Dataset	Both Sexes			Males			Females		
Character	PC1	PC2	PC3	PC1	PC2	PC3	PC1	PC2	PC3
Standard deviation	2.023249	1.558242	1.295387	2.216595	1.657350	1.181847	2.005975	1.984818	1.225493
Proportion of Variance	0.341130	0.202340	0.139840	0.409440	0.228900	0.116400	0.365810	0.358140	0.136530
Cumulative Proportion	0.341130	0.543470	0.683310	0.409440	0.638340	0.754740	0.365810	0.723950	0.860480
Eigenvalues	4.093536	2.428118	1.678028	4.913293	2.746809	1.396762	4.023936	3.939504	1.501833
TailLR	–0.447052	0.249969	0.093015	0.411575	0.080445	–0.030511	0.397780	0.281640	–0.097666
MSR	0.079393	0.451285	0.033150	–0.049786	0.399299	–0.488503	0.310159	–0.298034	–0.400251
VEN	0.121912	–0.218162	–0.658141	0.392885	0.137416	0.125126	–0.108163	0.466711	–0.090903
SC	–0.464651	0.195618	–0.067444	0.441817	0.061523	0.033930	0.244822	0.422401	–0.041109
TOTAL	–0.371280	0.051907	–0.458409	0.442466	0.092669	0.062183	0.021248	0.496294	–0.080813
SCR	–0.453981	0.232653	0.094943	0.427830	0.031792	0.007443	0.374383	0.239351	0.005688
SL	0.265283	0.414914	–0.134708	–0.094948	0.483870	0.244680	0.424064	–0.215350	0.195111
SLE	0.282019	0.464760	–0.157841	–0.098610	0.552936	0.030383	0.424064	–0.215350	0.195111
IL	0.174564	0.223896	–0.251328	–0.023924	0.327676	–0.458959	–0.013762	–0.178912	–0.724594
ILCS	–0.123575	–0.205080	–0.171953	0.193702	–0.111878	–0.573417	–0.376499	0.019319	–0.169292
PtO	0.126148	0.251417	0.251800	–0.168949	0.286459	0.131426	–0.178102	–0.082965	0.428848
PT	–0.086975	0.218224	–0.366335	0.119898	0.244964	0.349555	—	—	—

able overlap exists (Fig. 3A). PC1 accounted for 33.4% of the total variance and loaded most heavily for subcaudals and relative tail length (TAILR and SCR). PC2 accounted for 20.2% of the total variance and loaded most heavily for supralabials (SL and SLE) and midbody scale rows (MSR). PC3 accounted for 14.1% of the total variance and loaded most heavily for the number of ventral scales (VEN). More details on the PCA results can be found in Table 6. Contrary to the PCA, the results from the DFA show that neither species exhibit any overlap with one another in the density plots, and were clearly separated (Fig. 3B). The combined univariate and multivariate analyses show that *O. arenarius* from *O. macrurus* differ in body scalation and tail length, as previously mentioned by Vassilieva (2015).

Besides body scalation, two other morphological traits are considered distinct in *O. arenarius* and *O. macrurus*, specifically the hemipenes and the condition of the loreal scale (absent in *O. arenarius* vs. usually present in *O. macrurus*). However, Nguyen et al. (2021) reported a specimen of *O. arenarius* with a loreal scale on one side of the head. Our examination of additional specimens confirms that the loreal scale condition is variable within *O. arenarius*, with three of the nine specimens we examined bearing the scale on at least one side of the head. We also everted the hemipenes of freshly preserved *O. arenarius* and *O. macrurus* specimens and found that the organs more closely resemble the structuring described by Nguyen et al. (2021), rather than Vassilieva (2015) (Fig. 4). The hemipenes in *O. macrurus* specimens also match those in Smith (1943), who described the retracted organ of this species in-situ. We could not find any putative differences in ornamentation or overall shape between the organs of *O. arenarius* and *O. macrurus*. In both species the hemipenes

are deeply bilobed, with the point of bifurcation starting around one-third of the organ's length. No spinous calyces were found along the lobes or at the base of the hemipenes, nor myoectases. It is likely the eversion process attempted by Vassilieva (2015) failed to fully evert the organ, which resulted in the small unilobed looking hemipenes figured in the original description of *O. arenarius* (Fig. 4D).

The skulls of *O. macrurus* and *O. arenarius* are quite similar in cranial shape, bone structure, and number of teeth (Fig. 7). Nevertheless, some differences can be revealed. Between the two specimens examined, the neurocranium in *O. macrurus* is flat and elongated, whereas it is rounder and stouter in *O. arenarius*. The nasals in *O. macrurus* have a more humped profile and are fused anteriorly forming the sharp tip of the snout; in *O. arenarius* the nasals are less humped and blunter at the tip. The frontals in *O. macrurus* are well separated from each other and slightly concave laterally in dorsal view, but in *O. arenarius* are more ossified and less concave. The parietal segment of the skull in *O. macrurus* is longer, thus making the whole skull more elongated. The postorbitals in *O. macrurus* are also longer and thinner distally than *O. arenarius*. The total number of teeth in *O. macrurus* is higher: 12/12 maxillary teeth (vs. 11/10), 15/17 mandibular teeth (vs. 14/14), 12/10 pterygoid teeth (vs. 10/9). However, our analyses is still based on only two µCT-scans (one model per each species). Since intraspecific and interspecific variation within and between *Oligodon* taxa have not been investigated thoroughly, all the differences noted probably represent individual variation, and we interpret these differences with caution. We therefore consider the overall external morphological differences between *O. arenarius* and *O. macrurus* to be negligible.
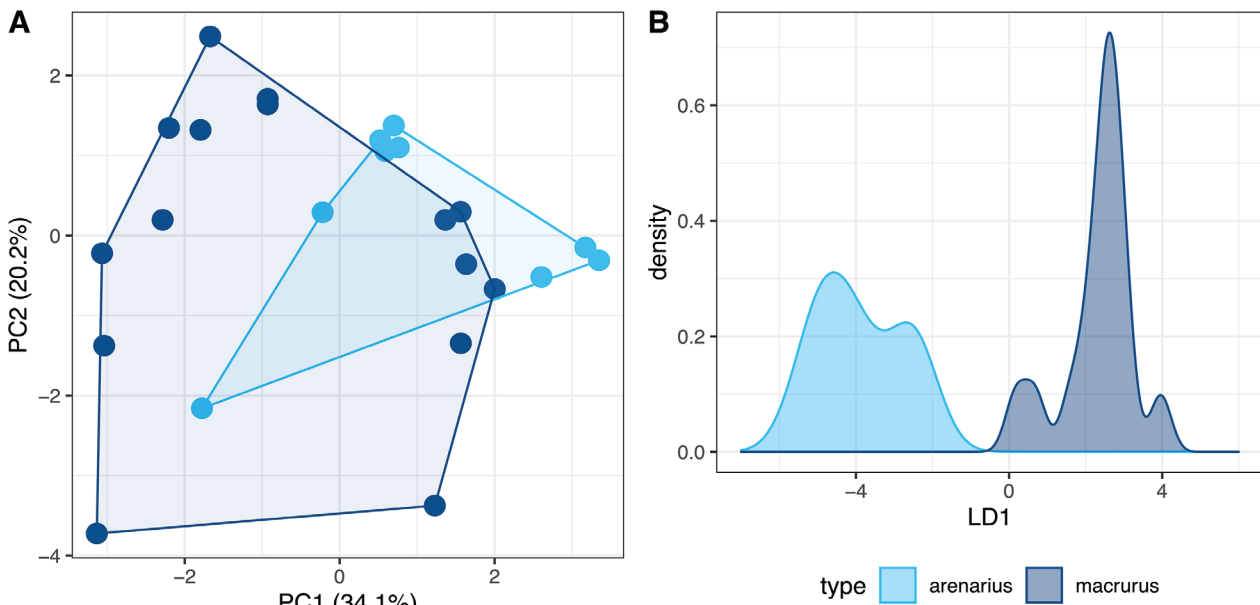
Figure 3. Multivariate analyses of morphology between *Oligodon arenarius* (light blue) and *O. macrurus* (dark blue) including: **A** plot of Principal Components Analysis (PCA) comprised of data from both sexes; **B** density plot of Discriminant Function Analysis (DFA) comprised of data from both sexes.

Taxonomic conclusions

Our phylogenetic analyses demonstrate that the genetic differentiation between *O. arenarius* and *O. macrurus* is much lower ($p = 0.5\%$) than the pairwise distances observed in other species within *Oligodon*. These results are more complex when our morphological data are incorporated (see above), which show significant differences in body scalation and relative tail length between *O. arenarius* and *O. macrurus*, but weak differences in other characters (i.e., color pattern, head scalation, hemipenial morphology and cranial osteology). Based on our species concept, delimitation criteria (see Materials and methods) and combined evidence, it is clear that the specific status *O. arenarius* should be downgraded. However, two taxonomic acts could be considered. Either *O. arenarius* could be synonymized with *O. macrurus* as a subjective junior synonym, or *O. arenarius* could be relegated as a subspecies of *O. macrurus*. The first decision would eliminate the paraphyly present between the two taxa and consider a single morphologically variable species, while the second would conserve the recognition of a potentially morphologically divergent population but maintain the paraphyly recovered in the phylogeny. We elect to choose the first decision and consider *O. arenarius* a morphologically divergent population within the variable *O. macrurus*. Synonymizing the two taxa would not affect the diagnosis of *O. macrurus* amongst other congeners, and stabilizes the paraphyly demonstrated by our phylogenetic results. Additional justifications for our decision are provided in the discussion section.

