

Kukri snakes *Oligodon Fitzinger, 1826* of the Western Palearctic with the resurrection of *Contia transcaspica* Nikolsky, 1902 (Reptilia, Squamata, Colubridae) (#80933)

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Kukri snakes *Oligodon* Fitzinger, 1826 of the Western Palearctic with the resurrection of *Contia transcaspica* Nikolsky, 1902 (Reptilia, Squamata, Colubridae)

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The kukri snakes of the genus *Oligodon* Fitzinger, 1826 reach the westernmost limits of their distribution in Middle and Southwest Asia (Pakistan, Afghanistan, Iran, and Turkmenistan). In this paper, we review the taxonomy and distribution of the two species native to this region, *Oligodon arnensis* (Shaw, 1802) and *Oligodon taeniolatus* Jerdon, 1853 based on an integrative approach combining morphological data, molecular data from mitochondrial DNA, and species distribution modeling (SDM). Phylogenetic analyses recover *O. taeniolatus* from Iran and Turkmenistan in the *O. arnensis* species group, rendering the species paraphyletic with respect to *O. taeniolatus* sensu stricto on the Indian subcontinent. To correct this, we resurrect the junior synonym *Contia transcaspica* Nikolsky, 1902 for the Middle/Southwest Asian populations and provide a formal redescription. So far, *Oligodon transcaspicus* **comb. et stat. nov.** is known only from the Köpet-Dag Mountain Range of northeast Iran and southern Turkmenistan, but SDM mapping suggests it may have a wider range. Genetic samples of *O. "arnensis"* from northern Pakistan are nested in a clade sister to the recently described *Oligodon churahensis* Mirza, Bhardwaj & Patel, 2021, and are phylogenetically separate from *O.*

arnensis sensu stricto in south India and Sri Lanka. Based on morphological similarity, the Afghanistan and Pakistan populations are assigned to *Oligodon russelius* (Daudin, 1803) and we synonymize *O. chuarhensis* with this species. Our investigation leads us to remove *O. taeniolatus* from the snake fauna of Afghanistan, Iran, and Turkmenistan, with the consequence that only *Oligodon transcaspicus* **comb. et stat. nov.** and *O. russelius* are present in these countries. Additional studies are needed to resolve the taxonomy of the *O. taeniolatus* and *O. arnensis* species groups on the Indian subcontinent.

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Abstract

The kukri snakes of the genus *Oligodon* Fitzinger, 1826 reach the westernmost limits of their distribution in Middle and Southwest Asia (Pakistan, Afghanistan, Iran, and Turkmenistan). In this paper, we review the taxonomy and distribution of the two species native to this region, *Oligodon arnensis* (Shaw, 1802) and *Oligodon taeniolatus* Jerdon, 1853 based on an integrative approach combining morphological data, molecular data from mitochondrial DNA, and species distribution modeling (SDM). Phylogenetic analyses recover *O. taeniolatus* from Iran and Turkmenistan in the *O. arnensis* species group, rendering the species paraphyletic with respect to *O. taeniolatus* sensu stricto on the Indian subcontinent. To correct this, we resurrect the junior synonym *Contia transcaspica* Nikolsky, 1902 for the Middle/Southwest Asian populations and provide a formal redescription. So far, *Oligodon transcaspicus* **comb. et stat. nov.** is known only from the Köpet–Dag Mountain Range of northeast Iran and southern Turkmenistan, but SDM mapping suggests it may have a wider range. Genetic samples of *O. “arnensis”* from northern Pakistan are nested in a clade sister to the recently described *Oligodon churahensis* Mirza, Bhardwaj & Patel, 2021, and are phylogenetically separate from *O. arnensis* sensu stricto in south India and Sri Lanka. Based on morphological similarity, the Afghanistan and Pakistan populations are assigned to *Oligodon russelius* (Daudin, 1803) and we synonymize *O. churahensis* with this species. Our investigation leads us to remove *O. taeniolatus* from the snake fauna of Afghanistan, Iran, and Turkmenistan, with the consequence that only *Oligodon transcaspicus* **comb. et stat. nov.** and *O. russelius* are present in these countries. Additional studies are needed to resolve the taxonomy of the *O. taeniolatus* and *O. arnensis* species groups on the Indian subcontinent.

Keywords

Oligodon transcaspicus, *Oligodon taeniolatus*, Middle Asia, Iran, Turkmenistan, Köpet–Dag Mountain Range, Indian subcontinent, Taxonomy, mtDNA, species distribution modeling

Introduction

Our knowledge of the snake fauna of Middle and Southwest Asia (herein considered the countries of Afghanistan, Iran, Pakistan, western China, Mongolia and the former Soviet Middle Asian republics fide Berg, 1931; Geptner, 1938; Chernov, 1949) has improved over the past decade as researchers continue to contribute species descriptions, range extensions, and natural history observations (Wagner et al., 2016a; Jablonski & Koleska, 2017; Farooq et al., 2018; Rajabizadeh, 2018; Shestopal & Rustamov, 2018a; Shestopal & Rustamov, 2018b; Orlov et al., 2018; Jablonski et al., 2019; Asadi et al., 2019; Rajabizadeh et al., 2020; Eskandarzadeh et al., 2020; Chen et al., 2021; Essote et al., 2022). Most snake species inhabiting these countries are associated with the Palearctic biogeographic realm. However, there also exist a few taxa originating from the Oriental realm (South and Southeast Asia) that reach their westernmost limits in this region (Wagner et al., 2016b; Orlov et al., 2018). The kukri snakes of the genus *Oligodon* Fitzinger, 1826 are one such example. Normally distributed across tropical portions of

South and Southeast Asia, two species of this diverse group extend into Afghanistan, northeastern Iran, Pakistan, and southern Turkmenistan (Latifi, 1991; Green, 2010; Wagner et al., 2016b; Orlov et al., 2018; Uetz et al., 2022).

The first species, the banded kukri snake *Oligodon arnensis* (Shaw, 1802), is commonly found across the Indian subcontinent, but is known from Afghanistan based on a single specimen (Král, 1969; Wagner et al., 2016b). This species was recently divided into several taxa by Bandara et al. (2022), who published a revision of *O. arnensis* sensu auctorum based largely on morphological data. These authors restricted *O. arnensis* sensu stricto to southern India and Sri Lanka, and described a new species *Oligodon tillacki* Bandara et al., 2022 (Tillack's kukri snake) for *O. arnensis* populations found along the western coast of India, and the resurrected the name *Oligodon russelius* (Daudin, 1803) (Russell's kukri snake) for populations in north/east India, Bangladesh (Barkat & Rabbe, 2022) and Nepal (Rai, Adhikari & Antón, 2022). Additionally, Mirza, Bhardwaj & Patel (2021) described a new species, the Churah Valley kukri snake *O. churahensis* Mirza, Bhardwaj & Patel, 2021 from Himachal Pradesh, India, which was recovered within *O. arnensis* species group based on mitochondrial DNA (mtDNA) sequences. These authors included genetic samples of *O. "arnensis"* collected from Pakistan but were unable to examine their specimen vouchers and tentatively identified them as *Oligodon cf. churahensis*. While these studies have shed light on the taxonomic nature of the *O. arnensis* and related taxa, both neglected the status of specimens from Pakistan and Afghanistan. We refer to these populations as *O. "arnensis"* until our clarifications in the results.

The second species, the streaked kukri snake *Oligodon taeniolatus* (Jerdon, 1853), is also widespread on the Indian subcontinent, but extends westward into northern Iran, southern Turkmenistan, and possibly Afghanistan (Latifi, 1991; Wagner et al., 2016b; Orlov et al., 2018). Like *O. "arnensis"*, *O. taeniolatus* exhibits substantial variation across its range, including multiple color phenotypes that have invariably been recognized as synonyms or subspecies by past authors (Wall, 1921; Wall, 1923; Smith, 1943; Taylor, 1950). Bauer (2003) reviewed the nomenclatural history of this taxon and designated a lectotype illustrated by Russell (1796) with the type locality "Vizagapatam" (=Visakhapatnam, Andhra Pradesh, India), thereby restricting 'true' (nominotypical) *O. taeniolatus* to eastern India. Outside of South Asia, populations of *O. taeniolatus* from Iran and Turkmenistan can be referred to the name *Contia transcaspica* Nikolsky, 1902, described based on a single specimen collected from "Köpet-Dag, Transcaspia" [=now Köpet-Dag Mountain Range, near Ashgabat, Ahal Province, Turkmenistan]. Chernov (1935) considered *C. transcaspica* to be a junior synonym of *O. taeniolatus*, owing to similarities between Turkmen and Indian specimens. Later authors would follow his recommendation and report these populations as *O. taeniolatus* in the subsequent literature (Terentjev & Chernov, 1949; Bogdanov, 1962; Bannikov et al., 1977; Dotsenko, 1984; Atayev, 1985; Szczerbak, Khomustenko & Golubev 1986; Latifi, 1991; Rustamov & Sopyev, 1994; Szczerbak, 1994; Atayev, Rustamov & Shammakov, 1994). The name *Contia transcaspica* has rarely been mentioned since and was even neglected in the synonymy of *O. taeniolatus* by Wallach et al. (2014). A few sources (Dotsenko, 1984; Latifi, 1991) would provide additional descriptive data

of collected specimens from this region. Their accounts showed that specimens from the Köpet–Dag Mountain Range had distinct differences in coloration and scalation from Indian subcontinent *O. taeniolatus* (Wall, 1921; Wall, 1923; Smith, 1943), although detailed comparisons between populations were not made.

In this study, we review the taxonomy, phylogenetic relationships, and distributional limits of the genus *Oligodon* at the westernmost end of its range. We aimed to clarify the taxonomic status of *O. taeniolatus* historically associated with the name *Contia transcaspica* from Iran and Turkmenistan and resolve the status of *Oligodon* “*arnensis*” populations from the countries of Pakistan and Afghanistan, which were neglected by past taxonomic revisors.

Materials & Methods

Sampling and species delimitation. Fieldwork which resulted in the collection of *Oligodon* in Iran was conducted by RAN and MR during a field trip in May 2017 to Razavi, Khorasan Province, Iran (locality 7, Figure 1). Fieldwork in Pakistan was conducted by DJ and RM during a field trip in September 2018 to Punjab Province, Pakistan. Fieldwork in Sri Lanka was conducted by SK and NAP during field trips in February 2018 to December 2020 to dry and wet zones of the country. Collected specimens were euthanized using a 20% solution of benzocaine and fixed in formalin before being transferred into 70% ethanol for storage. Before preservation, a small sample of muscle tissue was taken from each snake and stored in 95% ethanol for later DNA analyses. For molecular analysis, we included one sample of *O. taeniolatus* (= *Contia transcaspica*) from Iran (ZMMU Re-16687); one sample of nominotypical *O. taeniolatus* from India (CESS-180); four novel samples of *O. arnensis* sensu stricto from India (CESS-563) and Sri Lanka (SL-Os-1, SL-Oa-2; ZMMU Re-17331); two novel samples of *O. sublineatus* Duméril, Bibron & Duméril, 1854 from Sri Lanka (SL-Os-2; SL-Os-3); and one novel sample morphologically resembling *Oligodon russelius* from Punjab Province, Pakistan (CUHC 7904; locality 9, Figure 1). In addition, we included 34 publicly available samples of other *Oligodon* species retrieved from GenBank (Table 1). Bandara et al. (2022) noted that one sample (NCBS-NRC-AA-021) previously identified as *O. “arnensis”* may represent *O. tillacki* but did not examine this specimen. As such, we re-identify this specimen as *O. cf. tillacki* herein. For outgroup taxa, we chose one sample each of *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).

We examined the morphology of seven *O. taeniolatus* specimens available to us from the Iran and Turkmenistan, including the type specimen of *Contia transcaspica* (localities 1–7, Figure 1). To compare these populations with typical members of the *O. arnensis* species group, we examined two specimens within the range of *O. russelius* fide Bandara et al. (2022) from Andhra Pradesh, India, and southern Nepal (localities 14–16, Figure 1), five specimens of *O. arnensis* sensu stricto from southern India and Sri Lanka (localities 18–19, Figure 1) (see Supplementary Material 1), and the new specimen of *O. russelius* collected from Pakistan (locality 9, Figure 1). Additional morphological data for *O. taeniolatus*, the *O. arnensis* species group and other taxa were derived from relevant literature sources (see Morphological analysis).

For aspects of species concepts and delimitation, we follow an integrative taxonomic approach (Padial et al., 2010) where a species is supported by a combination of morphological and molecular evidence. In addition, we follow the General Lineage Concept (De Queiroz, 2007), where a species represents a single independent lineage following a separate evolutionary trajectory compared to its congeners. Discrete morphological separation, substantial genetic divergence using standard genetic markers, and evidence of monophyly are all used as supporting evidence for evolutionary independence.

Abbreviations for museum collections are as following: CAS: California Academy of Sciences, San Francisco, USA; CUHC: Comenius University Herpetological Collection, Bratislava, Slovakia; MMB: Department of Zoology, Moravian Museum, Brno, Czech Republic; USNM: National Museum of Natural History, Washington, DC, USA; ZISP: Zoological Institute of Russian Academy of Sciences, St. Petersburg, Russia; ZMMU: Zoological Museum of Moscow State University, Moscow, Russia. Additional abbreviations for genetic samples and voucher specimens can be found in Table 1.

Field works, including collection of the samples and animals in the field, was performed outside of any protected area, in the framework of a project contract signed by International Center for Science, High Technology and Environmental Sciences, Kerman, Iran (contract number 1.87, issued at 11.04.2008). The contract bears a permission to collect the reptile samples outside of any protected area of Department of the Environment (specified in www.doe.ir) that needed extra permissions. Specimen collection protocols and animal operations followed the Institutional Ethical Committee of International Center for Science, High Technology and Environmental Sciences, Kerman, Iran (certificate number 1.87-1).