Redescription of *Oligodon macrurus*

The addition of *O. arenarius* into the synonymy of *O. macrurus*, along with the paucity of known specimens,

prompts us to provide a formal redescription of this species. The type specimen of *Simotes violaceus macrurus*, collected from "Annam: Pointe Lagan (sur les dunes)" (now Cape Lagan or Mui La Gan, northeast Binh Thuan Province, Vietnam), was once part of the herpetological collection of the Muséum National d'Histoire Naturelle (MNHN) in Paris, but was lost between 1943 to 2009 (Nguyen et al. 2009; Geissler et al. 2011; Wallach et al. 2014; Uetz et al. 2019). Owing to the fact that the name-bearing type no longer exists and there is no other type material by the original author, we elect to designate a neotype for this species in compliance with the International Code of Zoological Nomenclature (ICZN; Article 72.2 and Article 75) (Anonymous 1999). We choose specimen ZFMK 88885 as the neotype for *Oligodon macrurus* (Angel, 1927) due to its close proximity to the original type locality and overall similarity with the lost holotype. As a result of this action, the type locality of *O. macrurus* is emended to the catalogued locality of this specimen in accordance with ICZN Article 76.3. The new type locality for *O. macrurus* is now the "coastal dune area about 1 km from the coast line, Mui Ne, Binh Thuan Province, Vietnam (near 10°57'59.6"N, 108°19'46.5"E)", based on ZFMK 88885 collected DOR by Peter Geissler on 27 April 2009. The neotype is on permanent loan to the herpetological collection of the Zoologisches Forschungsmuseum Alexander Koenig (ZFMK) in Bonn, Germany.

Oligodon macrurus (Angel, 1927)

Figs 2, 4–6; Tables 4–8

Simotes violaceus macrurus: Angel (1927: 496). *Holotype*: "Annam: Pointe Lagan (sur les dunes)" [= now Cape Lagan or Mui La Gan, Binh Thuan Province, Vietnam]

Synonymy. *Oligodon arenarius*: Vassilieva (2015: 212). *Holotype*: "Binh Chau–Phuoc Buu Nature Reserve, Xuyen Moc District, Ba Ria–Vung Tau Province, southern Vietnam, coordinates 10°29′46″N, 107°27′54″E, elevation 5 m a.s.l."

Holotype. MNHN-RA 1928.0119, an adult male from "Annam: Pointe Lagan (sur les dunes)" (now Cape Lagan or Mui La Gan, Binh Thuan Province, Vietnam, 11°10′N, 108°42′E), collected by M. Pierre Chevey on 17 May 1926 (Chevey 1927). Lost fide Nguyen et al. (2009) and Uetz et al. (2019).

Neotype. ZFMK 88885, an adult male from "coastal dune area about 1 km from the coast line", Mui Ne, Binh Thuan Province (10°57'N, 108°19'E), collected by Peter Geissler on 27 April 2009.

Referred specimens (n = 23). All from Vietnam. NHMUK 1938.8.7.39 male, "Nha Trang, S. Annam" (now Nha Trang, Khanh Hoa Province), collected by M. A. Smith; NHMUK 1969.1854 female, "Saigon" (now Ho Chi Minh City); NHMUK 1969.1855–1856 two females, "near Na Thrang" (now Nha Trang, Khanh Hoa Province); ZMMU Re-11561 female, Nui Chua National Park, Ninh Thuan Province (11°46′N, 109°09′E), collected by V. V. Bobrov on September 10, 2003; ZMMU Re-13857 male, Hon Tre Island, Khanh Hoa Province (12°11′N, 109°17′E), collected by A. B. Vassilieva on 2 January 2011; ZMMU Re-15136 female, paratype of *O. arenariu*s, Binh Chau–Phuoc Buu Nature Reserve, Binh Chau, Xuyen Moc District, Ba Ria–Vung Tau Province (10°29′N, 107°27′E), collected by A. B. Vassilieva on 9 November 2010; ZMMU Re-14502 male, paratype of *O. arenarius*, Binh Chau–Phuoc Buu Nature Reserve, Binh Chau, Xuyen Moc District, Ba Ria–Vung Tau Province (10°32′N, 107°28′E), collected by A. B. Vassilieva on 9 November 2010; ZMMU Re-14503 male, holotype of *O. arenarius*, Binh Chau–Phuoc Buu Nature Reserve, Binh Chau, Xuyen Moc District, Ba Ria–Vung Tau Province (10°29′N, 107°27′E), collected by A. B. Vassilieva on 14 November 2014; ZMMU Re-14504 female, paratype of *O. arenarius*, Binh Chau–Phuoc Buu Nature Reserve, Binh Chau, Xuyen Moc District, Ba Ria–Vung Tau Province (10°29′N, 107°27′E), collected by A. B. Vassilieva on 16 November 2014; VNMN 04274 female, paratype of *O. arenarius*, Binh Chau–Phuoc Buu Nature Reserve, Binh Chau, Xuyen Moc District, Ba Ria–Vung Tau Province (10°30′N, 107°28′E), collected by N. A. Poyarkov on 10 July 2012; UNS05001–05002, two males, Mui Ne, Binh Thuan Province (10°58′N, 108°20′E), collected by P. Geissler on 4–5 March 2011 respectively (Geissler et al. 2011); DTU 532, female, Mui Ne, Binh Thuan Province, collected by Hieu Minh Pham on July 2019; ITB-CZ 6884, male, on the coastal road near Ho Coc Resort, Xuyen Moc District, Ba Ria–Vung Tau Province, Vietnam (10°29′49.2″N, 107°27′36″E), collected on 15 June 2019 by Sang Ngoc Nguyen and Vu Dang Hoang Nguyen (Nguyen et al. 2021); ZMMU Re-16804–16806, three males, previously identified as *O. arenarius*, Binh Chau–
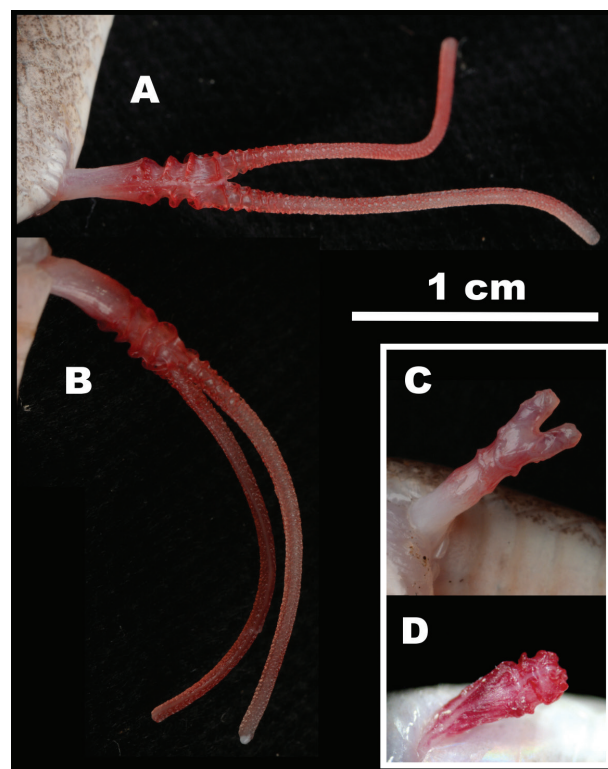

Figure 4. Hemipenes of *Oligodon arenarius*. **A** sulcal and **B** asulcal side of the fully everted hemipenis of ZMMU Re-16804; **C** partially everted hemipenis of the same specimen demonstrating the overall similar shape to the partially everted organ of the holotype figured by Vassilieva (2015); **D** partially everted hemipenis of the holotype ZMMU Re-14503 from the original description (Vassilieva 2015), copyright Magnolia Press, reproduced with permission from the copyright holder. Photographs A–C taken by Nikolay A. Poyarkov Jr.

Phuoc Buu Nature Reserve, Binh Chau, Xuyen Moc District, Ba Ria–Vung Tau Province (10°30′N, 107°28′E), collected by N. A. Poyarkov and P. V. Yushchenko on 24–28 December 2020; ZMMU Re-16807–16809, three males, Phan Thiet City, Binh Thuan Province (10°56′N, 108°17′E), collected by Hieu Minh Pham on October 2020; ZFMK 88884, female from Mui Ne, Binh Thuan Province (10°56′N, 108°17′E), collected by Peter Geissler on 27 April 2009 .

Revised diagnosis. An *Oligodon* species distinguished from all other members of the genus by having the following morphological characters: 1) medium body size in adults (TotalL 245–510 mm); 2) a very long relative tail length, especially in males (TAILR 25.4%–37.3% in males, 14.0–19.6% in females; SCR 29.3%–38.7% in males, 20.0%–25.0% in females); 3) head small and slightly spade-shaped, comparatively short and wide (HW/HL 0.53–0.90); 4) dorsal scale rows usually 17-17-15, rarely 18 scale rows anteriorly and 16 rows at midbody; 5) ventral scales 131–152 in males, 139–169 in females, with significant sexual dimorphism; 6) subcaudals 60–94 in males, 36–48 in females with significant sexual dimorphism; 7) total body scales trending towards sexual dimorphism, 191–243 in males, 178–214 in fe-

Figure 5. Photographs of the preserved neotype of *Oligodon macrurus* (ZFMK 88885), an adult male specimen. **A** dorsal and **B** ventral views of the whole specimen, and **C** dorsal **D** ventral, **E** right lateral and **F** left lateral views of the head. Scale bars for A–B represent 10.0 mm, and scale bars for C–F represent 5.0 mm. All photographs taken by Morris Flecks, used with permission.

males (178–243 in both sexes); 8) cloacal plate single; 9) 1 preocular and usually 2 postoculars (rarely 1 postocular); 10) nasal scale divided, loreal scale and presubocular condition variable (can be present or absent); 11) usually 8 supralabials (rarely 7), with the 4th and 5th scales in contact with the orbit (occasionally just the 4th supralabial contacting the orbit); 12) usually 9 infralabials (rarely 8 or 10), anterior 4th and 5th infralabials contacting the first

pair of chin shields; 12) internasals present, separate from prefrontals; 13) temporal scale formula 1+2 (rarely 1+3); 14) maxillary teeth 9–12, with posterior teeth enlarged and blade-like; 15) hemipenes deeply bilobed, retracted organ reaching the 29th subcaudal in-situ, without spinous calyces and with flounced structures across lobes; 16) dorsal color pattern variable, ochre brown or orange–brown above with light dark brown reticulations and a dark V-shaped nuchal collar present; 17) ventral color pattern pale gray and immaculate.

Comparisons. We compare *O. macrurus* to other members of *Oligodon* found in the *O. cyclurus–taeniatus* species group (Green et al. 2010; similar in composition to the *O. cyclurus* and *O. taeniatus* groups fide Smith 1943). We divide the *O. cyclurus–taeniatus* species-group into two further subgroups, the *O. cyclurus* subgroup and the *O. taeniatus* subgroup, since they are apparently closely related and are recovered sister to one another in the same clade (Leviton 1962; Green et al. 2010; Nguyen et al. 2020; Nguyen et al. 2022; present paper). It differs from all other species of the genus by the unique combination of the following characters: usually 17-17-15 dorsal scale rows; 134–169 ventrals; expressed sexual dimorphism in relative tail length (TAILR), varying from 14.0% in females and 37.3% in males and the number of subcaudals, varying from 36 in females to 94 in males; an entire cloacal plate; divided nasal scale; a deeply bilobed hemipenis without spines or obvious myoectases, and the absence of a specific dorsal coloration pattern (i.e., large blotches or bright longitudinal stripes). Additional comparisons between the *Oligodon* native to Vietnam can be found in Table 8.

Members of the informal *O. taeniatus* subgroup (sensu David et al. 2008b; Smith 1943; Vassilieva 2015) possess deeply bilobed hemipenes with myoectases visible when retracted, whereas *O. macrurus* does not possess myoectases on the retracted hemipenes. Furthermore, the *O. taeniatus* subgroup all have a dorsum with vertebral stripes or blotches (vs. dorsum without vertebral stripes or large blotches, reticulate and only with crossbars anteriorly). *Oligodon barroni* has a red venter with black quadrangular spots (vs. immaculate venter); *Oligodon deuvei* David, Vogel and Van Rooijen, 2008 by having the 3rd and 4th supralabials contacting the eye (vs. usually 4th and 5th contacting eye) and a venter with black rectangular blotches (vs. immaculate venter); *Oligodon moricei* David, Vogel & Van Rooijen, 2008 has a higher number of ventrals (175 vs. 131–169) and a venter with grayish–brown blotches (vs. immaculate venter); *Oligodon mouhoti* (Boulenger, 1914) and *O. pseudotaeniatus* David, Vogel & Van Rooijen, 2008 have a venter with black quadrangular spots (vs. immaculate venter); and *O. taeniatus* has 19 midbody scale rows (vs. usually 17).

The *O. cyclurus* subgroup (sensu David et al. 2008a; Green et al. 2010; Smith 1943; Vassilieva 2015) have deeply bilobed hemipenes without spines or myoectases, which greatly resemble the morphology observed in *O. macrurus*. Compared to *O. macrurus*, *O. chinensis* has a higher number of ventrals (170–206 vs. 131–169) and has a dorsum with large dark brown blotches (vs. dorsum without blotches); *Oligodon condaoensis* Nguyen et al., 2016 has a higher number of ventrals (168–176 vs. 131–169) and has a dark gray dorsum (vs. dorsum light brown, ochre brown or orange–brown); *O. culaochamensis* Nguyen et al., 2017 has a higher number of ventrals (167–182 vs. 131–169), 2+2 temporals (vs. 1+2 temporals), and a dorsum with large dark brown blotches (vs. dorsum without blotches), *O. cyclurus* has 19 midbody scale rows (vs. usually 17), a higher number of ventrals (167–197 vs. 131–169); *Oligodon fasciolatus* (Günther, 1864) has 21–23 midbody scale rows (vs. usually 17); *O. formosanus* has 19 anterior scale rows (vs. no more than 18); *Oligodon huahin* Pauwels et al., 2017 has a slightly higher number of ventrals (166–173 vs. 131–169), only 8 infralabials (vs. usually 9, rarely 8–10) and a distinct gray dorsum (vs. dorsum mostly ochre brown); *Oligodon juglandifer* (Wall, 1909) has 19 midbody scale rows (vs. usually 17), 7 supralabials (vs. usually 8, rarely 7), 8 infralabials (vs. usually 9, rarely 8–10), and a higher number of ventrals (162–208 vs. 131–169); *Oligodon kampucheaensis* Neang, Grismer & Daltry, 2012 has 15 midbody scale rows (vs. usually 17) and 8 infralabials (vs. usually 9, rarely 8–10); *Oligodon kheriensis* Achardji & Ray, 1936 has 19 midbody scales (vs. usually 17), and a bright red dorsum (vs. dorsum light brown, ochre brown or orange–brown); *O. ocellatus* has 19 midbody scale rows (vs. usually 17); and *Oligodon saintgironsi* David, Vogel & Pauwels, 2008 has a higher number of ventrals (166–184 vs. 131–169) and 2+2 temporals (vs. 1+2). A few species share a close relationship to the *O. cyclurus* and *O. taeniatus* subgroup, but are basal phylogenetically and are compared here. *Oligodon annamensis* has 13 dorsal scale rows (vs. usually 17-17-15), 6 supralabials and 6 infralabials (vs. usually 8 supralabials and 9 infralabials), and has a dorsal coloration with orange crossbars (vs. dorsum with dark brown crossbars only anteriorly); *O. rostralis* has 15 dorsal scales (vs. usually 17-17-15), 6 supralabials and 6 infralabials (vs. usually 8 supralabials and 9 infralabials) and a dorsal coloration with dark blotches (vs. dorsum with no blotches); *O. octolineatus*, which is seems to be the sister taxa to the informal *O. taeniatus–cyclurus* species group, usually has 6 (rarely 5–7) supralabials (vs. usually 8, rarely 7), 2+2 temporals (vs. 1+2), and a dorsum with bright longitudinal stripes (vs. dorsum without stripes).