Molecular analyses. We extracted total genomic DNA of novel samples from muscle tissue preserved in 95% ethanol using a Qiagen DNAeasy Blood and Tissue Kit following manufacturers protocols. We performed polymerase chain reactions (PCRs) on the extracted DNA 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 (total length up to 1930 bp), and a second fragment including the complete sequence of the gene Cytochrome *b* (*cyt b*) (1,091 bp). Primers used for both PCR and sequencing are summarized in Table S2. PCR protocols for 12S-16S rRNA fragments were adapted from Green et al. (2010). For both primer pairs of 12S and 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 of 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 Sciences (Moscow, Russia) and at MacroGen Europe (Amsterdam, The Netherlands; <http://www.macrogen-europe.com>). Sequences were assembled and checked using Sequencher 4.9 (GeneCodes). The obtained sequences are deposited in GenBank under the accession numbers OQ092426; OQ099833–OQ099837; and OQ116816–OQ116825 (Table 1).

To examine the position of *O. taeniolatus* from Turkmenistan and Iran in a matrilineal genealogy of the genus, we combined newly obtained sequences with all publicly available GenBank sequences of *O. arnensis*, *O. churahensis*, *O. taeniolatus*, *O. cf. tillacki* and one sequence per species of other *Oligodon* (summarized in Table 1). In total, we analyzed mtDNA sequences of 45 specimens, including 43 samples of 33 species of *Oligodon*, with outgroup sequences of *O. porphyraceus* and *H. vibakari* used to root the tree. Nucleotide sequences were initially aligned in MAFFT v.7 (Katoh et al., 2002) 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 IQ-TREE web server (<http://iqtree.cibiv.univie.ac.at/>; Trifinopoulos et al. 2016) to estimate optimal evolutionary models for the data set analysis using the Akaike Information Criterion (AIC). Mean uncorrected genetic distances (p-distances) were calculated in MEGA 7.0 (Kumar, Stecher & Tamura, 2016). The matrilineal genealogy was inferred using Bayesian inference (BI) and Maximum Likelihood (ML) approaches. The best-fitting model for both BI and ML analyses for 12S–16S rRNA fragments and for the second codon partition of cyt *b* was the GTR+G+I model as of DNA evolution suggested by the AIC. For the remaining portions of cyt *b*, the AIC suggested the GTR+G model for the first codon partition, and the HKY+G+I for the third codon partition.

ML was conducted using the IQ-TREE web server (Trifinopoulos et al., 2016). BI was conducted in MrBayes 3.2.2 (Ronquist et al., 2012); Metropolis-coupled Markov chain Monte Carlo (MCMCMC) analyses were run with one cold chain and three heated chains for one million generations and 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 exploring and examining likelihood plots in TRACER v1.6 (Rambaut et al., 2020), with effective sample sizes (ESS) all above 200. Nodal support for BI was assessed by calculating posterior probabilities (BI PP). We *a priori* regarded tree nodes with BI PP values over 0.95 as sufficiently resolved, while BI PP values between 0.95 and 0.90 were regarded as tendencies. For ML, confidence in nodal topology was estimated via the ultrafast bootstrap approximation algorithm (UFBS; Hoang et al., 2018) with 1,000 bootstrap pseudoreplicates. Nodes having ML UFBS values of 95 and above were *a priori* considered highly supported, while nodes with values of 90–94 were considered well-supported, and nodes with values of 70–89 were considered as tendencies. Lower values were regarded as indicating unresolved nodes (Huelsenbeck & Hillis, 1993).

Morphological analysis. Coloration and pattern were recorded during examination of preserved specimens. For some specimens, live coloration was also recorded from digital images taken before preservation. No statistical analyses were performed between species due to the low sample size of comparative material. All body measurements, except body and tail lengths, were taken under a dissecting microscope using a digital slide-caliper to the nearest 0.1 mm. Body and tail lengths were measured to the nearest millimeter by straightening snakes along a flexible ruler. Methodology for counting ventral and subcaudal scales follow Dowling (1951). The tail tip was not included in the number of subcaudals. Head scale suture angle terminology follows that of Kaiser, O'Shea & Kaiser (2019). Maxillary teeth were counted by examination of the dissected maxillary bone when available, or by carefully removing the gum layer of the maxilla. Sex was determined by ventral incision below the vent to detect the presence or absence of hemipenes. Our data on specimens referable to *Contia transcaspica* were compared and reviewed with relevant literature on *O. taeniolatus* across its distribution (Nikolsky, 1902; Nikolsky, 1903a; Wall, 1921; Wall 1923; Chernov, 1935; Smith, 1943; Minton, 1966; Dotsenko, 1984; Latifi, 1991; Khan, 2002).

The following linear measurements (all in mm) were taken: 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 mandible; 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); 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); anterior scale rows (ASR) — namely number of scale rows at one head length behind the head; midbody scale rows (MSR) — the number of scale rows at midbody; posterior scale rows (PSR) — 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 belly scales starting from the scale contacting 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) — the sum of ventral, 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. We also describe and abbreviate certain color pattern characteristics found in specimens, including the number of body blotches or crossbars from nape to vent (B-Blotch); the number of blotches or crossbars from vent to tail tip (T-Blotch); the width in vertebral (dorsal) scales of each blotch at midbody (BlotchW); and the distance between each blotch at midbody counted using vertebral (dorsal) scales (BlotchD). Abbreviations for these characters are used in Tables 3–4. Symmetric characters are given in left/right order.

Species distribution modeling. We used MaxEnt 3.3.3 (Phillips, Anderson & Schapire, 2006) and modelled the potential distribution of *Oligodon* population in Central Asia in the present as well as three previous historical epochs: the mid-Pliocene (ca 3.2 Mya), the Last Glacial Maximum (ca 21 Kya), and the mid-Holocene (ca 6 Kya). We used 23 unique georeferenced data points (Table S1), 23 bioclimatic and four landscape layers. Data were filtered and correlated variables were excluded using ENMTools 1.3. (Warren et al., 2010) and models assessed by computing the area under the CURVE (AUC). Further, we estimated the relative contribution of variables to the model. For the current climate projection, we used the CHELSA database (Karger et al., 2017). The PaleoCLIM database was used for the past conditions, the mid-Pliocene, the Last Glacial Maximum (LGM) and the Mid-Holocene (Fordham et al., 2017; Brown et al., 2018), at 5 km pixel size. The final maps were designed in QGIS Desktop 3.28 software (QGIS Development Team, 2021).

Results

Molecular analyses. The final concatenated alignment of the 12S–16S rRNA and cyt *b* gene sequences contained 3019 base pairs with 1812 conserved sites, 1191 variable sites, and 833 parsimony informative sites. The transition-transversion bias (R) was estimated as 1.2. Nucleotide frequencies were 36.7% (A), 23.0% (T), 25.7% (C), and 14.6% (G) (all data given for ingroups only). The uncorrected pairwise genetic distances (hereafter p-distances; given for the cyt *b* mtRNA gene fragment) between and within examined *Oligodon* species are presented in Table 4. Intraspecific genetic distances varied from $p = 0\%$ (in *O. sublineatus*) to $p = 2.2\%$ (*O. churahensis*, including samples of *O. cf. churahensis* and *O. russelius*). The interspecific genetic distances within examined *Oligodon* varied from $p = 3.3\%$ (between *O. arnensis* sensu stricto and *O. churahensis*) to $p = 21.0\%$ (between *O. sublineatus* and *O. churahensis*).

In general, our mtDNA-based genealogy of *Oligodon* (Figure 2) correlates well with the set of phylogenetic relationships obtained from previous authors (Green et al., 2010; Nguyen et al., 2020; Mirza, Bhardwaj & Patel, 2021; Das et al., 2022; Yushchenko & Lee et al., *in press*). Both ML and BI topologies of our mtDNA-genealogy of *Oligodon* support the specimen of *O.*

taeniolatus from Iran as a separate lineage sister to *Oligodon melaneus* Wall, 1909, the newly described species *O. churahensis*, and Pakistani specimens *O. russelius* and *O. cf. churahensis*, with strong support from both analyses (0.97/92). Genetic p-distances in this clade varied from 7.8% (between *O. taeniolatus* and *O. melaneus*), 6.3% (between *O. taeniolatus* and *O. russelius*), and 5.7% (between *O. taeniolatus* and *O. churahensis*) based on *cyt b*. Together with *O. arnensis* they form the most basal clade (1/100), while the three samples of *O. taeniolatus* from India and Sri Lanka form a distinct clade together with *O. sublineatus* and *Oligodon calamarius* (Linnaeus, 1758) also with strong support (1.0/100). This topology renders *O. taeniolatus* sensu lato as paraphyletic. Notably, the sample of *O. taeniolatus* from Sri Lanka is divergent (2.2% p-distance based on 16S rRNA) from the Indian sample, which suggests additional undescribed diversity is present in *O. taeniolatus* outside of Middle and Southwest Asia. Distances of such a percentage based on 16S rRNA are more significant than the *cyt b* gene as 12S–16S rRNA evolves at a slower rate (Mueller, 2006). The newly collected Pakistan sample (CUHC 7904) identified by us as *O. russelius* is recovered within a clade containing two other Pakistan samples from Genbank that were identified as *O. cf. churahensis* by Mirza, Bhardwaj & Patel (2021) with high support (1.0/99). Low genetic divergence ($p = 2.2\%$) exists between the three samples, suggesting they are conspecific. Additionally, the divergence between the Pakistan samples and the type series of *O. churahensis* from Himachal Pradesh, India is only 3.3% in *cyt b* gene (Table 5). The genetic distance between the sample re-identified as *O. cf. tillacki* and samples of *O. arnensis* sensu stricto was also low ($p = 3.6\%$).

Species distribution modeling. The species distribution model (SDM) maps based on geolocation points of *Oligodon* from Iran and Turkmenistan is shown in Figure 3. Variables that mostly account for the species presence are landscape uniformity, mean temperature of coldest quarter (Bio 11), slope, and precipitation seasonality (coefficient of variation) (Bio 15). The average test AUCs for the replicate runs was estimated as 0.988. The predicted distribution of *Oligodon* during past and present epochs expanded and contracted across the Plio-Pleistocene and Holocene and suggests that the current distribution of *Oligodon* in Middle/Southwest Asia is significantly different. The most suitable habitat for *Oligodon* mostly occurred during the last glacial maximum (LGM) period, with the range including more expansive areas of current day Turkmenistan, Afghanistan, and the southern edge of the Caspian Sea. Subsequent range reduction is visible since the mid-Holocene, with the model prediction expecting the most suitable habitat for this species in Köpet-Dag Mountain Range of northeast Iran and southwest Turkmenistan, and small parts of Afghanistan, Azerbaijan, and western Iran (Figure 3).

Resurrection and revalidation of *Contia transcaspica* Nikolsky, 1902. Re-examination of Turkmen and Iranian *O. taeniolatus* as well as past literature descriptions *O. taeniolatus* from this region by Dotsenko (1984) and Latifi (1991) revealed that individuals from these localities are morphologically identical to the type specimen of *Contia transcaspica* (ZISP 9868). These specimens differ from Indian subcontinent *O. taeniolatus* in several features, the most obvious

being the presence of only 5 (rarely 6) supralabial scales, and narrow contact between the 4th and 5th supralabials due to the bottommost posterior temporal scale. These specimens can also be diagnosed from all members of its sister clade, the *O. arnensis* species group (*O. arnensis*, *O. churahensis*, *O. melaneus*, *O. russelius*, and *O. tillacki*), based on several coloration and scalation features, namely the presence of 15 dorsal scale rows throughout the body (*versus* 17–17–15). In terms of color pattern, these specimens also differ from typical *O. taeniolatus* (and most *Oligodon* species across Asia) by the presence of brown transverse crossbars across the dorsal surface. Phylogenetically, the sample of *O. taeniolatus* from northern Iran is monophyletic and separate from all other congeners in the *O. arnensis* species group. Genetic distances between its closest relatives, *O. churahensis*, *O. melaneus*, *O. russelius* are also substantial (5.7%–7.8% based on *cyt b*) are also substantial. Since the combination of molecular and morphological evidence support the distinct status of Iranian and Turkmen *O. taeniolatus*, we resurrect the name *Contia transcaspica* from the subjective junior synonymy of this species. *O. taeniolatus* sensu stricto is no longer paraphyletic and is now restricted to the Indian Subcontinent in Bangladesh, India, Sri Lanka, and Pakistan. The Iranian and Turkmen populations from the Köpet–Dag Mountain Range shall now be referred to as *Oligodon transcaspicus* **comb. et. stat. nov.** and a detailed redescription, including the holotype of *Contia transcaspica*, is provided below.

***Oligodon transcaspicus* comb. et stat. nov. (Nikolsky, 1902)**

(Figures 4–6; Table 2)

Contia transcaspica: Nikolsky (1902: 839–840). **Holotype**: "Köpet–Dag, Transcaspia" [= now Köpet–Dag Mountain Range, near Ashgabat, Ahal Province, Turkmenistan], Nikolsky (1903a: 11–13), Bobrinskoy (1923: 8), Chernov (1935: 351) (in part), Welch (1983: 77) (in part), Green (2010: 139) (in part), Bandara et al. (2022: 68) (in part), Uetz et al. (2022) (in part)

Oligodon taeniolatus (in part): Chernov (1935: 351), Filippov (1947), Terentjev & Chernov (1949), Bogdanov (1962), Brück (1968: 201), Nurgeldyev, Shammakov & Atayev (1970: 187–190), Rustamov & Atayev (1976: 47–53), Bannikov et al. (1977) Atayev, Gorelov & Shammakov (1978), Szczerbak (1979: 68–70), Welch (1983: 77), Dotsenko (1984: 23–26), Atayev (1985), Szczerbak, Khomustenka & Golubev (1986: 68–70), Latifi (1991: pl. 52 & 117), Rustamov & Sopyev (1994: 224), Atayev, Rustamov & Shammakov (1994: 337), Szczerbak (1994: 312), Ananjeva et al. (2006: 175), Green (2010: 139), Rustamow (2011), Safaei-Mahroo et al. (2015: 280), Shestopal & Rustamov (2018a: 40), Orlov et al. (2018: 58–67), Rajabizadeh (2018: 242).

Holotype. ZISP 9868, adult female from "Köpet–Dag, Transcaspia" [= now Köpet–Dag Mountain Range, near Ashgabat, Ahal Province, Turkmenistan] collected by N. Kinschin in 1901 (Figure 4).