Description of the neotype (ZFMK 88885). An adult male specimen in good condition, found DOR. Partial incision anteriorly and a longer incision made posteriorly before the cloaca. SVL 279 mm, TailL 146 mm (TotalL 425 mm). HeadL 12.5 mm, HeadW 7.9 mm, SnoutL 3.9 mm, EyeD 1.9 mm, FrontalL 3.5 mm, FrontalW 2.9 mm, IOD 4.4 mm, IND 3.3 mm. TailLR 34.4%, HeadW/L 0.63, SnoutL/HeadL 0.31, EyeD/SnoutL 0.49, EyeD/HeadL 0.15, FrontalL/W 1.21, IND/IOD 0.21, IOD/HeadW 0.56. Body elongated but somewhat flattened due to preservation state, slightly robust anteriorly and at midbody; head ovoid, slightly distinct from neck; snout narrowing in dorsal view, depressed and truncate towards the rostral
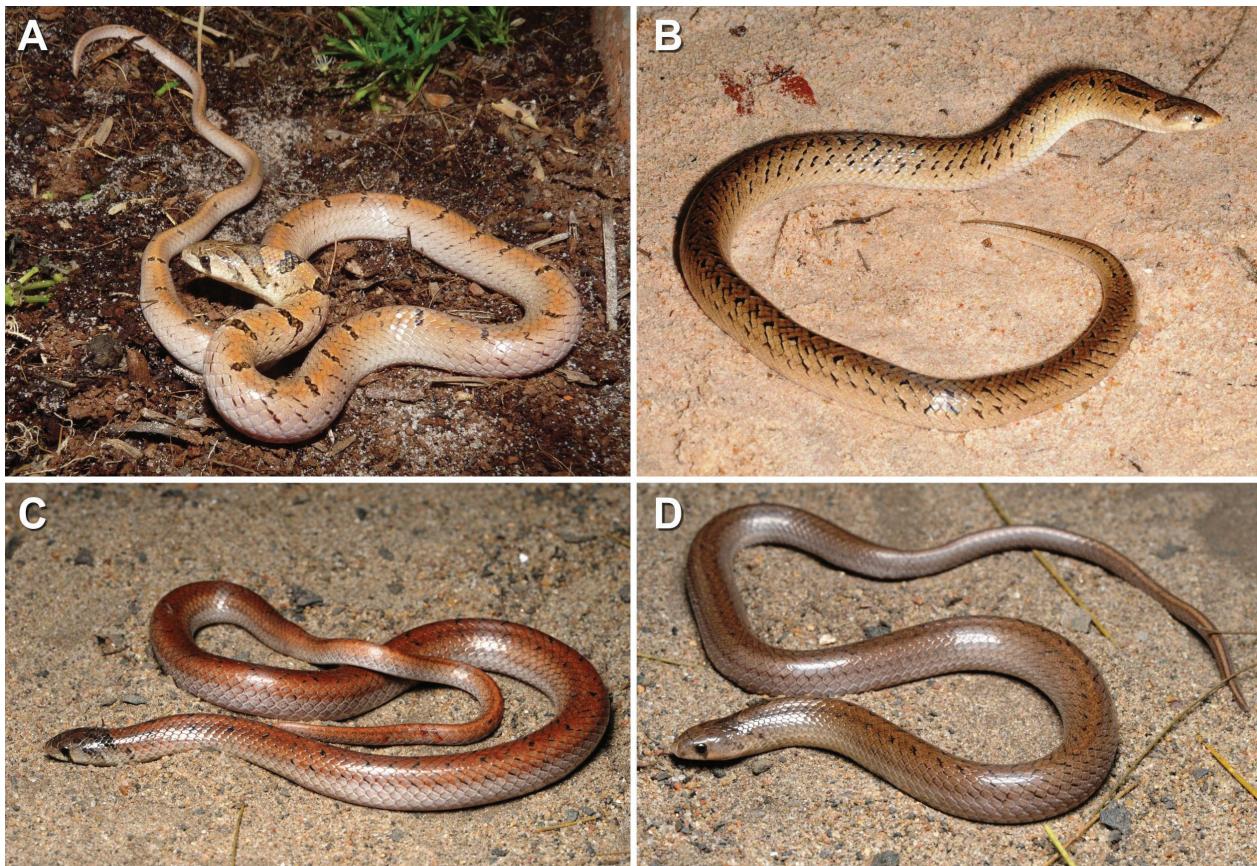
Figure 6. Living specimens of *Oligodon macrurus* sensu stricto from various locations in southern Vietnam. **A** adult male ZMMU Re-16807 from Mui Ne, Binh Thuan Province, representing the 'middle' color phase; **B** adult female VNMN 04724 (formerly ZMMU NAP-03884) from Binh Chau-Phuoc Buu Nature Reserve; **C** and **D** two adult males ZMMU Re-16804 and ZMMU Re-16805 from Binh Chau-Phuoc Buu Nature Reserve, Ba Ria-Vung Tau Province, B–D formerly identified as *Oligodon arenarius*. Photographs taken by Hieu Minh Pham **A** and Nikolay A. Poyarkov Jr. B–D.

in dorsolateral view; snout tip terminating past lower jaw; eyes moderately-sized with a round pupil; nostrils pointed laterally; mouth flat, curving slightly posteriorly; tail long, consistent in diameter until the posterior half where it tapers gradually to a sharp terminal scute.

Rostral distinctly enlarged and truncate laterally, wider than high and triangular in dorsal view, partially separating internasals; posterior scale suture of rostral with internasals "deep-V" shaped, vertex of rostral rising far onto the dorsal surface of the head in-line with nostrils as a narrow obtuse angle (~97º); internasals subrectangular, longer than wide, internasal suture shorter than prefrontal suture, anterior border with rostral and nasal concave; prefrontals subpentagonal, longer than wide, wider than internasals; frontal subpentagonal and shield shaped; length of frontal longer than prefrontals and internasals; anterior suture of frontal bordering prefrontals straight but somewhat indented; eyes placed posterior relative to the anterior edge of the frontal; angle formed by the sutures producing the posterior vertex of the frontal narrowly obtuse (~94º); supraoculars subrectangular, longer than wide, narrower anteriorly than posteriorly; length of frontal longer than supraoculars; parietals subpentagonal, slightly longer than wide, width of each scale wider than length of parietal suture; length of parietal scale slightly longer than length of frontal; parietal suture shorter than

length of frontal; anterior parietal angle formed by the sutures between the parietal/frontal and the suture between the supraocular/parietal an obtuse angle (~122º) with the lateral ray of the angle pointing posterolaterally; nasal scale subrectangular, longer than wide and fully divided; loreal scale present (1/1), also subrectangular, slightly longer than wide, around half the size of nasal; supralabials 8/8, with the 4th and 5th scales in contact with the orbit; 7th supralabials largest, 1st supralabial smallest; preoculars 1/1; presuboculars (1/1), smaller and less wide than preocular; postoculars 2/2, uppermost postocular larger in size on left side, bottommost postocular on right side slightly wider; temporal scale formula 1+2, uppermost posterior temporal longer with 6/6 scales surrounding scale; infralabials 9/9, first pair contacting eachother; 4/4 infralabials contacting the first pair of chin shields; 5th infralabial largest, 2nd infralabial smallest; mental subtriangular, wider than long; small mental groove present starting below the mental scale where the first pair of infralabials contact, then terminating at the level of the posterior chin shields; anterior pair of chin shields longer than the posterior pair; anterior chin shields slightly wider than posterior chin shields.

Dorsal scale rows 17-17-15, smooth throughout; reduction from 17 to 15 scale rows occurring on 87th ventral on either side; ventral scales 142, subcaudals 87, cloa-

cal plate divided (total body scales 230); subcaudal ratio 38.0%. Maxillary teeth not counted (see General description and variation for details on dentition). The hemipenes were partially everted in an unilobed state, but not fully prepared. The base of the organ is relatively naked with a few flounces present and the sulcus spermaticus partially visible.

In preservative, dorsum light brown with small dark brown or black reticulations formed by dark edges along the dorsal scales; dorsal reticulations concentrated anteriorly and at midbody, whereas the posterior portion of the dorsum is mostly immaculate; vertebrally a series of crossbars, beginning anteriorly as a pair of dark brown spots and continuing as narrow black bars around one or one-half a scale wide, slowly fading in size by midbody and continuing up to the tail as small subrectangular spots. The head is brown dorsally with a poorly defined gray–brown ocular bar edged posteriorly with black, extending across the eyes then meeting at the prefrontals and anterior portion of the frontal; a grayish brown and black-edged temporal streak present on each side of the head starting from the medial portion of each parietal through the posterior temporals and supralabials before dissipating at the gular region. The frontal and parietals have small dark vermiculations present on the scales, along with a dark brown irregularly-shaped spot on the posterior vertex of the frontal and on the suture of the parietals. Along the nape there is a large gray–brown V-shaped nuchal chevron beginning at the posterior end of the parietals around six dorsal scales in length before forking at the nape as a dark brown streak terminating along the flanks of the first two dorsal scale rows. The remainder of the head, including the labial and ventral regions, are beige and mostly immaculate. Ventral surface light brown to beige, immaculate without any spotting or makings. Dorsal surface of tail light brown, immaculate laterally and vertebrally between two dark brown longitudinal stripes originating from the dorsum and extending posteriorly from the cloaca as a pair of stripes extending across the tail to its tip. Ventral surface of tail beige and immaculate.

General description and variation. All examined specimens agree with the original description of the lost holotype and the newly designated neotype (ZFMK 88885). A summary of morphological data for all presently known specimens of *O. macrurus* is presented in Table 7. In all specimens, body elongated and semi-cylindrical, slightly robust anteriorly and at midbody; head ovoid, slightly distinct from neck; snout narrowing in dorsal view, depressed towards the rostral in dorsolateral view; snout tip terminating past lower jaw; eyes moderately-sized with a round pupil; nostrils pointed laterally; mouth flat, curving slightly posteriorly; tail long in males, consistent in diameter until the posterior half before tapering gradually to a sharp terminal scute; in females, tail still elongate but much shorter than males, tapering gradually starting anteriorly from the cloaca to the terminal scute.

SVL 210–320 mm (212–320 mm in males, 210–319 mm in females); TailL 35–190 mm (72–190 mm in males, 35–75 mm in females); TotalL 245–510 mm (284–510 mm in males, 345–385 mm in females). The largest specimen is an adult male (UNS 5001) with a SVL of 320 mm and TailL of 190 mm (TotalL 510 mm; TailLR 37.3%). HeadL 8.9–14.3 mm, HeadW 6.1–10.3 mm, SnoutL 3.1–4.9 mm, EyeD 1.5–2.1 mm, FrontalL 2.8–4.2 mm, FrontalW 2.3–3.4 mm, IOD 3.6–5.6 mm, IND 2.1–3.8 mm; TailLR 14.0%–37.3% (25.4%–37.3% in males, 14.0–19.6% in females), HeadW/L 0.53–0.90, SnoutL/HeadL 0.30–0.40, EyeD/SnoutL 0.35–0.52, EyeD/HeadL 0.13–0.18, FrontalL/W 1.10–1.35, IND/IOD 0.44–0.73, IOD/HeadW 0.48–0.64. Rostral distinctly enlarged and truncated laterally, wider than high, triangular shaped in dorsal view, partially separating internasals; posterior scale suture of rostral with internasals "deep-V" shaped; internasals subrectangular, longer than wide, internasal suture longer than prefrontal suture, anterior border with rostral and nasal concave; prefrontals subpentagonal, longer than wide, wider than internasals; frontal subpentagonal and shield shaped, length longer than prefrontals; anterior suture of frontal bordering prefrontals broad, either concave or straight; eyes placed posterior to the anterior margin of frontal; angle formed by the sutures producing the posterior vertex of the frontal a narrow obtuse angle; supraoculars subrectangular, longer than wide, length of frontal longer than supraoculars; parietals subpentagonal, slightly longer than wide, width of each scale wider than length of parietal suture; length of each parietal scale equal or slightly longer than length of frontal, but length of the parietal suture shorter than length of frontal; anterior parietal angle formed by the sutures between the parietal/frontal and the suture between the supraocular/parietal a broad obtuse angle with the lateral ray of the angle pointing posterolaterally. Nasal scale subrectangular and longer than wide, fully divided; loreal scale condition variable, 1/1 or 0/0 (0/1 in two specimens); when present, loreal square or subrectangular-shaped, slightly longer than wide, around half the size of nasal; supralabials usually 8/8 (7/7 in one specimen, 7/8 in four specimens, 8/7 in one specimen), with the 4th and 5th scales in contact with the orbit (3rd and 4th scale in contact on one side in one specimen, just the 4th scale in contact on both sides in one specimens, on one side in four specimens); 7th supralabial largest, 1st supralabial smallest; preoculars 1/1; presubocular usually present (1/1) but sometimes absent (0/0 in five specimens), when present smaller than preocular; postoculars usually 2/2 (rarely 2/1 in one specimen, 1/2 in two species, 1/1 in one specimen), uppermost postocular usually larger in size when two scales are present (occasionally the bottommost postocular is wider); temporal scale formula 1+2, with one specimen having 2/3 posterior temporals; infralabials usually 9/9 (rarely 8/8 in two specimens, 8/9 in two specimens, 7/9 in one specimen, 10/10 in one specimen); first pair of infralabials in contact with each other; usually 4/4 or 5/5 infralabials contacting the first pair of chin shields, one specimen with 4/5 and another with 3/4 infralabials in contact; 5th infralabial largest, 2nd infralabial smallest; mental subtriangular, wider than long; small mental groove present, starting below the mental scale where the first pair of infralabials contact and extending until the posterior chin shields;

Table 7. Summary of examined morphological characters for all known specimens of *O. arenarius* and *O. macrurus*, with the third column including all specimens under *Oligodon macrurus* sensu stricto (herein redescribed including *O. arenarius* as a synonym). All characters include data for both sexes except TailLR, VEN, SC, TOTAL and SC, which are separated based on male (m) and female (f) material. Abbreviations are listed in the materials and methods. Cells denoted with a "/" symbol were unavailable or not examined.

Character	*O. arenarius*	*O. macrurus*	Combined (*O. macrurus* s. str.)
n	6 (m) 3 (f)	9 (m) 6 (f)	15 (m) 9 (f)
TailLR	14.0–27.5 22.09±6.27	14.3–37.3 28.07±8.58	14.0–37.3 25.62±7.96
TailLR (m)	25.4–27.5 26.49±0.80	30.0–37.3 34.06±2.18	25.4–37.3 31.03±4.21
TailLR (m)	14.0–15.1 14.56±0.54	14.3–19.6 17.61±1.95	14.0–19.6 16.59±2.18
DSR	17-17-15 (18-17-15)	17-17-15 (17-16-15)	17-17-15 (18-17-15, 17-16-15)
VEN	131–143 135.9±4.8	135–169 149.0±10.3	131–169 144.1±10.5
VEN (m)	131–136 133.2±1.8	135–152 142.7±5.6	131–152 138.9±6.5
VEN (m)	139–143 141.3±2.1	150–169 158.7±6.5	139–169 152.9±10.1
SC	36–60 50.8±10.7	44–94 70.3±18.3	36–94 62.5±17.8
SC (m)	55–60 58.3±1.9	75–94 82.9±6.3	55–94 73.1±13.4
SC (m)	36–40 38.0±2.0	44–53 48.2±3.4	36–53 44.8±5.9
TOTAL	178–195 187.6±6.5	203–243 220.3±12.3	178–243 207.5±18.5
TOTAL (m)	188–195 192.5±2.7	211–243 226.6±10.6	188–243 212.9±19.1
TOTAL (f)	178–183 180.3±2.5	201–214 207.7±5.1	178–214 198.6±14.3
SCR	20.0–31.3 26.91±4.89	20.6–38.7 31.64±7.00	20.0–38.7 29.72±6.39
SCR (m)	29.3–31.3 30.30±0.71	34.72–38.68 36.55±1.43	29.3–38.7 34.05±3.38
SCR (f)	20.00–21.86 21.07±0.96	20.56–25.37 23.22±1.86	20.0–25.4 22.50±1.88
SL	8/8 (7/7)	7/8 or 8/8 (8/7)	8/8 (7/7, 7/8, 8/7)
SLE	4+5 (4/4)	4/4+5 or 4+5/4+5 (3+4/4+5)	4+5/4+5 or 4/4+5 (4/4, 3+4/4+5)
IL	9/9 (7/9)	9/9 (8/8, 8/9 or 10/10)	9/9 (7/9, 8/8, 8/9, 10/10)
ILCS	4/4 (3/4, 4/5 or 5/5)	4/4 or 5/5	4/4 (3/4, 4/5, 5/5)
PtO	2/2	2/2 (1/1, 1/2 or 2/1)	2/2 (1/1, 1/2 or 2/1)
PT	2/2	2/2 (2/3)	2/2 (2/3)

length of anterior pair of chin shields longer than posterior pair; anterior chin shields slightly wider than posterior chin shields.

Dorsal scale rows 17-17-15 (rarely 18-17-15 in two specimens, or 17-16-15 in two specimens), smooth throughout; reduction from 17 to 15 scale rows occurring on ventrals 71–98; ventral scales 131–169 (131–152 in males, 139–169 in females); subcaudals 36–94 (60–94 in males, 36–48 in females); total body scales 178–243 (191–243 in males, 178–214 in females); subcaudal ratio

20.0%–38.7% (29.3%–38.7% in males, 20.0%–25.0% in females). Maxillary teeth 9–12, all blade-like, with the posterior two or three greatly enlarged. Vassilieva (2015) provided lower tooth counts ranging from 6–9 for the type series of *O. arenarius*, however our examination of the maxilla using μCT-scanning revealed that the number of teeth is likely higher by at least three. These differences can reflect the difficulties of counting dislodged teeth on the maxilla, especially when the gum layer can obscure views of the upper jaw when examined carelessly. Significant sexual dimorphism was observed in the number of ventrals, subcaudals, TailLR and subcaudal ratio (Table 5). In general, the tails of male specimens are much longer and less tapered in female *O. macrurus* and are some of the longest tails out of any members of the genus *Oligodon*. The hemipenes are deeply bilobed in both retracted and everted specimens examined, in-situ extending from the 25th to 29th subcaudal (fide. Smith 1943 and our own data); myoectases absent on retracted organ. When partially everted the hemipenis may appear unilobed with small apical flounces. Fully everted, the organ is obliquely flounced until the point of bifurcation, which occurs at the first fourth or third of the organ; lobes calyculate and without spines, becoming smoother posteriorly; lobes terminating as blunt apices; base of organ nude without ornamentation; sulcus spermaticus bifurcate (forked), extending straight from the base and then dividing at the point of bifurcation and continuing along the lobes to the apices.