Referred Specimens. Turkmenistan: Ahal Province. CAS 180042, adult female from “the Iran border south of Goalon, Ashkabad (Ashkhabad) Region” collected in May 1989 by Soviet Border Patrol (obtained by J. R. Macey); ZMMU Re-5589, subadult female from “Karanki”, collected on 1 May 1979; ZMMU Re-6155, juvenile male from “Aidere” unknown collection date; ZMMU Re-7318, adult female from “Chuli, Geok-Tepe” collected on 20 June 1990; ZISP 18334, juvenile of undetermined sex from “Geok-Tepe”, collected on May 1971; ZISP 18976, subadult male from “Geok-Tepe”, collected on 05 August 1968. **Iran:** Khorasan Province. ZMMU Re-16687 (field number RAN-3264), adult male from Bazangan Lake, Razavi (36.3044°N, 60.4751°E, WGS 84; 900–950 meters a.s.l.) collected by Roman A. Nazarov and Mehdi Radjabizadeh on 27 May 2017. See Table S1 for more details.

Diagnosis. A Kukri Snake in the genus *Oligodon* that is distinguished from all other congeners by the following combination of morphological characters: 1) 7–9 maxillary teeth, with posterior two teeth enlarged and blade-like; 2) dorsal scales in 15–15–15 rows; 3) cloacal plate divided; 4) ventral scales 179–188 in males, 193–214 in females; 5) subcaudals 48–52 in males, 44–51 in females; 6) total body scales 232–240 in males, 240–266 in females (232–266 scales combined); 7) subcaudal ratio 0.203–0.224 in males, 0.177–192 in females; 8) almost always 5 supralabials (sometimes 6 according to Latifi, 1991), with 3rd supralabial in contact with orbit; 9) loreal and preocular scales present, presubocular sometimes present; 10) posterior temporal scales 3 (rarely 2), with lowest temporal causing 4th and 5th supralabial to contact narrowly; 11) dorsal color pattern beige or light brown with of 42–57 dark transverse crossbands on body and 12–17 crossbands on the tail; 12) dorsal color pattern on tail similar to rest of body, with no vertebral stripe along tail.

Comparisons. We compare *Oligodon transcaspicus* **comb. et stat. nov.** to all species of *Oligodon* found in Middle and Southwest Asia, which may be confused with this species, particularly *O. taeniolatus* sensu stricto, with which it was previously confused with, and members of its sister clade in the *O. arnensis* species group. We base our comparisons primarily on data from the following literature sources (Wall, 1921; Wall, 1923; Smith, 1943; Khan, 2002; Mirza, Bhardwaj & Patel, 2021; Bandara et al., 2022) as well as data from our own examined specimens (Supplementary Material 1). *Oligodon transcaspicus* **comb. et stat. nov.** can be morphologically assigned to the genus *Oligodon* by having a subcylindrical body, enlarged blade-like maxillary teeth, two prefrontals and internasals present, a blunt and subterminal-shaped rostral scale, length of rostral scale visible from above two times as long as the internasal suture, two temporal scales bordering edge of parietals (generic diagnosis modified from Wall 1923).

The closest relatives of *O. transcaspicus* **comb. et stat. nov.** include members of the *O. arnensis* species group. Of these, *O. transcaspicus* **comb. et stat. nov.** can be distinguished from *O. arnensis* sensu stricto by having 15 dorsal scale rows (*versus* 17–17–15), 179–202 ventrals in both sexes (*versus* 164–188 in both sexes), loreal scale present (*versus* loreal absent), 5–6 supralabials (*versus* 7–8, rarely 6), usually 3 posterior temporal scales (*versus* always 2), 7–9 maxillary teeth (*versus* 12–16), and irregular dorsal mottling with 47–57 transverse body

blotches (*versus* dorsum immaculate, less than 20 black body bands). *O. transcaspicus* **comb. et stat. nov.** can be distinguished from *O. churahensis* (later synonymized with *O. russelius*) by having 15 dorsal scale rows (*versus* 17–17–15), 179–202 ventrals in both sexes (*versus* 170–175 in both sexes), 5–6 supralabials (*versus* 7–8), usually 3 posterior temporal scales (*versus* always 2), and irregular dorsal mottling with 42–57 transverse body blotches 1.5–3.0 dorsal scales wide and 12–16 tail blotches (*versus* 37–45 broad black body crossbars, all edged with a cream color, 1.0–2.0 dorsal scales wide and 9–11 tail bars). *O. transcaspicus* **comb. et stat. nov.** is distinguished from *O. melaneus* by having 15 dorsal scale rows (*versus* 17–15–15), 5–6 supralabials (*versus* usually 7, rarely 6), usually 3 posterior temporal scales (*versus* always 2), and irregular dorsal mottling with 42–57 transverse body blotches 1.5–3.0 dorsal scales wide and 12–16 tail blotches (*versus* black dorsum without conspicuous blotches or markings and a distinct blue ventral coloration in life). *O. transcaspicus* **comb. et stat. nov.** can be distinguished from *O. russelius* by having 15 dorsal scale rows (*versus* 17–17–15), 5–6 supralabials (*versus* 7–8, rarely 6), usually 3 posterior temporal scales (*versus* always 2), and irregular dorsal mottling with 42–57 transverse body blotches 1.5–3.0 dorsal scales wide (*versus* dorsum immaculate with narrow black body bands or crossbars usually edged with white, 1.0–2.0 dorsal scales wide). *O. transcaspicus* **comb. et stat. nov.** can be distinguished from *O. tillacki* by having 15 dorsal scale rows (*versus* 17–17–15), 5–6 supralabials (*versus* 7–8), usually 3 posterior temporal scales (*versus* always 2), and irregular dorsal mottling with 42–57 transverse body blotches 1.5–3.0 dorsal scales wide (*versus* dorsum immaculate with 25–35 broad black body bands 4.0–6.0 dorsal scales wide).

In addition, *O. transcaspicus* **comb. et stat. nov.** can be distinguished from *O. taeniolatus*, which it was previously confused with, by having 5 (rarely 6) supralabials (*versus* always 7–8) with only the 3rd supralabial contacting the orbit (*versus* usually the 3rd and 4th in contact with orbit), two posterior supralabials (4th and 5th) in narrow contact due to the lowest posterior temporal scale abutting the two scales (*versus* all supralabials in broad contact), temporal scale formula 1+3 (*versus* temporals 1+2), and a dorsal color pattern with irregular transverse crossbars and no distinct vertebral stripe on the body or tail (*versus* dorsal color pattern variable, but usually with irregular non-transverse crossbars or body blotches, and a small thin vertebral stripe on the body and tail).

Redescription of the Holotype (ZISP 9868). Adult female specimen in good condition after 118 years of preservation. Small portion of midbody in slightly poor condition, large ventral incision posteriorly until vent (Figure 4). SVL 304 mm, TailL 53 mm (TotalL 357 mm). HeadL 9.6 mm, HeadW 5.6 mm, SnL 2.6 mm, EyeL 1.4 mm, FrontalL 3.2 mm. TailLR 0.148, HeadW/HeadL 0.58, SnL/HeadL 0.29, EyeL/SnL 0.54, EyeL/HeadL 0.15. Body elongated and cylindrical in cross section; head ovoid, slightly distinct from neck; snout narrowing in dorsal view, depressed very slightly towards the tip with rostral appearing rounded in lateral profile; snout tip subterminal near mouth; eyes moderately sized compared to head, with a round pupil; nostrils small and subelliptical, pointed in lateral view; mouth flat with lips curving upwards posteriorly along last supralabial; tail gradually tapering to a sharp terminal scute.

Rostral distinctly enlarged, wider than high, triangular in dorsal view, partially separating the anterior half of internasals; posterior scale suture of rostral with internasals “deep-V” shaped, with vertex of rostral in-line with nostrils as a narrow obtuse angle ($\sim 99^\circ$); internasals subpentagonal, wider than long, internasal suture equal in length compared to prefrontal suture; prefrontals subhexagonal, wider than long, wider and longer than internasals; frontal subpentagonal, shield shaped, anterior suture with prefrontals concave and angled; frontal longer than prefrontals; eyes placed posterior relative to the anterior edge of the frontal; angle formed by sutures producing the posterior vertex of the frontal a right angle, almost acute ($\sim 90^\circ$); supraoculars subrectangular, longer than wide, shorter in length than frontal; parietals subpentagonal, longer than wide, width of scale wider than parietal suture, posterior sutures bordering occipital region strongly concave and curved; length of parietals approximately equal in length of frontal; parietal suture shorter than 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 a broad obtuse angle ($\sim 130^\circ$) with lateral ray of angle pointing posterolaterally. Nasal scale rectangular-shaped, longer than wide, fully divided; loreal 1/1, small and square shaped, slightly wider than than long, less than half the size of the nasal; supralabials 5/5; 3rd supralabial in contact with orbit; 5th supralabial largest, first supralabial smallest; all supralabials in broad contact, except for supralabials 4–5, which are in narrow contact due to abutting posterior temporal; preoculars 1/1, wider than long; presubocular 1/1, smaller than preocular; postoculars 2/2, uppermost postocular largest; anterior temporal 1/1; posterior temporals 3/3, bottommost temporal large and subpentagonal in shape, blocking the 4th and 5th supralabial from broadly contacting each other; infralabials 7/7 in all specimens, first in contact with each other, 4/4 infralabials in contact with anterior chin shields; mental subtriangular, wider than long; small mental groove present, starting from border of 1st infralabial and mental terminating at the posterior chin shields; length and width of both chin shields equal in size.

Dorsal scale rows 15–15–15, smooth throughout without apical pits; ventral scales 202; subcaudals 47, paired; total body scales 250; subcaudal ratio 0.19; cloacal plate divided; tail tip a sharp pointed scute. Maxillary teeth 7, posterior two teeth enlarged and blade-like.

Coloration in Preservation. After 121 years in preservation fluids, dorsal ground color cream, margins of some dorsal scales brown forming indistinct and irregular mottling along flanks; 47 indistinct transverse bars along dorsum, broadest vertebrally and slightly narrowing laterally, around 1.5–2.0 dorsal scales at their widest; along tail 12 transverse bands of similar color with any additional markings. Dorsal portion of head is cream, indistinct beige ocular-bar edged with brown starting along 3rd and 4th supralabial scale, past eye covering first half of supraocular, prefrontals and anterior suture of frontal; a second beige and brown-edged temporal bar starting near gulars and first dorsal scales, extending across posterior portion of the fifth supralabial before meeting medially at the parietals and frontal forming a “V” shaped mark; brown nuchal chevron present medially starting at the parietal suture as a small lanceolate tip broadening along the nape as a thick tripartite-shaped blotch, extending laterally on each side of



the flanks, ending before reaching the ventral surface. Ventral surface an immaculate cream, faint beige spotting or mottling along edge of ventral scales, more prominent along the tail.

General Description and Variation. The additional six specimens examined agree with the description of the holotype in most aspects of coloration, scalation and morphometric characteristics. SVL 145–312 mm in male, 267–361 mm in females; TailL 27–70 mm in male, 42–64 mm in females; TotalL in male 195–382 mm, 309–425 mm in females. The largest specimen is an adult female (ZMMU Re-7318) with a SVL of 361 mm and TailL of 64 mm. HeadL 5.9–9.6 mm; HeadW 3.6–6.0 mm, SnL 2.3–3.5 mm, EyeL 0.8–1.4 mm, FrontalL 1.4–3.2 mm. TailLR 0.157–0.183 in males, 0.136–0.159 in females, HeadL/HeadW 0.53–0.72, SnL/HeadL 0.27–0.42, EyeL/SnL 0.34–0.54, EyeL/HeadL 0.12–0.15. Body elongated and cylindrical, slightly robust along midbody in some specimens; head ovoid, slightly distinct from neck; snout narrowing in dorsal view, depressed only slightly towards the tip in dorsolateral view; head oblong in lateral profile; snout tip subterminal near mouth; eyes moderately sized compared to head; nostrils pointed in lateral view; mouth flat, lips slightly curved posteriorly; tail tapering to a sharp terminal scute.

Rostral distinctly enlarged, wider than high, triangular in dorsal view, extending posteriorly partially separating internasals; posterior scale suture of rostral with internasals “deep-V” shaped, with vertex of rostral in-line with nostrils obtuse angled (95°–115°); internasals subpentagonal, wider than long, suture roughly equal or slightly longer than prefrontal suture; prefrontals subhexagonal, wider than long, longer and wider than internasals; frontal subhexagonal, shield shaped, anterior margin of scale clearly angled in most specimens but sometimes more concave; the posterior border of the frontal of one specimen (ZMMU Re-16687) is slightly notched with two pores near the border of the parietals and two similar notched “pores” in the center of the scale (Figure 5); frontal around twice the length of prefrontals; supraoculars subrectangular, longer than wide, shorter in length and width than frontal; eyes placed posterior relative to the anterior edge of the frontal; angle formed by sutures producing the posterior vertex of the frontal right or acute-angled (80°–90°); oftentimes the posterior portion of the frontal truncates, giving the vertex a notched appearance in dorsal profile; parietals subpentagonal, posterior portion concave and usually curved, occasionally straight; parietals slightly longer than wide, width of scale wider than parietal suture; length of parietals equal or slightly longer than length of frontal; parietal suture shorter than frontal length; anterior parietal angle formed by the sutures between the parietal/frontal and the suture between the supraocular/parietal a broad obtuse angle (120°–130°) with lateral ray of angle pointing posterolaterally. Nasal scale rectangular to square shaped, fully divided and usually longer than wide; loreal 1/1, square-shaped, around a quarter or half the size of nasal; supralabials 5/5 in all examined specimens, although Latifi (1991) mentions specimens with 6 supralabials; 3rd supralabial always in contact with orbit; 5th supralabial largest, 1st supralabial smallest; all supralabials in broad contact, except for supralabials 4–5, which contact narrowly due to abutting posterior temporal; preoculars 1/1, uppermost preocular slightly larger; presubocular 1/1 present in four specimens (including holotype), absent in rest; postoculars 2/2, uppermost postocular

largest; anterior temporal 1/1; posterior temporals 3/3 (in one specimen, CAS 180042, 3/2),
bottommost temporal large and subpentagonal in shape, blocking the 4th and 5th supralabial from
broadly contacting each other; infralabials 7/7 in all specimens, first in contact with each other,
4/4 infralabials in contact with anterior chin shields; mental subtriangular, wider than long; small
mental groove present, starting from border of 1st infralabial and mental terminating at the
posterior chin shields; length and width of both chin shields equal in size.