Most *O. macrurus* specimens exhibit a similar color pattern, but some intraspecific variation is present. The dorsum in-life is ochre brown, light brown or orange–brown, and all specimens have small dark-brown reticulations across the body formed by dark edges along the dorsal scales; dorsum usually darker vertebrally, occasionally with two darker lines creating a small weakly-distinguished and dusky pair of longitudinal stripes, especially distinct on the tail. The head is marked with a dark ocular bar that extends across the eyes and meeting at the prefrontals and anterior portion of the frontal, a temporal streak on each side of the head starting from the parietals to the supralabials and flanks, and a V-shaped nuchal chevron. The ventral surface is plain white or beige and without any spots or blotches. Three main color variants can be observed, well correlated with geographic location. The first is a "north" form observed in specimens from Khanh Hoa Province (NHMUK 1938.8.7.39, 1969.1855–56, ZMMU Re-13857). In these individuals, the ocular bar is indistinguishable or barely distinguishable from the rest of the head, the temporal streak is faint (and reduced to the lower half of its length in NHMUK 1938.8.7.39 and NHMUK 1969.1855), and the narrow V-shaped nuchal collar is only 2–4 dorsal scales in length and of equal width. There are no dark markings on the frontal scale, and the dorsum has small dark brown crossbars starting posterior to the nuchal collar fading by midbody to small indistinguished reticulations. The second "middle" form (Figs 5, 6A) is found in specimens from Binh Thuan Province (ZFMK 88885 [neotype], UNS05001-05002, the lost holotype and

ZMMU Re-14502), where the ocular bar is dark brown and fairly distinct (faint in ZMMU Re-14502, but this is probably due to preservation conditions), the temporal stripe is also distinct (divided on two parts in ZMMU Re-14502), and V-shaped nuchal collar is more elongated (4–6 scale rows long) and widest medially before narrowing laterally, including the posterior portion of the parietals. The frontal spot is present and usually distinct (with exception of the lost holotype), and the remainder of the dorsum has several paravertebral pairs of narrow spot-shaped crossbars on the anterior half of the body. The "south" form (Figs 6B–D) occurs in specimens from Ba Ria–Vung Tau (ZMMU Re-11561, Re-14503–04 and VNMN 04724) and Ho Chi Minh City (NHMUK 1969.1854), where the ocular bar is distinct and dark-brown (faint in NHMUK 1969.1854, but again probably due to conditions of preservation), the temporal stripe is also usually distinct (faint in NHMUK 1969.1854) and the V-shaped nuchal collar is 4–5 scales long but wide both medially and on the flanks and fused with markings on the frontal. The dorsum has paravertebral pairs of dark-brown spots present mostly anteriorly (ZMMU Re-11561, R-14503, NHMUK 1969.1854) or throughout the whole body (ZMMU Re-14504 and VNMN 04724). Oblique lateral streaking on the dorsum are also displayed on a few specimens (with exception of NHMUK 1969.1854). The specimen ZMMU Re-15136 (from Ba Ria–Vung Tau) stands out for its saturated orange color in life and black speckling evenly distributed along the body. However, it seems to share more in common with the "south" form. The presence of more or less distinct vertebral stripe, especially on the tail, seems to be the common feature for all three groups with exception of ZMMU Re-15136 and, apparently, the lost holotype. It should be noted that the color present in the "south" form includes specimens previously referred to *O. arenarius*, as well as specimens identified as *O. macrurus*.

Osteological description. The description of the skull of *Oligodon macrurus* is based on 3D reconstructed μCT-scans of two specimens: ZMMU Re-13857 and ZMMU Re-14502 (one of the paratypes of *O. arenarius*); (Fig. 7). The skull of *O. macrurus* is short, rounded, and well ossified. The snout is composed of the premaxilla, nasals, septomaxillae and vomers. The circumorbital bones include the prefrontals and postorbitals. Premaxilla single, flat and curved anteriorly, representing the front tip of the snout; deeply wedged in the space between and beneath the septomaxillae and the nasals. Nasals spatulate-shaped and sharpened at the tip with an S-shaped profile; left and right articulated nasals form median septum between the nasal cavities covering them dorsally; ventrally nasals form a posterior process lying between the anterior edge of the frontals. Septomaxillae paired and plate-like, in contact medially, forming the floor of nasal cavity, partially fused with vomers; conchal processes of septomaxillae well defined; each septomaxilla in contact with nasal septum medially and form a posterior process contacting anterior edge of frontals through the prokinetic joint. Vomers toothless, positioned beneath and behind the two
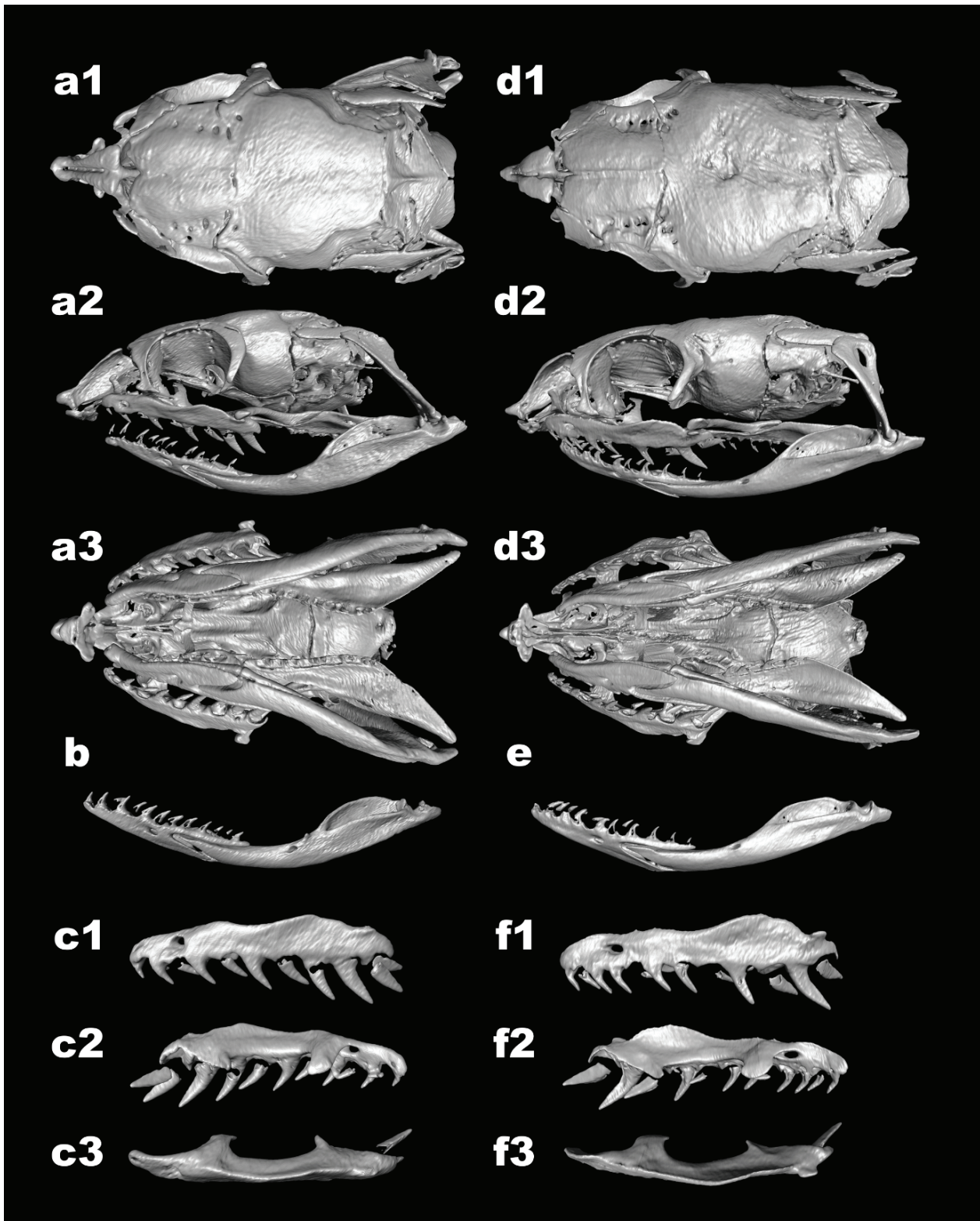
Figure 7. Three-dimensional CT reconstruction of the skull, lower jaw and maxilla of **A–C** *Oligodon arenarius* (ZMMU Re-14502, paratype) and **D–F** *O. macrurus* (ZMMU Re-13857) showing **A1**, **D1** dorsal, **A2**, **D2** lateral, and **A3**, **D3** palatal view of the skull labial view. **B**, **E** of the lower jaw, **C1**, **F1** labial, **C2**, **F2** lingual, and **C3**, **F3** dorsal view of the maxilla. Reconstructions by Elena V. Syromyatnikova.

septomaxillae and forming a pair of spherical fenestrae, in which lies the vomeronasal organs, opened by paired orifices into the buccal cavity. Prefrontals on either side of the head, block shaped and obliquely positioned forming the anterior edge of the orbit; dorsally prefrontals in broad contact with the anterolateral surface of the frontals, ventrally in loose contact with the maxillae. Left and right postorbitals articulate with the anterolateral surfaces of the parietal and form the dorsoposterior boundary of each orbit.

The braincase is composed of compactly ossified bones consisting of the frontals, parietal, basisphenoid, basioccipital, prootics, supraoccipital and exoccipital; partially fused to each other forming the complete enclosure of the brain. Frontals well separate. Parietals elliptical shaped and the largest cranial element, fused together to form a single bone that dorsally roofs the braincase, bearing no elaborated crests; laterally parietal extends far down contacting the basisphenoid and the prootics. Basisphenoid and parasphenoid fused with each other, forming the posterior snout and anterior floor of braincase. Basioccipital forms the floor of the posterior portion of the brain cavity, and completes the foramen magnum creating a large and raised occipital condyle. Left and right prootics large, subrectangular ventrally and dome contoured dorsally, partly fused with the parietal and forming the anterior walls of each internal otic capsule; prootics form the anterior half of each fenestra ovalis and the posterolateral wall of the braincase. Supraoccipitals fused together to form a single bone, externally roofing the posterior brain cavity, internally expanding to form the posterior part of each otic capsule. Exoccipital forming the posterolateral wall of the braincase and part of its roof; exoccipital fused with the opisthotics, surrounding the jugular foramen and extending forward to form the posterior border of the fenestra ovalis, the entire oval foramen magnum, and a small ventral portion of the occipital condyle along with most of the basioccipital. Stapes slender, rod like, proximally enlarged and form a footplate fitting into the fenestra ovalis and distally connect to the inner surface of the quadrate at about mid length level.