Dorsal scale rows 15–15–15, smooth throughout and without apical pits; ventral scales
179–188 in males, 193–202 in females; subcaudals 48–52 in male, 44–51 in females; total body
scales 232–240 in male, 240–266 in females; subcaudal ratio 0.203–0.224 in males, 0.177–192 in
females; anal plate divided; tail tip tapers to a sharp tip. Maxillary teeth 7 in two specimens
(including the holotype) and 9 in one specimen (CAS 180042), posterior two teeth enlarged and
blade-like. Teeth unavailable for examination in other specimens. We did not examine the
hemipenis of any specimens as all organs were retracted. The structure of hemipenes is a rather
conservative feature. Therefore, despite the lack of any information about hemipenial
morphology of *O. transcaspicus* **comb. et stat. nov.**, we expect that the fully everted and
expanded hemipenes of this species will likely share the same structure with its closest relatives
in the *O. arnensis* species group, namely a short and slightly bilobed hemipenes with spinous
calyces and a simple sulcus spermaticus. Our sample size is too low to make statistical
comparisons between sexes, however a few instances of putative sexual dimorphism are noted.
First, the number of ventral scales appear to be higher in the single male specimen. The male
specimens also have a higher number of subcaudals, TailLR ratio and subcaudal ratio than the
females. The number of total body scales appears to be higher in females.

All specimens in preservative have a cream to beige colored dorsum, with brown
mottling mostly well-defined and restricted across the flanks, some vertebral portions of dorsum
also with white mottling; 47–57 transverse crossbars, usually light brown with the margins of
dorsal scales along bars dark-brown or black and the edges of each bar surrounded weakly edged
by white; all crossbars more well-defined compared to the holotype, widest in the vertebral
region and are narrower laterally, at widest between 1.5–3.0 dorsal scales in length; crossbar
counts on body are not sexually dimorphic; tail blotches range from 12–16 and are similar in
coloration. Dorsal surface of the head tan to cream, lower portions of snout sometimes grayish-
brown; occasional vermiculations present along supralabials and underside of head; the position
of the ocular and temporal bars are consistent amongst all specimens, but are usually brown or
dark-brown and edged with black; the nuchal chevron in some specimens is lanceolate-shaped at
its anterior origin along the parietals, but in two specimens it is blunt or obtuse-pointed,
terminating before the ventral surface along the nape as a thick tripartite or triangular-shaped
blotch. No vertebral stripe is present along the tail in preserved specimens. The ventral surface is
tan to cream, with three specimens bearing irregular margins of dorsal cross-bands visible on
lateral sides of the ventral scales, but in other specimens the ventral surface is immaculate. The
color in life based on ZMMU Re-16687 (Figure 5) and two specimens photographed in
Turkmenistan by A. V. Pavlenko (Figure 6) resembles the coloration in preservative, but its

dorsal patterning and blotching are more pronounced. In these specimens, the dorsum is brown to reddish-brown with white mottling concentrated on the vertebral region and white and dark-brown mottling concentrated on the flanks; the transverse bars are brown and have small dark-brown edges on the dorsal scales of each bar; the nuchal chevron and ocular bars are darker than the bars on the dorsum; iris of eyes gold-brown, pupils black; ventral surface and areas between head markings plain white.

Distribution and Natural History. The known distribution of *Oligodon transcaspicus* **comb. et stat. nov.** is summarized in Figure 1 and Table S1. This species is currently known from the Köpet–Dag region of northern Iran and southern Turkmenistan. In Turkmenistan, it is known from the present-day Balkan, Ahal and Mary provinces. The distribution of the species in Turkmenistan was recently reviewed by Orlov et al. (2018). They report *O. transcaspicus* **comb. et stat. nov.** from ten localities in the foothills of the Köpet–Dag Mountains: Balkan and Ahal Provinces (Danata spring; Eldere Gorge north from Kara–Kala; Chandyr Valley; Makhmumkala village; Kara–Elchi and Eishem gorges; Aidere, Kurygol; Arvaz Valley; 7 km northwards from Saivan; Firuza and Chuli villages; Shamly, near Babazo) and from two localities in Mary Province (Dana–Germab spring, and Nardyvanly spring; environs of Badkhyz). In Iran, *Oligodon transcaspicus* **comb. et stat. nov.** is known definitively from Razavi Khorasan Province from two localities (ZMMU Re-16687 from Bazangan Lake; and another sight record we confirm from ~5 km SW of Mashahd), and Golestan Province (town of Dashliburun [Dashil Borun]). The Golestan Province records originates from Latifi (1991), who reported the locality as “Mazandaran Province (Ghonbad Kavoos) ... in Dashley Boron region”. At the time of Latifi’s writings, the locality “Ghonbad Kavoos... Dashley Boron” (the romanized spelling of Gonbad-e Kavus county) was included within Mazandaran Province before being separated into Golestan Province in 1997. We here confirm this locality in Golestan Province as “Dashliburun” (sometimes spelled as “Dashil Boron”), close to the Turkmenistan border. Rajabizadeh (2018) reported the species in Northeastern Iran close to border of Turkmenistan from eastern Golestan Province to north of Khorasan Razavi Province. Latifi (2000) and Safaei-Mahroo et al. (2015) also reported this species from North Khorasan, and from Zanjan and West Azarbaijan Provinces, although the occurrences in western Iran require further verification (see Discussion).

The natural history of *Oligodon transcaspicus* **comb. et stat. nov.** is somewhat well-known in the literature (Dotsenko, 1984; Atayev, 1985; Szczerbak, Khomustenka & Golubev, 1986; Rustamov & Sopyev, 1994; Szczerbak, 1994; Atayev, Rustamov & Shammakov, 1994; Orlov et al., 2018) and several additional specimens have been recorded. Two specimens photographed by A. Pavlenko (pers. comm.) were found in the daytime amongst rocky outcrops (Figure 6); however, Orlov et al. (2018) noted most specimens were strictly nocturnal or crepuscular. These authors found *Oligodon transcaspicus* **comb. et stat. nov.** was most abundant between elevations of 400–700 meters, but also noted a few specimens that were found at lower and higher altitudes. Most animals were captured at the base of gradually sloping mountain gorges, riverbeds and open habitats with shrubs and tree vegetation that maintain enough surface moisture. Based on this, Orlov et al. (2018) posited that the activity period of *Oligodon*



transcaspicus **comb. et stat. nov.** is highly dependent on high moisture and relative humidity and will only come up on the surface when these conditions are met. Like other *Oligodon*, this species probably feeds on reptile and bird eggs. Atayev, Rustamov & Shammakov (1994) and sources therein record this species laying one to two eggs between the months of May and June, suggesting the reproductive season is in the spring and early summer. It is assumed like other *Oligodon* that its diet primarily consists of reptile eggs.

Remarks. Most sources that mention *O. transcaspicus* **comb. et stat. nov.** have cited Nikolsky (1903a) as the source of original description. However, we have discovered an earlier book that was also authored by Nikolsky describing *Contia transcaspica* dated to 1902. Thus, the year of original description and its publication source should be fixed, and we do so here in the present paper.

Etymology. The species epithet “*transcaspicus*” is a latinized toponymic adjective in genitive singular and given in reference to the type locality of this species, which during the time of its description, was called the Transcaspian Region (Zakaspiyskaya Oblast or Zakaspiyskiy Krai) and was part of the Turkestan Governor–Generalship of the Russian Empire. The Transcaspian Region later became known as Turkmenistan during its time as a constituent republic of the Soviet Union (Turkmen S.S.R.) and now as an independent nation. The epithet is fixed to agree with the gender of the generic name *Oligodon*, which is masculine. We recommend the English common name “Köpet–Dag Kukri Snake” for this species, followed by the Russian, Farsi, and Turkmen common names “Zakaspiyskiy oligodon”, “داغ کپه مار لوس” [Loos Mār-e Kopet Dagh], and “Goňurja ýylanjyk”, respectively (see Rustamow, 2011; Rajabizadeh, 2018).

The taxonomic status of *Oligodon* “arnensis” in Pakistan. Because the revision of *O. arnensis* sensu auctorum by Bandara et al. (2022) only focused on material from India and Sri Lanka, we use this section to review the status of these snakes in neighboring Pakistan. We examined one specimen of *O. “arnensis”* (CUHC 7904) recently collected by DJ and RM on 16 September 2018 from Kallar Kahar, Punjab Province, Pakistan (32.7695°N, 72.7065°E, 613 m a.s.l.). Based on the presented mtDNA phylogeny, this specimen was recovered in a clade with two additional samples from Pakistan that were previously identified as *O. cf. churahensis* by Mirza, Bhardwaj & Patel (2021). These authors only briefly commented on the status of these genetic samples and could not examine voucher specimens from Pakistan in their study. A brief description of CUHC 7904 is as follows (Figure 7): adult male, SVL 345 mm, TailL 65 mm (TotalL 410 mm; TailLR 0.159) 16–17–15 dorsal scale rows, 183 ventrals, 49 subcaudals (233 total body scales), subcaudal ratio of 0.21, 1/1 loreal present, 1/1 divided nasal, 7/7 supralabials with the third and fourth in contact with the eye, 7/7 infralabials, and an immaculate brown dorsum with 37 black crossbands across the body and 13 tail bands approximately 1.0–1.5 dorsal scales wide at midbody and interspaces between each band approximately 4.0 dorsal scales long. In addition to this specimen, multiple authors who have conducted fieldwork in Pakistan (Minton, 1962; Minton, 1966; Mertens, 1969; Khan, 2002) have recorded *O. “arnensis”* specimens. Both

Minton (1962) and Khan (2002) figure an *O. "arnensis"* (with Khan, 2002 swapping the images of *O. "arnensis"* and *O. taeniolatus* by mistake) bearing small narrow black crossbars with white edges. Based on these characteristics, along with other scalation features (see Table 3), the literature descriptions of Pakistani *O. "arnensis"* are very similar to CUHC 7904 and specimens *O. russelius* fide Bandara et al. (2022). Therefore, based on our specimen and previous reports of *O. "arnensis"*, we refer the northern Pakistan populations of *O. "arnensis"* to *O. russelius*.

Records of *Oligodon* in Afghanistan. Literature reports of *O. "arnensis"* and *O. taeniolatus* from Afghanistan are sparse but have been the subject of confusion for decades. Brück (1968) first reported a juvenile Kukri Snake he identified as *O. taeniolatus* from “dem Gebiete um Djelalabad” [= vicinity of Jalalabad]. This record was plotted by Sindaco et al. (2013) but rejected due to imprecision by Wagner et al. (2016b). Although Brück (1968) identified this specimen as *O. taeniolatus*, data he provided for this specimen indicates it bears 17 dorsal scale rows, contra the 15 dorsal scales normally observed in *O. taeniolatus*. This was noticed quickly by Král (1969), who subsequently corrected its identification to *O. arnensis*. Nevertheless, both Sindaco, Venchi & Grieco (2013) and Wagner et al. (2016b) recorded both *O. arnensis* and *O. taeniolatus* as inhabitants of Afghanistan, failing to realize that their records refer to the same specimen (MMB 28497). Brück (1968)’s account provided additional morphological data that allow us to confirm its identification. He notes that the specimen bears the following features: juvenile (unsexed, but based on relative tail length and subcaudal ratio, possibly an immature female), SVL 153 mm, TailL 24 mm (TotalL 177 mm, TailLR 0.136), dorsal scales in 17 rows, 198 ventrals, 44 subcaudals, (243 total body scales, subcaudal ratio 0.181), 7/7 supralabials (3–5 contacting eye), 6/6 infralabials, 1 preocular, 2 postocular, 1+2 temporals, and 49 dark crossbars across the body and tail. These characteristics confirm that the specimen should not be identified as *O. taeniolatus* and that Král’s re-identification as *O. "arnensis"* was correct (see Table 3 for more comparisons). A second *Oligodon* record from Afghanistan was recently documented on the citizen science platform iNaturalist (2022). This specimen (obs. 110932106, user mohammadfarooq) was observed from Dara-i-Pech district, Kunar Province, Afghanistan (35.0553°N, 70.9561°E; 1,700–1,800 meters a.s.l.) on 9 April 2022. While photographs of the specimen are too poor in quality to discern any scalation features, its color pattern consisting of approximately 51 black crossbars and 13 tail bars (64 total crossbars) greatly resembles *O. "arnensis"*, specifically *O. russelius* (and to some extends *O. churahensis* but see Discussion). Because of this, we conclude that the Afghanistan populations previously recorded as *O. arnensis* (Khan, 2002; Wagner et al., 2016b) should also represent *O. russelius*. All records of this species from the country are restricted to the western portion of the Hindu Kush.

The only other report of an Afghan *Oligodon* is a record of *O. taeniolatus* from Afghanistan noted by Wagner et al. (2016b) from “Kars, Kandahar Province” based on specimen USNM 194971. We attempted to trace the voucher of this specimen and discovered that the museum catalog number USNM 194971 refers to a scincid lizard *Eurylepis taeniolatus* Blyth, 1854a, and not a kukri snake. No collection records of *Oligodon* from Afghanistan have been

found within the USNM collections ledger (E. Langan, 2022, pers. comm.), and so we consider the Kandahar Province record of *O. taeniolatus* to be erroneous. The similar species epithets between *E. taeniolatus* and *O. taeniolatus* may have caused Wagner et al. (2016b) to mistake its identity, resulting in a *lapsus calami*. Therefore, we formally remove *O. taeniolatus* from the herpetofauna of Afghanistan, Iran, and Turkmenistan. However, we note that the presence of *O. transcaspicus* **comb. et stat. nov.** in Afghanistan is still possible, particularly in northwestern provinces bordering with Iran and Turkmenistan (suggested also by the SDM analysis).

Discussion

The phylogenetic analysis of 12S–16S rRNA, *cyt b* fragments, morphological data and SDM mapping data support the resurrection of *Contia transcaspica* as *Oligodon transcaspicus* **comb. et stat. nov.** for Iranian and Turkmen populations previously ranked under *O. taeniolatus*. This analysis also revealed substantial genetic differentiation between populations of *O. taeniolatus* on the Indian subcontinent warranting additional revisionary work from future authors. We cannot provide a valid description for the deeply divergent lineages in Sri Lanka and mainland India due to a lack of broad morphological and genetic sampling. However, we note that the names *Oligodon fasciatus* Günther, 1864 (now considered a subspecies of *O. taeniolatus*) and *Oligodon taeniolatus* var. *ceylonicus* Wall, 1921 are both available names for Sri Lankan populations if they indeed prove to be distinct from others on the island, and/or the remainder of the Indian subcontinent. While the taxonomy of *O. taeniolatus* remains unresolved, the position of *O. transcaspicus* **comb. et stat. nov.** outside of this clade in the *O. arnensis* species group justifies its separation as a distinct species. The distribution of *O. transcaspicus* **comb. et stat. nov.** is probably more expansive than currently ascertained, and we expect that this species will eventually be found in additional localities across the Köpet–Dag Mountain region.

The SDM models identified some patches of suitable habitat across the Western Caspian region and Central Iranian Desert in areas where Latifi (1991, 2000) and Safaei-Mahroo et al. (2015) reported its presence. Unfortunately, we could not trace any specimen vouchers of Latifi's collection in the Razi Vaccine and Serum Research Institute associated with these Iranian records. Since these Latifi's specimens come from snake hunters of the institute (and were not collected by Latifi himself) and the locality data is given only at province level, researchers must be very cautious about them. Only subsequent fieldwork in these areas might verify such reports, particularly in adjacent Iranian provinces bordering Turkmenistan.

Verified vouchers specimens of *O. transcaspicus* **comb. et stat. nov.** also exist close to the border of Afghanistan in Mary Province, Turkmenistan. Since SDM modelling also predicts suitable habitat in this region, it is possible that this species also persists in the northwestern portion of Afghanistan (specifically Herat, Badghis, Faryab and Jowzan provinces), but a lack of survey effort due to security concerns makes it difficult to ascertain whether this species will be found here anytime soon (see Jablonski et al., 2021). The conservation of *O. transcaspicus* **comb. et stat. nov.** does not seem to be under any significant threats, although factors such as habitat degradation and human encroachment could pose a threat to some populations. Climate



projections also state that aridification and a reduction of river runoff is expected across the southern portion of Turkmenistan over the following decades (Lioubimtseva et al., 2012; Duan et al., 2019). Because the SDM mapping analyses indicated temperature and precipitation seasonality were major factors influencing the distribution of *O. transcaspicus* **comb. et stat. nov.**, climate change may also negatively impact populations. Under listings provided by the International Union for Conservation of Nature (IUCN) we would recommend classifying this species as “Least Concern”. Continued monitoring of existing populations and additional field surveys across the Köpet–Dag Mountain Range would improve our understanding of the ecology and conservation of this species.

Although our sampling is very limited, the results from our study suggest the three-taxon statement of the *O. arnensis* sensu auctorum by Bandara et al. (2022) requires additional scrutiny. Specimens we included from Ganjam district, Odisha, India (CAS 17224–225) are well within the distribution of *O. russelius* (fide Bandara et al., 2022) and both morphologically resemble *O. arnensis* sensu stricto, bearing 18–20 dark black body bands that are 2.0–3.0 dorsal scales wide. Another specimen collected near Rajamahendravaram, Andhra Province, India (CAS 94375) is close to the type locality of *O. russelius* but has 22 dorsal body bands that are 1.5–2.0 dorsal scales wide (band count resembling the species diagnosis of *O. arnensis* sensu stricto fide Bandara et al., 2022). Either the ranges of *O. arnensis* sensu stricto and *O. russelius* are sympatric in parts eastern India, or a broad contact zone between the two species may exist. This could explain why some specimens we examined have more variable color pattern conditions than previously described. The distribution map of *O. arnensis*, *O. russelius* and *O. tillacki* in Bandara et al. (2022)’s clearly separates the three taxa on the Indian subcontinent; however, we note that the collection localities in their map combine collection localities with observations identified from iNaturalist. We agree that such citizen scientist databases have great utility in documenting rare and understudied herpetofauna, but they still can suffer from data quality issues (i.e., limited number of visible morphological features, misidentification errors). It is difficult to discern which locations in Bandara et al. (2022)’s map are voucher specimens or iNaturalist observations because the authors do not provide a geolocation appendix in their paper and do not denote a distinction between their location datapoints. Furthermore, we note that the p-distance (based on cyt *b*) between Sri Lankan *O. arnensis* samples and the GenBank sample identified as *O. cf. tillacki* is only 3.6%, lower than most normal p-distances separating species-level lineages of *Oligodon*. We conservatively retain the species status of *O. tillacki* as we have not directly examined the voucher specimen of this sample to verify its identity. Subsequent treatments of *O. arnensis* sensu stricto, *O. russelius*, and *O. tillacki* should emphasize increased specimen and tissue collection for an integrative taxonomic approach.

Our analysis also confirmed the taxonomic identity of *O. “arnensis”* populations in northern Pakistan and Afghanistan as *O. russelius*. Nevertheless, several authors (Minton, 1966; Mertens, 1969; Khan, 2002) note the distribution of *O. “arnensis”* extends into central and southern Pakistan close to the border of western India. These locations come close to the known distribution of *O. tillacki*, especially near Gujarat State, India. However, Minton (1966) noted

that all his specimens have black bars with white edges, a phenotypic trait that Khan (2002) also described. Both illustrations by these authors show a “V-shaped” marking on the nape, although it is not a thick triangular blotch that is observed in *O. tillacki*. We believe there is little indication that *O. “arnensis”* populations in southern and central Pakistan match the description *O. tillacki* and we maintain the identity these populations as *O. russelius* for the time being. It is still possible that *O. tillacki* could range into this part of the country due to the continuity of habitat within this region, and we suggest future herpetological survey work and the examination of additional material to confirm this. Such a discovery could align with recent studies that have denoted a biogeographic break between the right and left banks of the Indus River seen in several Pakistani amphibians and reptiles (Gowande et al., 2021; Agarwal et al., 2022; Dufresnes et al., 2022).

Our study has taxonomic implications for the recently described *O. churahensis*, as Mirza, Bhardwaj & Patel (2021) tentatively associated Pakistani samples of *O. “arnensis”* with this species. Like the genetic distances between *O. cf. tillacki* and *O. arnensis sensu stricto*, the *cyt b* p-distance between the Pakistani clade of *O. russelius* (= *O. cf. churahensis*) and the clade containing the type series of *O. churahensis* is low for species-level divergence, standing at only 3.3%. *Oligodon churahensis* was described by Mirza, Bhardwaj & Patel (2021) based on two specimens collected at the foothills of the western Himalayas in Himachal Pradesh, India. Bandara et al. (2022) correctly noted that literature descriptions of kukri snakes similar to *O. churahensis* were reported as *O. arnensis sensu lato* (= now *O. russelius*) by past authors (Wall, 1921; Deraniyagala, 1936; Constable, 1949; Deraniyagala, 1955). However, because Bandara et al. (2022) include data from these historical sources into their conception of *O. churahensis* (as seen in their supplementary material), diagnosing this species from *O. russelius* becomes puzzling. In the comparisons section of *O. russelius*, Bandara et al. (2022) separated this species from *O. churahensis* by the presence of 30–45 crossbars (*versus* 48–54 in *O. churahensis*) the distance between each crossbar measured in vertebral dorsal scales (4–6 scales *versus* 2–4 in *O. churahensis*), and by a different head shape marking (inverted Y-shaped marking *versus* heart-shaped symbol in *O. churahensis*). However, the authors note that *O. churahensis* has 56–62 crossbars in the remaining text, especially in Table 1, where it is again compared to the 30–45 crossbars of *O. russelius*. It appears that the authors confused the true number of crossbars found in *O. churahensis* and *O. russelius*, failed to specify between “total crossbars” (including body and tail bars) and “body crossbars” (restricted from nape to vent) and did not completely summarize the color pattern traits observed in all of the sources they believe comprise *O. churahensis* (Wall, 1921; Deraniyagala, 1936; Constable, 1949; Deraniyagala, 1955; Mirza, Bhardwaj & Patel 2021). Per the original description (Mirza, Bhardwaj & Patel 2021), the actual number of body crossbars in *O. churahensis* is 37–45, with the total crossbars noted as 48–54. Furthermore, Bandara et al. (2022) state in the written description that *O. russelius* has 30–45 body crossbars and 6–10 tail bars. This indicates that the supposed differences in crossbar numbers are a lot less significant than previously considered. As argued by Mahony & Kamei



(2021), errors and inconsistencies in taxonomic articles are inevitable, but authors should practice great care to make sure data inputted into descriptions and tables is consistent.

When we combine our own data on *O. russelius* from Afghanistan, Pakistan with the clarified characters of Bandara et al. (2022) and existing data in the literature (Wall, 1921; Constable, 1949), most color pattern and scalation traits between this taxon and *O. churahensis* overlap (Table 3). Combined with the low genetic divergence revealed by our molecular data, our study does not support the species-rank status of *O. churahensis*. It is plausible that specimens identified as *O. churahensis* represent the high-end of a geographic cline of cross-banded phenotypes found within *O. russelius* across its range, as suggested in part by Wall (1921). Alternatively, it is possible that the *O. churahensis* and *O. russelius* clades could maintain their reciprocal monophyly, albeit with low genetic divergence that would support the existence of two lineages at the subspecies level. In the absence of additional samples from the type locality of *O. churahensis* and adjacent regions of northern India and Pakistan, we believe the most appropriate decision is to relegate the species to the junior synonymy of *O. russelius*, which we do so here.

Our resurrection of *O. transcaspicus* **comb. et stat. nov.** and the clarification of *O. "arnensis"* and *O. taeniolatus* records from Middle and Southwest Asia represents a small step of a long journey in our goal of understanding the evolutionary history of snakes and other herpetofauna of this region. Interestingly, several reptiles found in Middle and Southwest Asian countries that are Oriental realm elements of the region's herpetofauna are recognized as separate taxa. Such examples include *Boiga trigonata melanocephala* (Annandale, 1904), *Lycodon striatus bicolor* Nikolsky, 1903b and *Ptyas mucosa nigriceps* Terentjev & Chernov, 1949. Other reptile taxa found in Middle/Southwest Asia whose close relatives are of Oriental realm origin include *Naja oxiana* Eichwald, 1831 and *Eublepharis macularius* Blyth, 1854b. For these latter species, phylogeographic evidence indicates minimal genetic differentiation between populations opposite of the Hindu Kush suggesting rapid range expansion from the Indian subcontinent into Middle/Southwest Asia due to suitable environmental conditions formed by steppe habitats west of the Hindu Kush mountains (Kazemi et al., 2021; Agarwal et al., 2022). The uniqueness of the evolutionary lineage representing *O. transcaspicus* **comb. et stat. nov.** paints a different picture, as the presented molecular, morphological and SDM evidence implies that the divergence of its common ancestor into present-day Iran and Turkmenistan occurred much earlier. The high topography surrounding the Hindu Kush and the south-adjacent Registan-North Pakistan sandy deserts present formidable biogeographic barriers, and probably limited dispersal opportunities periods when climatic and habitat conditions were suitable. The diversity and cladogenesis of other Oriental-affiliated elements of Middle and Southwest Asia's amphibians and reptiles are still poorly understood by herpetologists, and present numerous intriguing questions for future research. The acquisition of new material along with more comprehensive phylogeographic analyses will undoubtedly shed light on these unique animals and their taxonomic and evolutionary status.

Conclusions

We carefully reviewed the status of the two kukri snake species found in Middle and Southwestern Asia, the banded kukri snake *O. "arnensis"* and the streaked kukri snake *O. taeniolatus*, leading to several taxonomic and distributional clarifications. For *O. taeniolatus*, we found that specimens from the Köpet-Dag Mountain Range of northern Iran and southern Turkmenistan were phylogenetically recovered in a different intrageneric grouping compared to nominotypical *O. taeniolatus* on the Indian subcontinent. To fix this paraphyly, we resurrected the junior synonym *Contia transcaspica* and provided a thorough morphological redescription supplemented with SDM mapping to explore its potential range. We also found that Afghanistan and northern Pakistan records of kukri snakes previously recognized as *O. arnensis* should in fact be allocated to the species *O. russelius*. This latter species forms a clade sister to the recently described *O. churahensis* from northern India, but is only separated by a small genetic divergence of 3.3% based on cytochrome *b*. Because the morphology between *O. russelius* and *O. churahensis* exhibits substantial overlap, we consider both species to be conspecific, and relegate *O. churahensis* to junior synonymy. Our investigation further revealed that there are no records of *O. taeniolatus* from Afghanistan, as the two past reports from the literature refer to a misidentified specimen of *O. russelius*, and a misidentified scincid lizard, respectively. As a consequence, we remove *O. taeniolatus* from the snake fauna of Afghanistan, Iran, and Turkmenistan. The two kukri snakes found in Middle and Southwestern Asia now consist of *transcaspicus* **comb. et stat. nov.** and *O. russelius*. These two species represent key Oriental herpetofaunal elements in a region that primarily consists of Palearctic amphibians and reptiles. Their ranges in Middle and Southwest Asia appear to be influenced by past climate change across the Hindu Kush Mountain range, in addition to past biotic and abiotic fluctuations that occurred during the Plio-Pleistocene. Future studies that explore the biogeographic origins of these animals are recommended. We also suggest that additional taxonomic work on *O. arnensis* and *O. taeniolatus* are needed on Indian subcontinent populations. The number of recognized species in *Oligodon* remains at 89.

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Competing Interests

Nikolay A. Poyarkov serves as an Academic Editor for PeerJ. The other authors declare that they have no competing interests.