The palatomaxillary arches consists of the palatine, pterygoid, ectopterygoid and maxilla. Palatines long and narrow, in contact with the prefrontal process of the maxilla laterally and pterygoid posteriorly; 7 small sized palatine teeth. Pterygoids long and slightly bent bones, narrower anteriorly, flattened posteriorly, and extend from the posterior palatines to the posterior mandible. Each pterygoid bears 10–12/9–10 teeth. Ectopterygoids flat, bifurcate anteriorly, notched posteriorly and connect the maxillae to the pterygoids. Left and right maxillae comparatively straight and posteriorly broadened due to the dorsal ridge, connected to the flattened ventral surface of the ectopterygoid by a mesial process; the maxilla medially contacts the ventral surface of the prefrontal. Each maxilla almost has no edentulous region anteriorly, and bears 10 to 12 teeth, with the posterior 2–3 enlarged and blade-like. This number of maxillary teeth agrees well with the known data for *O. macrurus* and differs from the data represented in the original description of *O. arenarius* (Vassilieva 2015).

The suspensorium contains the quadrate and supratemporal, connecting to the mandibles by elastic tissue. Supratemporals narrow, flattened, dermal elements, connected to the proximal end of quadrates and the posterolateral part of braincase by fibrous connective tissue; each is long, straight, slightly bent toward the braincase, and overlay the exoccipital and prootic. Quadrates long, widely flattened, concave dorsally with a fenestra found posterolaterally; proximal end contacting the posterolat-

eral edge of each supratemporal; distally articulated surface of each quadrate narrow, extended transversely and directed backward. Mandibles long and connected to each other anteriorly by an elastic ligament; each composed of the compound, angular, splenial and dentary. The compound is strongly concave dorsally, narrow distally, and massive and laterally flattened proximally; prearticular crest higher than subarticular crest. Angular and splenial both triangular shaped elements that fuse at their broadest point of contact. Dentaries somewhat dorsally curved, bearing sockets for closely set 14–15/14–17 small teeth that decrease in size posteriorly.

Distribution and natural history. To date *O. macrurus* is reliably known from five provinces in southern Vietnam (Khanh Hoa, Ninh Thuan, Binh Thuan, Ba Ria–Vung Tau and possibly the vicinity of Ho Chi Minh City), where it is only found in coastal ecosystems associated with the Mui Ne dunefields and sandy coastlines to its north and south (Fig. 1). The locality of Ho Chi Minh City (based on specimen NHMUK 1969.1854) has no precise information associated with it, and requires additional confirmation; although, suitable habitat may exist within the region. Vassilieva (2015) described aspects of behavior and habitat of *O. arenarius*. One specimen was found feeding on a frog *Microhyla pulchra* Hallowell, 1861 (Vassilieva 2015). During the collection of new material, we found specimens crossing roads at night and on the crawl in habitat during daytime searches, including a few that were recovered DOR. Based on collection records with dates, this species appears to be surface active year-round, although there is a slight increase in records between the months of November to March, corresponding with the end of southern Vietnam's monsoon season. Habitats where *O. macrurus* were found include low-sloped littoral dunefields with short vegetation and ecotones with sandy clearings along lowland dipterocarp forests adjacent to dune habitats.

Etymology. The specific name "*macrurus*" is a Greek adjective derived from the words "makrós" (μακρός) meaning "long", and "oúrá" (οὐρά) meaning "the tail", here latinized as -*urus* and thus literally denoting "long-tailed". Common names previously attributed to this species include "*Angel's kukri Snake*" (English) and "*Oligodon anzhela*" (Russian). The synonym *O. arenarius* was not given a common name during its description, although "*Dune kukri snake*" has sometimes been attributed, due to its epithet translating to "coast" or "dunes". Since this species now includes this combination, we herein suggest the common name "*Long-tailed kukri snake*" (English), "*Rắn khiếm đuôi dài*" (Vietnamese), and "*Dlinnohvostiy oligodon*" (Russian), respectively, for *O. macrurus*, which directly translates to its Greek species epithet.

Conservation status. This species is now known specifically from seven localities across the coast of southern Vietnam. A few of these sites are found within nature reserves and other preserved tracts of land, however human development and increased tourism around these areas

could pose a significant threat to this species. Geissler et al. (2011) collected two specimens as roadkill indicating that road mortality could be a potential hazard in some locations. Additionally, Vassilieva (2015) noted that the type locality of the synonym *O. arenarius* was highly disturbed, with surrounding areas where specimens were collected consisting of hotels and residential properties. The protection and management of dunefield habitats across the known localities of *O. macrurus* should be of conservation priority. Based on the assessment criteria adopted by the International Union for Conservation of Nature (IUCN), we suggest that *O. macrurus* should be listed as "Vulnerable" on the IUCN Red List, due to the risks associated with habitat destruction and disturbance. Additional research understanding the population dynamics and ecology of this species would greatly improve conservation efforts.

Discussion

Using an integrative taxonomic approach, we found that the recently described kukri snake *O. arenarius* represents a junior synonym of the species *O. macrurus*. Our study also provides new data on the distribution, taxonomy and phylogenetic position of *O. macrurus* and confirms its confinement to the coastal dunefields and sandy regions of southern Vietnam. The weak genetic divergence (less than 1.0% pairwise distance) and non-monophyly of *O. arenarius* certainly justifies its demotion from species rank. However, the significant differences in body scalation and relative tail length may lead some readers to question whether *O. arenarius* should be considered a subspecies of *O. macrurus* instead of a junior synonym. In herpetology, the contemporary application, criteria and usage of subspecies is controversial (Hawlitschek et al. 2012; Torstrom et al. 2014; Kindler and Fritz 2018; De Queiroz 2020; Hillis 2020; Burbrink et al. 2022) and a discussion of its utility is beyond the scope of this paper. Recent designations of subspecies generally follow the suggestions of Mayr and Ashlock (1991) and Braby et al. (2012), who define subspecies as a distinct metapopulations that are phenotypically diagnosible and are on a trajectory towards evolutionary independence. Following these standards, we offer the following justifications for treating *O. arenarius* as a synonym rather than a subspecies: (1) Our phylogeny demonstrates that *O. arenarius* is paraphyletic with respect to *O. macrurus*, whereas other snake taxa recently described as subspecies with weak genetic divergence still display clear monophyly based on traditional genetic markers (Hawlitschek et al. 2012; Göçmen et al. 2017; Hofmann et al. 2018; Kindler and Fritz 2018). (2) When subspecies are nonmonophyletic, as is the case for North American night snakes (*Hypsiglena*) and the Southeast Asian pit viper subspecies of *Trimeresurus* (*Popeia*) *sabahi* Regenass & Kramer, 1981, they usually display allopatric or parapatric distributions with different habitat preferences (Mulcahy 2008; Mulcahy et

al. 2017) and are still exhibit morphological diagnosibility (Vogel et al. 2004). *Oligodon arenarius* so far is known from one population at the southern end of the range of *O. macrurus* and occupies a very similar habitat and ecological role. Furthermore, there exists one record of *O. macrurus* directly south of *O. arenarius* in the vicinity of Ho Chi Minh City, albeit with imprecise locality information. Pending its rediscovery in this province, it would eliminate any sense of allopatry between the two taxa. (3) All other morphological features examined between *O. arenarius* and *O. macrurus*, besides body scalation and tail length, show broad overlap (color pattern, dentition, and hemipenial morphology). Regardless of whether *O. arenarius* is treated as a synonym or subspecies, the overall diagnosis of *O. macrurus* would not be affected, as its combination of morphological characteristics readily separate it from all other members of the genus, especially its uniquely elongate tail found in males (Table 8).

Our study attempted to examine all material available for *O. macrurus*, but still has limitations related to sample size and geographic scope. In total, we examined 24 specimens of *O. macrurus* and *O. arenarius*, yet it is still difficult to conduct analyses related to geographic variation with such a sample size, which could reveal clinal patterns in the number of body scales and body size (sensu Ashton 2001; Lee et al. 2016). Both traits are known to vary within snakes, and are often influenced by environmental pressures, directional selection, and phenotypic plasticity (Kelley et al. 1997; Krause et al. 2003; Fornasiero et al. 2007; Martínez-Freiría et al. 2009). On one hand, these factors could explain why the *O. arenarius* population has such a divergent number of body scales (178–195 total scales) compared to other *O. macrurus* populations (203–243 total scales). On the other hand, the addition of more specimens may cause the differences in body scalation to disappear. Besides morphology, results recovered in our molecular analyses could be influenced by mitochondrial introgression, which is a plausible explaination for the nonmonophyly of *O. arenarius* and *O. macrurus* in the mtDNA phylogeny. Finer scale population genomics using rapidly-evolving markers such as nuclear SNPs or microsatellites, along with denser sampling between the southernmost localities of *O. macrurus*, might present different patterns of genetic variation in this species. If there is evidence that *O. arenarius* is headed on a trajectory towards evolutionary independence, then designating the taxon as a subspecies could be considered. However, we are currently convinced that it is most appropriate to consider *O. arenarius* a synonym of *O. macrurus*, given the evidence at hand.