Author Contributions

Justin L. Lee collected data, conceived and designed the experiments, analyzed the data, prepared figures and tables, prepared the drafts of the paper, reviewed drafts of the paper, and approved the final draft.



Platon V. Yushchenko collected data, conceived and designed the experiments, analyzed the data, prepared figures and tables, prepared the drafts of the paper, reviewed drafts of the paper, and approved the final draft.

Konstantin D. Milto collected data, prepared figures, reviewed drafts of the paper, discussion of the results

Mehdi Radjabizadeh collected data, prepared figures, reviewed drafts of the paper, discussion of the results

Eskandar Rastegar Pouyani analyzed the data, reviewed drafts of the paper, discussion of the results

Daniel Jablonski collected data, contributed analysis tools, prepared figures, prepared the drafts of the paper, reviewed drafts of the paper, and approved the final draft, discussion of the results

Rafaqat Masroor collected data for the paper, contributed analysis tools, reviewed drafts of the paper, approved the final draft, discussion of the results

Suranjan Karunarathna collected data for the paper, contributed analysis tools, reviewed drafts of the paper, approved the final draft, discussion of the results

Ashok Kumar Mallik analyzed the data, contributed analysis tools, reviewed drafts of the paper, discussion of the results

Princia Dsouza collected data for the paper, reviewed drafts of the paper, approved the final draft, discussion of the results

Nikolai L. Orlov analyzed the data, reviewed drafts of the paper, discussion of the results

Roman A. Nazarov collected data, prepared figures, reviewed drafts of the paper, discussion of the results

Nikolay A. Poyarkov conceived and designed the experiments, analyzed the data, prepared the drafts of the paper, reviewed drafts of the paper, and approved the final draft.

Animal Ethics

The following information was supplied relating to ethical approvals (i.e., approving body and any reference numbers):

Specimen collection protocols and animal operations followed the Institutional Ethical Committee of International Center for Science, High Technology and Environmental Sciences, Kerman, Iran (Certificate #1.87-1).

Field Study Permissions

The following information was supplied relating to field study approvals (i.e., approving body and any reference numbers):

Field works, including collection of the samples and animals in the field, was performed outside of any protected area, in the framework of a project contract signed by International Center for Science, High Technology and Environmental Sciences, Kerman, Iran (contract number 1.87, issued at 11.04.2008). The contract bears a permission to collect the reptile samples outside of any protected area of Department of the Environment (specified in www.doe.ir) that needed

extra permissions. Specimen collection protocols and animal operations followed the Institutional Ethical Committee of International Center for Science, High Technology and Environmental Sciences, Kerman, Iran (certificate number 1.87-1).

DNA Deposition

The following information was supplied regarding the deposition of DNA sequences: Sequences of 12S–16S rRNA and *cyt b* genes presented here are accessible via GenBank accession numbers OQ092426; OQ099833–OQ099837; and OQ116816–OQ116825 (Table 1).

Data Availability

The following information was supplied regarding data availability: Specimens examined in this study are deposited in herpetological collections of the following museums:

1. CAS: California Academy of Sciences, San Francisco, USA;
2. CUHC: Comenius University Herpetological Collection, Bratislava, Slovakia;
3. MMB: Department of Zoology, Moravian Museum, Brno, Czech Republic;
4. USNM: National Museum of Natural History, Washington, DC, USA;
5. ZISP: Zoological Institute of Russian Academy of Sciences, St. Petersburg, Russia;
6. ZMMU: Zoological Museum of Moscow State University, Moscow, Russia.

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1409 Supplementary Material and Table Legends:

1410

1411 **Supplementary Material 1.** Other Specimens of *Oligodon* examined, organized based on their
1412 morphological identification based on Bandara et al. (2022).

1413

1414 **Supplementary Table 1.** Tabled list of localities of *Oligodon transcaspicus* **comb. et stat. nov.**
1415 with latitude and longitude coordinates used for species distribution modelling.

1416

1417 **Supplementary Table 2.** Primers used in this study

1418

Table Legends:

Table 1. Sequences and voucher specimens of *Oligodon* and outgroup taxa used in molecular analyses of this study.

Note that the numbers (column one) included in this table are not the same as those found in other tables or figures. Acronyms present here that are not noted in the materials and methods include the following: CHS, unknown field tag series; KIZ, Kunming Institute of Zoology, Chinese Academy of Sciences, Kunming, China; NCBS, National Center for Biological Sciences, Bangalore, India; RAP, field tags of R. Alexander Pyron; ROM, Royal Ontario Museum, Toronto, Canada; RS, field tags of Ruchira Somaweera; SIEZC, Department of Zoology, Southern Institute of Ecology, Ho Chi Minh City, Vietnam; SYNU, Shenyang Normal University, Shenyang, China; TNHC, Texas Natural History Collections, Austin, USA; UMMZ, University of Michigan Museum of Zoology, Ann Arbor, USA; ZMUVAS, Zoological Museum of the University of Veterinary and Animal Sciences, Punjab, Pakistan. Additional abbreviations include NP: National Park, NR: Nature Reserve, and WS: Wildlife Sanctuary.

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Table 3. Morphological comparisons of *Oligodon russelius* specimens from Afghanistan, northern India, and Pakistan hitherto recognized as *Oligodon “arnensis”* or *Oligodon churahensis*.

Data from the literature are combined from multiple authors unless denoted with an asterisk (*), which indicates that only a single source was used. Abbreviations for males and females are denoted by (m) or (f) respectively and (total) is used to indicate that the data combines both sexes or combines the total number of body and tail blotches.

Table 4. Pairwise matrix of genetic distances between and within *Oligodon* species sampled in this study.

Uncorrected p-distances (given as percentages) are based on sequences of the cytochrome *b* mtDNA gene are shown below the diagonal. Intraspecific genetic p-distances are shown along the diagonal and are highlighted in bold. See Table 1 for the list of samples used to create this matrix.

Figure Legends:

Figure 1. Approximate distribution and location of samples utilized in this study for molecular and morphological analyses (A); and approximate distribution of *Oligodon transcaspicus* comb. et stat. nov in the Köpet–Dag Mountain range of Iran and Turkmenistan (B).

Triangle icons denote specimens with only molecular data; square icons denote specimens with only morphological data; rhombic icons denote specimens without molecular and morphological data (only locality is known); round icons denote specimens with both molecular and morphological data. Stars/asterisks next to numbers indicate type localities. Localities: (1) Ashgabat, Ahal Prov., Turkmenistan (type locality of *Oligodon transcaspicus* **comb. et stat. nov**); (2) Chuli, Ahal Prov., Turkmenistan; (3) Geok-Tepe, Ahal Prov., Turkmenistan; (4) Karanki, Ahal Prov., Turkmenistan; (5) “Goalon” (Goudan), Ahal Prov., Turkmenistan; (6) Aidere, Ahal Prov., Turkmenistan; (7) Bazangan Lake, Razavi Khorasan Prov., Iran; (8) Punjab Prov., Pakistan; (9) Kallar Kahar, Punjab Prov., Pakistan; (10) Chamba Distr., Himachal Pradesh, India (type locality of *Oligodon churahensis*); (11) Jalalabad, Nangarhar Prov., Afghanistan; (12) Dara-i-Pech district, Kunar Prov., Afghanistan; (13) Maharashtra, India; (14) Chitwan NP, Bagmati Prov., Nepal; (15) Ganjam, Odisha, India; (16) 24.1 km SW of Rajamahendravaram, Andhra Pradesh, India; (17) Bangalore, Karnataka, India; (18) Tamil Nadu, India; (19) Puttalam Distr., North Western Prov., Sri Lanka; (20) Udawalawe National Park, Uva Prov.; (21) Monargala Distr., Southern Prov., Sri Lanka; (22) Hambantota Distr., Southern Prov., Sri Lanka; (23) Gampaha Distr., Western Prov., Sri Lanka; (24) Polonnaruwa Distr., North Central Prov., Sri Lanka; (25) Paramikulam, Kerala, India; (26) Barengabari, Assam, India.

Figure 2. Phylogenetic 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; n-dash denotes no support. Outgroup taxa are not shown. Colors of clades and locality numbers correspond to Figure 1.

Figure 3. Species distribution model (SDM) map based on geolocation points of *Oligodon transcaspicus* comb. et stat. nov. from Iran and Turkmenistan.

Darker red coloration indicates more suitable habitat, whereas lighter colors indicate less suitable habitat.

Figure 4. Photographs of the preserved holotype specimen of *Contia transcaspica* (ZISP 9868) now *Oligodon transcaspicus* comb. et stat. nov. from “Köpet–Dag, Transcaspica”.

Scale bars equal 10 millimeters. Photos by Konstantin D. Milto.

Figure 5. Live photographs of *Oligodon transcaspicus* comb. et stat. nov. (ZMMU Re-16687; field number RAN-3264) from Khorasan Province, Iran.

(a) Right lateral, (b) left lateral, (c) ventral, (d) ventral views of the head, and (e) general habitus. Photographs by Roman A. Nazarov.

Figure 6. Two unvouchered specimens of *Oligodon transcaspicus* comb. et stat. nov.

Specimens photographed from (a) Podere, Sumbar Valley, Turkmenistan and (b) Seqiz-Khan Gorge, Turkmenistan. Photographs taken by Alexander V. Pavlenko.

Figure 7. Photographs of *Oligodon russelius* from Pakistan (a–e) and Afghanistan (f).

Shown in a–e is specimen CUHC 7904 from Kallar Kahar, Punjab Province, Pakistan, showing (a) general habitus in life, (b) right lateral, (c) left lateral, (d) dorsal, and (e) ventral views of the head in preservative. Shown in (f) is a cropped image of *O. russelius* from Kunar Province, Afghanistan observed on iNaturalist (obs. 110932106, user mohammadfarooq). Photographs a–e by Daniel Jablonski, photograph f taken by Mohammad Farooq from iNaturalist.org.

Table 1 (on next page)

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No.	Sample ID	GenBank Accession No.	Species	Country	Locality	Reference
1	ZMMU Re-16687	OQ116823; OQ116816	<i>Oligodon transcaspicus</i> comb. et stat. nov.	Iran	Razavi Khorasan Prov., Bazangan Lake	<i>this work</i>
2	CUHC 7904	OQ092426; OQ116817	<i>Oligodon russelius</i>	Pakistan	Punjab Prov., Kallar Kahar	<i>this work</i>
3	SL-Os-1	OQ099833; OQ116819	<i>Oligodon arnensis albiventer</i>	Sri Lanka	Sabaragamu Prov., Ratnapura Distr., Udawalawe	<i>this work</i>
4	SL-Oa-2	OQ116825; OQ116820	<i>Oligodon arnensis albiventer</i>	Sri Lanka	Uva Prov., Monargala Distr., Thanamalwila	<i>this work</i>
5	ZMMU Re-17331	OQ116824; OQ116818	<i>Oligodon arnensis albiventer</i>	Sri Lanka	Western Prov., Gampaha Distr., Ganemulla	<i>this work</i>
6	SL-Os-2	OQ099834; OQ116821	<i>Oligodon sublineatus</i>	Sri Lanka	Central Prov.	<i>this work</i>
7	SL-Os-3	OQ099835; OQ116822	<i>Oligodon sublineatus</i>	Sri Lanka	Central Prov., Kandy Distr.	<i>this work</i>
8	CESS 563	OQ099837	<i>Oligodon arnensis</i>	India	Karnataka, Bangalore	<i>this work</i>
9	CESS 180	OQ099836	<i>Oligodon taeniolatus</i>	India	Kerala, Paramikulam	<i>this work</i>
10	WII-ADR980	ON262767, ON241309	<i>Oligodon melaneus</i>	India	Assam, Barengabari	Das et al. (2022)
11	NCBS NRC-AA-019	MZ675817	<i>Oligodon churahensis</i>	India	Himachal Pradesh, Chamba Distr.	Mirza et al. (2021)
12	NCBS NRC-AA-020	MZ675818	<i>Oligodon churahensis</i>	India	Himachal Pradesh, Chamba Distr.	Mirza et al. (2021)
13	ZMUVAS 10	MK941834	<i>Oligodon russelius</i>	Pakistan	Punjab Prov.	Mirza et al. (2021)
14	Saeed 5	MZ403752	<i>Oligodon russelius</i>	Pakistan	-	Ahmed et al. (unpublished)
15	RAP 483	KC347327; KC347365; KC347464	<i>Oligodon arnensis</i>	Sri Lanka	Southern Prov., Hambantota Distr.	Pyron et al. (2013)
16	NCBS-NRC-AA-021	MZ675819	<i>Oligodon cf. tillacki</i>	India	Maharashtra	Mirza et al. (2021)
17	RS136	KC347330; KC347368; KC347484;	<i>Oligodon taeniolatus ceylonicus</i>	Sri Lanka	Central Prov., Polonnaruwa Distr.	Pyron et al. (2013)