As mentioned previously, members of *Oligodon* have traditionally been partitioned into several informal groupings based on hemipenial morphology, scalation, and dentition (Wall 1923; Smith 1943; Leviton, 1962; David et al. 2008a, 2008b; Green et al. 2010; Neang et al. 2012; Vassilieva et al. 2013; Vassilieva 2015). The role of the hemipenis in delimiting clades within *Oligodon* was partially confirmed by the phylogenetic analyses of Green et al. (2010), although the sampling in their study was quite limited. Among the species with available data on

Table 8. Morphological comparisons between *Oligodon macrurus* sensu stricto and the other species of *Oligodon* native to Vietnam. Characters highlighted in bold are considered diagnostic. Abbreviations for characters can be found in the materials and methods. Data for other species are based on the following literature sources: Pope (1935), Smith (1943), Wagner (1975, 1976), David et al. (2008a, 2008b, 2011, 2012), Orlov et al. (2010), Vassilieva et al. (2013), Pham et al. (2014), Vassilieva (2015), Nguyen et al. (2016, 2017, 2022), Nguyen et al. (2020), Lalbiakzuala and Lalremsanga (2020), Lee (2022), Yushchenko and Lee et al. (2023).

Character	*O. macrurus*	*O. annamensis*	*O. barroni*	*O. catenatus*	*O. chinensis*	*O. cinereus*	*O. condaoensis*	*O. culaochamensis*	*O. deuvei*	*O. eberhardti*
TailLR	25.4–37.3 (m) 14.0–19.6 (f)	**16.5–19.7 (m)** **11.6–13.5 (f)**	**17.0–18.9 (m)** 13.7–14.9 (f)	**12.0–13.3 (m)** 10.2–10.7 (f)	**18.7–19.5 (m)** 15.2–15.8 (f)	**12.1–15.6 (m)** 9.4–13.3 (f)	**12.8–13.2 (m)** 12.6 (f)	**21.8–21.9 (m)** 16.6–16.9 (f)	**15.8–17.2 (m)** 13.2–14.9 (f)	**10.8–15.1 (m/f)**
MT	9–12	**7–8**	10–12 (13)	**7**	9	10–13	11–13	9	**12–15**	—
DSR	17(18)–17(16)–15	**13-13-13**	17-17-15	**13-13-13**	17-17-15	17-17(15)-15(13)	17-17-15	17/19-17-15	17-17-15	13-13-13
VEN	131–152 (m) 139–169 (f)	146–157 (m) 155–170 (f)	136–147 (m) 141–160 (f)	179–203 (m) 190–212 (f)	175–184 (m) 182–206 (f)	155–182 (m) 162–185 (f)	168–172 (m) 169–176 (f)	175–184 (m) 179–182 (f)	140–147 (m) 147–155 (f)	165–174 (m) 179–187 (f)
SC	60–94 (m) 36–48 (f)	**43–46 (m)** **30–34 (f)**	36–48 (m) 28–35 (f)	31–37 (m) 30–43 (f)	60–64 (m) 47–53 (f)	33–45 (m) 29–39 (f)	37 (m) 33–34 (f)	63–66 (m) 51–52 (f)	36–47 (m) 31–38 (f)	37–40 (m) 31–34 (f)
CP	Single	Single	Single	Divided	Single	Single	Single	Single	Single	Divided
SL	8 (7)	**6 (5)**	**7–8**	6	8 (7)	7–8	8	8	7 (8)	6
SLE	4+5 (3+4)	3+4	3+4 4+5	3+4	4+5 (3+4)	3+4 4+5	4+5	4+5	3+4	3+4
IL	9 (7–10)	6	**8–9 (7)**	6	9 (8)	**7–8 (9)**	**8 (7)**	9	8–9	6
LOREAL	0–1	0	1	0	1	1	1	1	1	0
PtO	2	**1**	2	2	2	2 (1)	2	2	2	**1**
AT	1	1	1	1	1–2	1–2	1	**2–3**	1 (2)	1
PT	2 (3)	2	2	2	2	2–3	2	**2–3**	2	2

Character	*O. fasciolatus*	*O. formosanus*	*O. lacroixi*	*O. moricei*	*O. mouhoti*	*O. nagao*	*O. ocellatus*	*O. rostralis*	*O. saintgironsi*	*O. taeniatus*	*O. tuani*
TailLR	**15.5–21.6 (m)** 11.6–15.8 (f)	**16.5–19.5 (m)** 14.9–16.4 (f)	**10.5–12.4 (m/f)**	13.3 (f)	**17.2–18.5 (m)** 12.2–13.1 (f)	13.9–14.6 (m)	**11.6–14.2 (m)** 10.6–11.4 (f)	19.6 (m)	19.1–20.3 (m) 16.1 (f)	**16.5–20.4 (m)** **12.8–15.1 (f)**	**18.4–18.8 (m)** **12.3–14.2 (f)**
MT	8–10	7–10	8–12	12	14–16	9–10	9	6	10–12	15–18	10
DSR	21/23-21/19-17/15	19-19/17-15	15-15-15	17-17-15	17-17-15	17-17-15	19-17-15(13)	15-15-13	19-17(18)-15	19-19-15	19-19-15
VEN	160–186 (m) 163–196 (f)	155–176 (m) 164–189 (f)	162–178 (m/f)	175 (f)	145–152 (m) 154–163 (f)	184–193 (m)	159–166 (m) 157–180 (f)	167 (m)	166–170 (m) 184 (f)	142–159 (m) 151–165 (f)	173–179 (m) 187–193 (f)
SC	43–61 (m) 34–48 (f)	49–55 (m) 43–48 (f)	25–34 (m/f)	41 (f)	39–43 (m) 29–33 (f)	43–47 (m)	32–44 (m) 26–33 (f)	47 (m)	55–59 (m) 53 (f)	38–48 (m) 31–39 (f)	58–59 (m) 44–45 (f)
CP	Single	Single	Divided	Single	Single	Single	Single	Single	Single	Single	Single
SL	8	7–8 (6)	**5**	8	8	8 (7)	8 (7)	**6**	8	8	8
SLE	4+5 (3+4)	3+4 4+5	**2+3**	4+5	4+5	4+5 (3+4)	4+5	3+4	4+5	4+5	4+5
IL	8–9	9	**6**	9	9–10	**8 (7)**	9–10	**6**	9	9	9
LOREAL	1	1	0	1	1	1	1	0	1	1	1
PtO	2	2	2	2	2	2	2	**1**	2	2	2
AT	**2–3 (1)**	1 (2)	1	1	1 (2)	1	**1–3**	1	**2**	1	**2**
PT	2–3	2	2	2	2	3	2	2	2	2 (1)	2

hemipenial morphology, only select members of the *O. cyclurus–taeniatus* species grouphave bilobed hemipenes without spinous calyces or myoectaces (papillae). Smith (1943), describing the hemipenial morphology of male specimen NHMUK 1938.8.7.39, showed that *O. macrurus* has a deeply bilobed hemipenis without spines or myoectases, and suggested this species should be part of his informal *O. cyclurus* species group (interchangeable with the *O. cyclurus–taeniatus* species group). Our observations of the same specimen confirm the presence of deeply bilobed hemipenes. In some later works (Pauwels et al. 2017; Sumontha et al. 2017), *O. macrurus* was considered as part of the *O. cinereus* group, however such an allocation was not confirmed by any data and was an accidental mistake (P. David, pers comm). Our phylogenetic analysis places *O. macrurus* in one clade with the members of the "*taeniatus–cyclurus*–complex" (sensu Green et al. 2010; Nguyen et al. 2020), thereby confirming the earlier hypothesis of Smith (1943). By this notion, in combination with the discoveries pointed out by Nguyen et al. (2021) on what was *O. arenarius*, we are confident allocating *O. macrurus* into the *O. cyclurus–taeniatus* species group.

So far, all recent reports of *O. macrurus* have been from dunefields and adjacent sandy habitats surrounding the southern coast of Vietnam. Based on geological evidence, most of the dunefields in southern Vietnam were formed during the last interglacial period of the late Pleistocene, with deposits continuing throughout the Holocene as a result of climate change and alterating monsoon conditions in the South China Sea (Murray-Wallace et al. 2002; Quang-Ming et al. 2010; Tamura et al. 2020). These findings substantiate Geissler et al. (2011), who suggested that the lack of sand-adapted reptiles (namely, burrowing skinks and sand-swimming lizards) indicated that these coastal regions were comparatively young in age. It is possible that the formation of these dunefields over the course of the Quarternary period may have influenced the phylogeography and evolutionary history of *O. macrurus*, however these conjectures remain speculative until more detailed studies can be conducted. A few reptile species, such as *Dibamus deharvengi* Ineich, 1999, *Dixonius aaronbaueri* Ngo & Ziegler, 2009, *Dixonius vietnamensis* Das, 2004, and *Leiolepis ngovantrii* Grismer & Grismer, 2010 also appear endemic to the sandy coastal habitats of southern Vietnam like *O. macrurus*. The continued conservation of these animals could be jeopardized in the future by increased tourist and development activities. We recommend the pursuit of additional studies and continued herpetological surveys in these regions to understand and conserve these animals.

Acknowledgements

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