		KC347521; KC347408; KC347445				
18	RS-OC	KC347328; KC347366	<i>Oligodon calamarius</i>	Sri Lanka	Central Prov., Kandy Distr.	Pyron et al. (2013)
19	RAP 504	KC347329; KC347367	<i>Oligodon sublineatus</i>	Sri Lanka	Central Prov., Kandy Distr.	Pyron et al. (2013)
20	ROM37092	HM591504	<i>Oligodon cinereus</i>	Vietnam	Dong Nai Prov., Cat Tien NP	Green et al. (2010)
21	UMMZ201913	HM591519	<i>Oligodon octolineatus</i>	Brunei	Tutong Distr., 3 km E of Tutong	Green et al. (2010)
22	ROM 35626	HM591526	<i>Oligodon chinensis</i>	Vietnam	Cao Bang Prov., Quang Thanh	Green et al. (2010)
23	ROM35629	HM591533	<i>Oligodon formosanus</i>	Vietnam	Cao Bang Prov., Quang Thanh	Green et al. (2010)
24	ROM32261	HM591534	<i>Oligodon ocellatus</i>	Vietnam	Dak Lak Prov., Yok Don NP	Green et al. (2010)
25	ROM32260	HM591521	<i>Oligodon taeniatus</i>	Vietnam	Dak Lak Prov., Yok Don NP	Green et al. (2010)
26	ROM32464	HM591523	<i>Oligodon barroni</i>	Vietnam	Gia Lai Prov., Krong Pa	Green et al. (2010)
27	CAS204963	HM591535	<i>Oligodon cyclurus</i>	Myanmar	Ayeyarwady Reg., Mwe Hauk	Green et al. (2010)
28	CAS204855	HM591509	<i>Oligodon splendidus</i>	Myanmar	Mandalay Reg., Kyauk Se	Green et al. (2010)
29	CAS215976	HM591513	<i>Oligodon torquatus</i>	Myanmar	Mandalay Reg., Min Gone Taung WS	Green et al. (2010)
30	CAS213822	HM591514	<i>Oligodon planiceps</i>	Myanmar	Magwe Reg., Shwe Set Taw WS	Green et al. (2010)
31	CAS213896	HM591516	<i>Oligodon theobaldi</i>	Myanmar	Magwe Reg., Shwe Set Taw WS	Green et al. (2010)
32	CAS213271	HM591517	<i>Oligodon cruentatus</i>	Myanmar	Yangon Reg., Hlaw Ga NP	Green et al. (2010)
33	ROM27049	HM591518	<i>Oligodon eberhardti</i>	Vietnam	Cao Bang Prov., Quang Thanh	Green et al. (2010)
34	TNHC59846	HM591511	<i>Oligodon maculatus</i>	Philippines	Mindanao, Barangay Baracatan	Green et al. (2010)
35	SIEZC 20201	MN395604; MN396765	<i>Oligodon rostralis</i>	Vietnam	Lam Dong Prov., Bidoup–Nui Ba NP	Nguyen et al. (2020)
36	ZMMU Re-14304	MN395601; MN396762	<i>Oligodon annamensis</i>	Vietnam	Dak Lak Prov., Chu Yang Sin NP	Nguyen et al. (2020)
37	KIZ014591	MW090140; MW133297	<i>Oligodon nagao</i>	-	-	Xu et al. (2021)
38	KIZ011002	MW090139; MW133296	<i>Oligodon lipipengi</i>	China	Tibet, Medok	Che et al. (2020)
39	CHS850	MK194265; MK201568; MK065694	<i>Oligodon albocinctus</i>	China	-	Li et al. (Unpublished)
40	CHS668	MK194135; MK201461; MK065563	<i>Oligodon fasciolatus</i>	China	-	Li et al. (Unpublished)
41	CHS304	MK194038; MK201386; MK065470	<i>Oligodon lacroixi</i>	China	-	Li et al. (Unpublished)
42	CHS683	MK194147; MK065575	<i>Oligodon ornatus</i>	China	-	Li et al. (Unpublished)
43	SYNU 1907027	MW489824	<i>Oligodon bivirgatus</i>	China	Hainan, Shangxi NR	Qian et al. (2021)
Outgroups						
44	-	KP684155	<i>Hebius vibakari</i>	-	-	-
45	-	GQ181130	<i>Oreocryptophis poryphyraceus</i>	-	-	-

Table 2 (on next page)

Table 2. Selected morphological characters of *Oligodon transcaspicus* comb. et stat. nov. based on examined specimens.

Abbreviations for males and females are denoted by (m) or (f) respectively. For abbreviations of characters, see materials and methods section for details.

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3 section for details.

Morphology	ZISP 9868 (holotype)	ZMMU Re-7318	ZMMU Re-5589	ZMMU Re-6155	CAS 180042	ZISP 18334	ZISP 18976	ZMMU Re-16687
Sex	f	f	f	f	f	m	m	m
SVL	304	361	267	166	338	145	252	312
TailL	53	64	42	29	64	27	53	70
TotalL	357	425	309	195	402	172	305	382
TailLR	0.148	0.151	0.136	0.149	0.159	0.157	0.174	0.183
DSR	15–15–15	15–15–15	15–15–15	15–15–15	15–15–15	15–15–15	15–15–15	15–15–15
VEN	202	198	203	193	214	188	188	179
SC	47	45	44	46	51	48	51	52
TOTAL	250	244	248	240	266	237	240	232
SCR	0.188	0.184	0.177	0.192	0.192	0.203	0.213	0.224
LOREAL	Present	Present	Present	Present	Present	Present	Present	Present
SL	5/5	5/5	5/5	5/5	5/5	5/5	5/5	5/5
SL-eye	3/3	3/3	3/3	3/3	3/3	3/3	3/3	3/3
IL	7/7	7/7	7/7	7/7	7/7	7/7	7/7	7/7
IL-CS	4/4	4/4	4/4	4/4	4/4	4/4	4/4	4/4
PrO	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1
PsO	1/1	1/1	0/0	0/0	0/0	0/0	1/1	1/1
PtO	2/2	2/2	2/2	2/2	2/2	2/2	2/2	2/2
Ate	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1
Pte	3/3	3/3	3/3	3/3	2/2	3/3	3/3	3/3
B-Blotch	47	52	57	54	54	47	43	42
T-Blotch	12	16	15	14	15	17	17	14

Table 3 (on next page)

Table 3. Morphological comparisons of *Oligodon russelius* specimens from Afghanistan, northern India, and Pakistan hitherto recognized as *Oligodon "arnensis"* or *Oligodon churahensis*.

Data from the literature are combined from multiple authors unless denoted with an asterisk (*), which indicates that only a single source was used. Abbreviations for males and females are denoted by (m) or (f) respectively and (total) is used to indicate that the data combines both sexes or combines the total number of body and tail blotches.

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Data from the literature are combined from multiple authors unless denoted with an asterisk (*), which indicates that only a single source was used. Abbreviations for males and females are denoted by (m) or (f) respectively and (total) is used to indicate that the data combines both sexes or combines the total number of body and tail blotches.

Morphology	CUHC 7904	MMB 28497	<i>O. churahensis</i>	<i>O. russelius</i>	Pakistan <i>O. “arnensis”</i>	West Himalayan <i>O. “arnensis”</i>
Location	Kallar Kahar, Punjab Province, Pakistan	Jalalabad, Nangarhar, Afghanistan	Churah Valley, Himachal Pradesh, India	Northern and Eastern India	Northern and Southern Pakistan	Punjab and Himachal Pradesh, India
TailLR	0.159	0.136	0.180	0.157–0.185	0.160–175	0.163
VEN	183 (m)	198 (juv)	170 (m) 175 (f)	169–180 (m) 183–207 (f)	175–191 (m&f)	187–190* (m&f)
SC	49 (m)	44 (juv)	46 (m) 47 (f)	46–54 (m) 49–51 (f)	47–52 (m) 40 (f)	39–52* (m&f)
LOREAL	Present	Present	Present	Present	Present (rarely absent)	Present
SL	7	7	7	7	7	6–7
IL	7	6	7	7	7–8	7
B-Blotch	37	49 (total)	37–45	30–45	31–42	41–54
T-Blotch	13	—	9–11	6–10	—	9–13
Blotch edges	Present	—	Present	Mostly present	Present	Present
BlotchW	1.0–1.5	—	1.0–2.0	1.0–2.0	—	—
BlotchD	4.0	—	3.0–4.0	4.0–6.0	—	—
Source	This study	Brück (1968)	Mirza, Bhardwaj & Patel (2021)	Bandara et al. (2022)	Minton (1966); Mertens (1969); Khan (2002)	Wall (1921), Constable (1949*)

Table 4(on next page)

Table 4. Pairwise matrix of genetic distances between and within *Oligodon* species sampled in this study.

Uncorrected p-distances (given as percentages) are based on sequences of the cytochrome *b* mtDNA gene are shown below the diagonal. Intraspecific genetic p-distances are shown along the diagonal and are highlighted in bold. See Table 1 for the list of samples used to create this matrix.

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No.	Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1	<i>O. transcaspicus</i>	—														
2	<i>O. russellus</i>	6.3	2.2													
3	<i>O. arnensis</i>	6.9	6.1	0.0												
4	<i>O. melaneus</i>	7.8	6.4	6.3	—											
5	<i>O. sublineatus</i>	18.9	20.9	19.8	20.1	0.0										
6	<i>O. taeniolatus</i>	17.1	18.5	18.3	18.3	19.5	—									
7	<i>O. churahensis</i>	5.7	3.3	5.1	5.1	21.0	18.0	0.0								
8	<i>O. tillacki</i>	8.7	7.9	3.6	7.5	18.6	20.1	6.3	—							
9	<i>O. calamarius</i>	17.4	19.3	17.4	17.7	11.4	17.4	19.2	18.3	—						
10	<i>O. annamensis</i>	18.0	17.9	16.8	18.3	17.7	16.5	16.8	16.2	16.5	—					
11	<i>O. rostralis</i>	17.7	19.1	17.4	18.3	18.9	17.1	17.7	16.8	17.7	6.9	—				
12	<i>O. octolineatus</i>	16.8	16.7	16.2	16.2	16.5	16.2	15.9	15.9	16.8	12.9	12.0	—			
13	<i>O. albocinctus</i>	18.0	18.9	18.3	20.1	16.5	20.1	18.6	18.6	16.8	16.2	16.2	15.0	—		
14	<i>O. fasciolatus</i>	17.1	17.3	18.0	16.8	16.5	17.4	16.5	17.7	16.8	12.3	12.6	11.4	15.0	—	
15	<i>O. lacroixi</i>	16.2	16.8	15.6	17.4	16.8	16.8	16.2	15.6	15.3	13.2	15.0	11.7	15.9	15.6	—

Figure 1

Figure 1. Approximate distribution and location of samples utilized in this study for molecular and morphological analyses (A); and approximate distribution of *Oligodon transcaspicus* comb. et stat. nov in the Köpet-Dag Mountain range of Iran and Tur

Triangle icons denote specimens with only molecular data; square icons denote specimens with only morphological data; rhombic icons denote specimens without molecular and morphological data (only locality is known); round icons denote specimens with both molecular and morphological data. Stars/asterisks next to numbers indicate type localities. Localities: (1) Ashgabat, Ahal Prov., Turkmenistan (type locality of *Oligodon transcaspicus* **comb. et stat. nov**); (2) Chuli, Ahal Prov., Turkmenistan; (3) Geok-Tepe, Ahal Prov., Turkmenistan; (4) Karanki, Ahal Prov., Turkmenistan; (5) “Goalon” (Goudan), Ahal Prov., Turkmenistan; (6) Aidere, Ahal Prov., Turkmenistan; (7) Bazangan Lake, Razavi Khorasan Prov., Iran; (8) Punjab Prov., Pakistan; (9) Kallar Kahar, Punjab Prov., Pakistan; (10) Chamba Distr., Himachal Pradesh, India (type locality of *Oligodon churahensis*); (11) Jalalabad, Nangarhar Prov., Afghanistan; (12) Dara-i-Pech district, Kunar Prov., Afghanistan; (13) Maharashtra, India; (14) Chitwan NP, Bagmati Prov., Nepal; (15) Ganjam, Odisha, India; (16) 24.1 km SW of Rajamahendravaram, Andhra Pradesh, India; (17) Bangalore, Karnataka, India; (18) Tamil Nadu, India; (19) Puttalam Distr., North Western Prov., Sri Lanka; (20) Udawalawe National Park, Uva Prov.; (21) Monargala Distr., Southern Prov., Sri Lanka; (22) Hambantota Distr., Southern Prov., Sri Lanka; (23) Gampaha Distr., Western Prov., Sri Lanka; (24) Polonnaruwa Distr., North Central Prov., Sri Lanka; (25) Paramikulam, Kerala, India; (26) Barengabari, Assam, India.

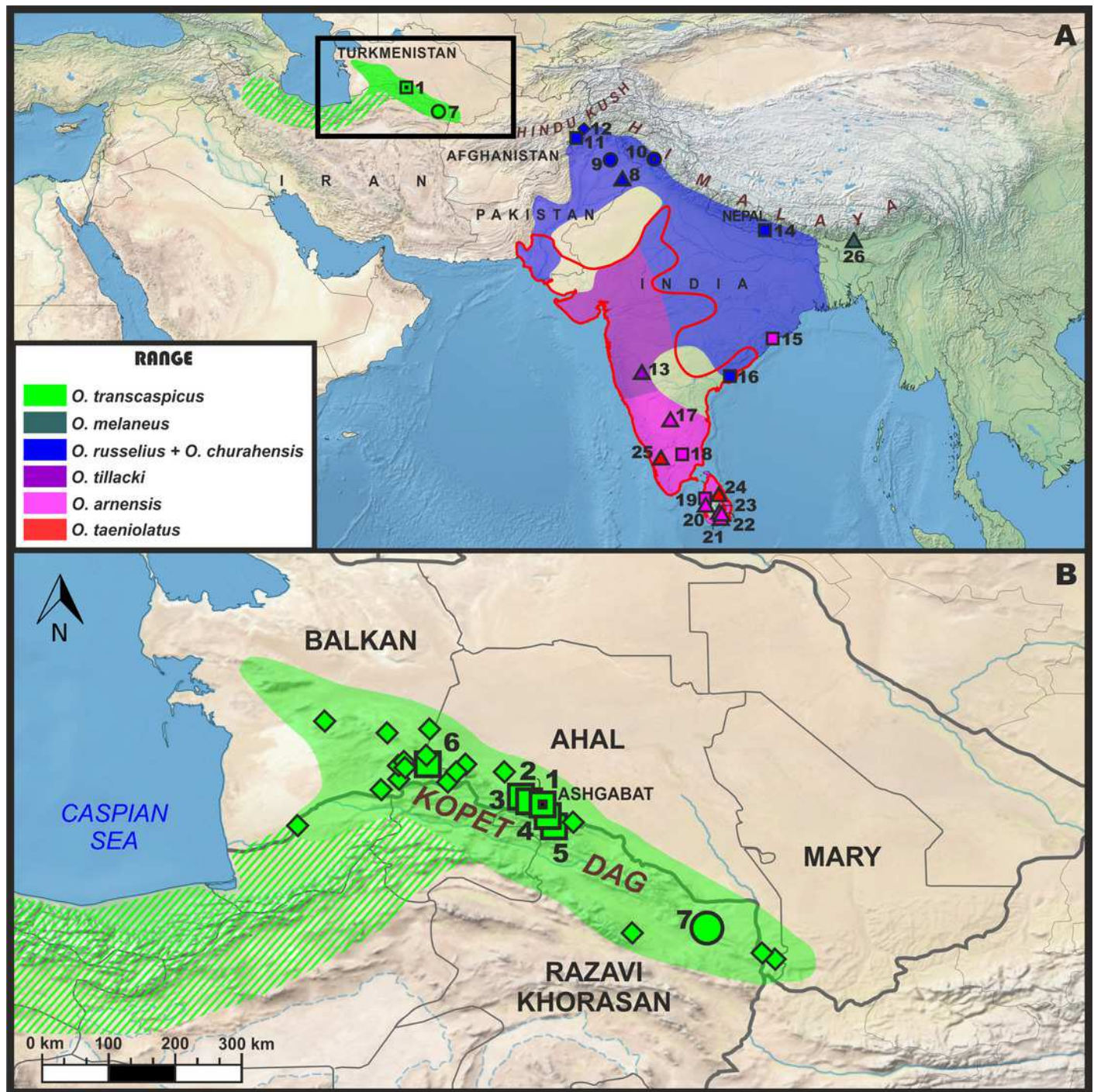


Figure 2

Figure 2. Phylogenetic 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; n-dash denotes no support. Outgroup taxa are not shown. Colors of clades and locality numbers correspond to Figure 1.

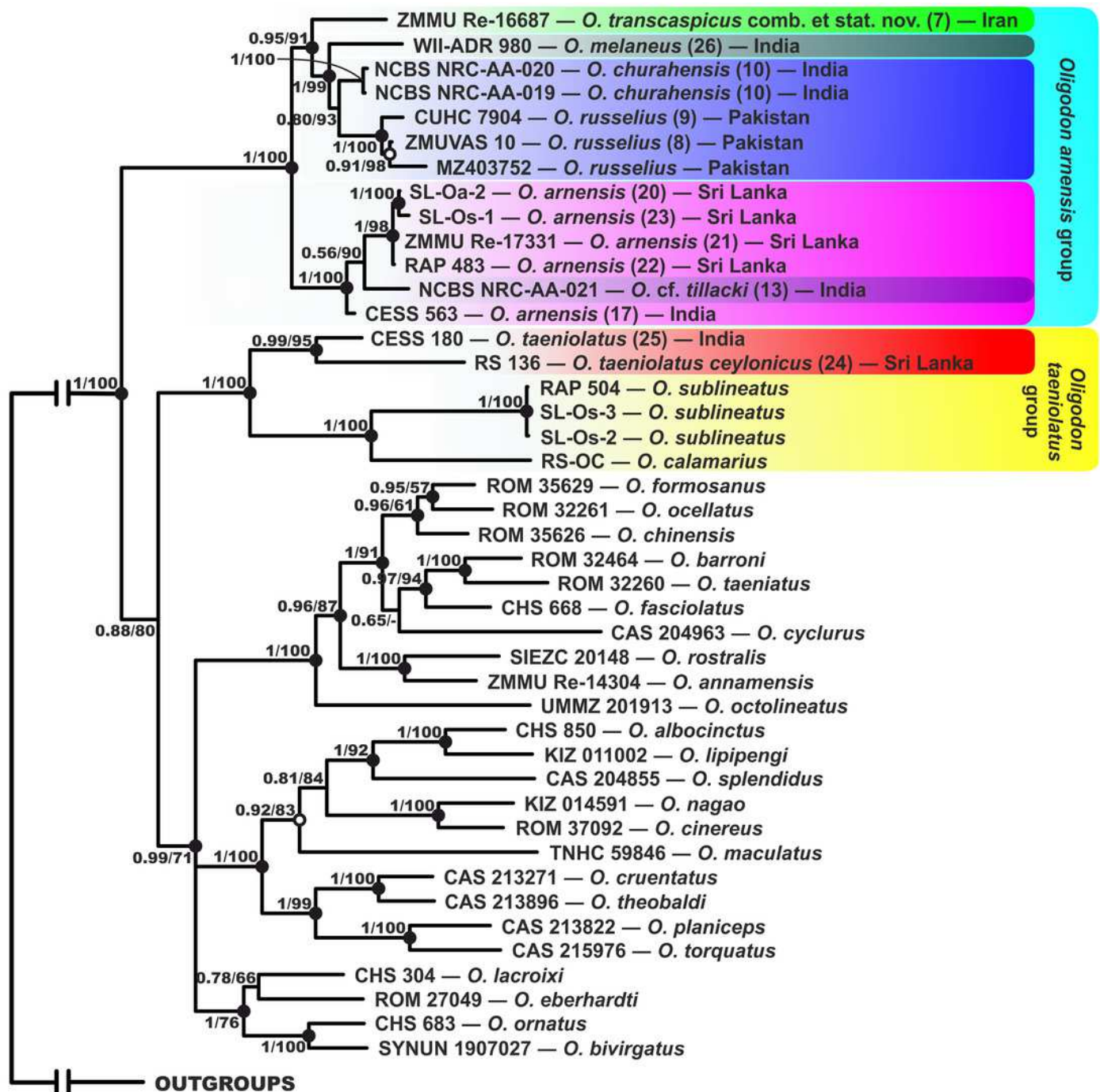


Figure 3

Figure 3. Species distribution model (SDM) map based on geolocation points of *Oligodon transcaspicus* comb. et stat. nov. from Iran and Turkmenistan.

Darker red coloration indicates more suitable habitat, whereas lighter colors indicate less suitable habitat.

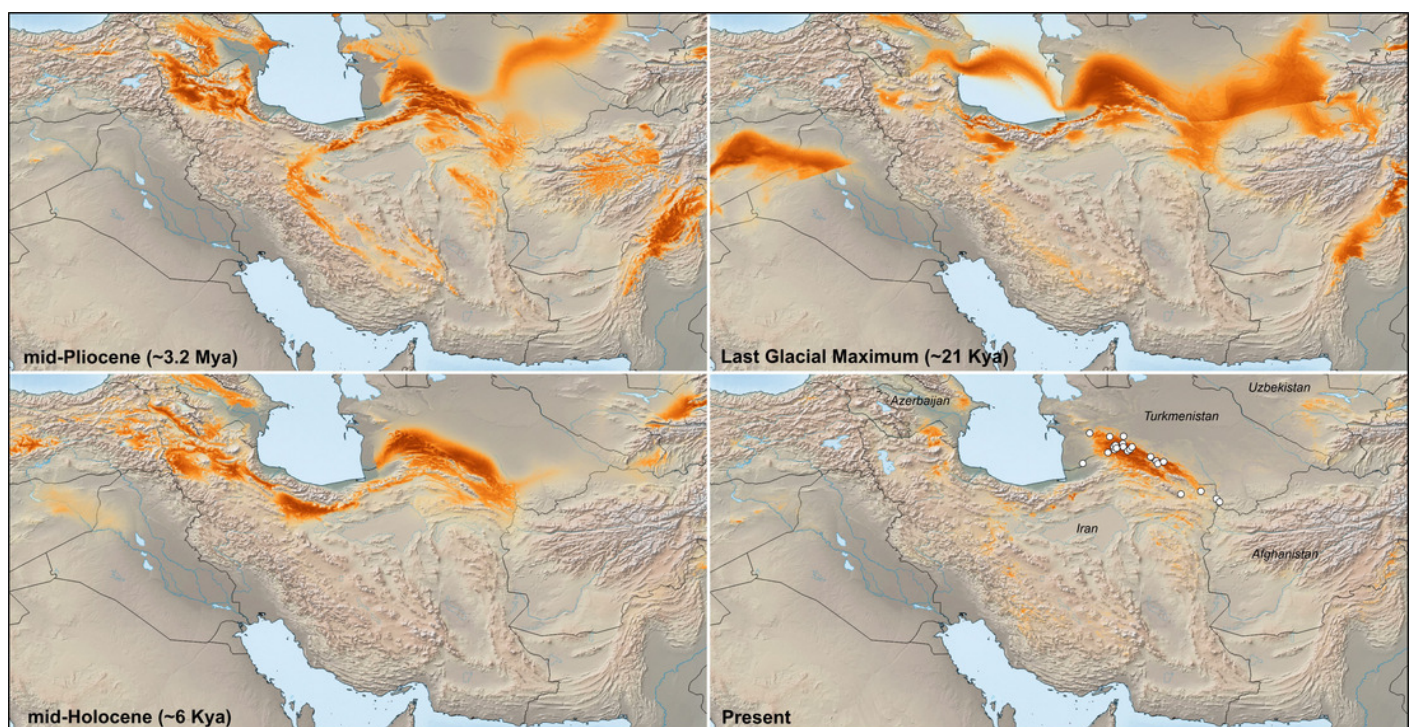


Figure 4

Figure 4. Photographs of the preserved holotype specimen of *Contia transcaspica* (ZISP 9868) now *Oligodon transcaspicus* comb. et stat. nov. from “Köpet-Dag, Transcaspica”.

Scale bars equal 10 millimeters. Photos by Konstantin D. Milto.



Figure 5

Figure 5. Live photographs of *Oligodon transcaspicus* comb. et stat. nov. (ZMMU Re-16687; field number RAN-3264) from Khorasan Province, Iran.

(a) Right lateral, (b) left lateral, (c) ventral, (d) ventral views of the head, and (e) general habitus. Photographs by Roman A. Nazarov.

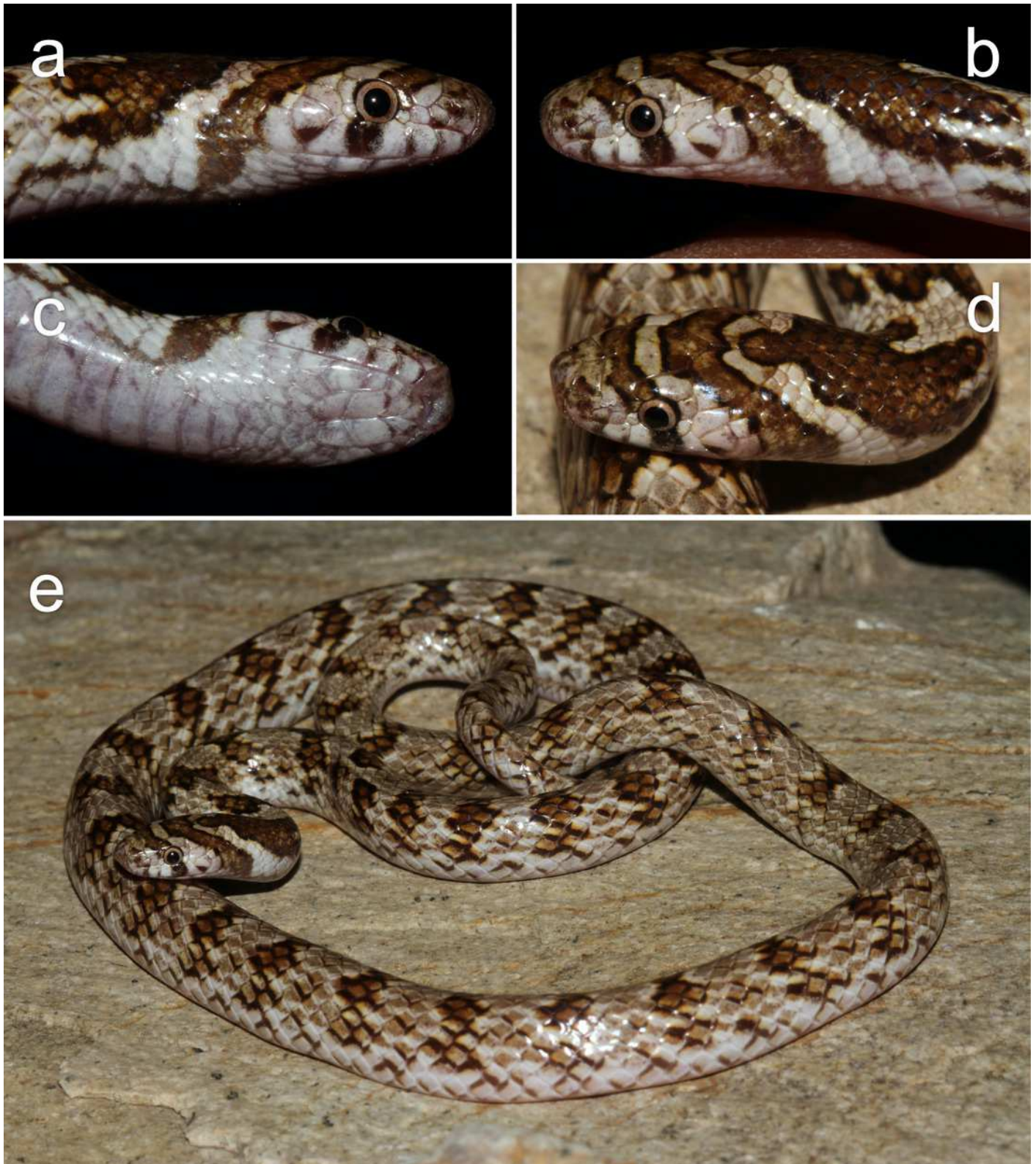


Figure 6

Figure 6. Two unvouchered specimens of *Oligodon transcaspicus* comb. et stat. nov.

Specimens photographed from (a) Podere, Sumbar Valley, Turkmenistan and (b) Seqiz-Khan Gorge, Turkmenistan. Photographs taken by Alexander V. Pavlenko.



Figure 7

Figure 7. Photographs of *Oligodon russelius* from Pakistan (a–e) and Afghanistan (f).

Shown in a–e is specimen CUHC 7904 from Kallar Kahar, Punjab Province, Pakistan, showing (a) general habitus in life, (b) right lateral, (c) left lateral, (d) dorsal, and (e) ventral views of the head in preservative. Shown in (f) is a cropped image of *O. russelius* from Kunar Province, Afghanistan observed on iNaturalist (obs. 110932106, user mohammadfarooq). Photographs a–e by Daniel Jablonski, photograph f taken by Mohammad Farooq from iNaturalist.org.

