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 Turkmenisan, 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

34 The kukri snakes of the genus *Oligodon* Fitzinger, 1826 reach the westernmost limits of their

35 distribution in Middle and Southwest Asia (Pakistan, Afghanistan, Iran, and Turkmenistan). In

36 this paper, we review the taxonomy and distribution of the two species native to this region,

37 *Oligodon arnensis* (Shaw, 1802) and *Oligodon taeniolatus* Jerdon, 1853 based on an integrative

38 approach combining morphological data, molecular data from mitochondrial DNA, and species

39 distribution modeling (SDM). Phylogenetic analyses recover *O. taeniolatus* from Iran and

40 Turkmenistan in the *O. arnensis* species group, rendering the species paraphyletic with respect to

41 *O. taeniolatus* sensu stricto on the Indian subcontinent. To correct this, we resurrect the junior

42 synonym *Contia transcaspica* Nikolsky, 1902 for the Middle/Southwest Asian populations and

43 provide a formal redescription. So far, *Oligodon transcaspicus* **comb. et stat. nov.** is known only

44 from the Köpet–Dag Mountain Range of northeast Iran and southern Turkmenisan, but SDM

45 mapping suggests it may have a wider range. Genetic samples of *O. "arnensis"* from northern

46 Pakistan are nested in a clade sister to the recently described *Oligodon churahensis* Mirza,

47 Bhardwaj & Patel, 2021, and are phylogenetically separate from *O. arnensis* sensu stricto in

48 south India and Sri Lanka. Based on morphological similarity, the Afghanistan and Pakistan

49 populations are assigned to *Oligodon russelius* (Daudin, 1803) and we synonymize *O.*

50 *chuarhensis* with this species. Our investigation leads us to remove *O. taeniolatus* from the snake

51 fauna of Afghanistan, Iran, and Turkmenistan, with the consequence that only *Oligodon*

52 *transcaspicus* **comb. et stat. nov.** and *O. russelius* are present in these countries. Additional

53 studies are needed to resolve the taxonomy of the *O. taeniolatus* and *O. arnensis* species groups

54 on the Indian subcontinent.

Keywords

56 *Oligodon transcaspicus*, *Oligodon taeniolatus*, Middle Asia, Iran, Turkmenistan, Köpet–Dag

57 Mountain Range, Indian subcontinent, Taxonomy, mtDNA, species distribution modeling

Introduction

59   Our knowledge of the snake fauna of Middle and Southwest Asia (herein considered the

60 countries of Afghanistan, Iran, Pakistan, western China, Mongolia and the former Soviet Middle

61 Asian republics fide Berg, 1931; Geptner, 1938; Chernov, 1949) has improved over the past

62 decade as researchers continue to contribute species descriptions, range extensions, and natural

63 history observations (Wagner et al., 2016a; Jablonski & Koleska, 2017; Farooq et al., 2018;

64 Rajabizadeh, 2018; Shestopal & Rustamov, 2018a; Shestopal & Rustamov, 2018b; Orlov et al.,

65 2018; Jablonski et al., 2019; Asadi et al., 2019; Rajabizadeh et al., 2020; Eskandarzadeh et al.,

66 2020; Chen et al., 2021; Essote et al., 2022). Most snake species inhabiting these countries are

67 associated with the Palearctic biogeographic realm. However, there also exist a few taxa

68 originating from the Oriental realm (South and Southeast Asia) that reach their westernmost

69 limits in this region (Wagner et al., 2016b; Orlov et al., 2018). The kukri snakes of the genus

70 *Oligodon* Fitzinger, 1826 are one such example. Normally distributed across tropical portions of

71   South and Southeast Asia, two species of this diverse group extend into Afghanistan,
72   northeastern Iran, Pakistan, and southern Turkmenistan (Latifi, 1991; Green, 2010; Wagner et
73   al., 2016b; Orlov et al., 2018; Uetz et al., 2022).
74   The first species, the banded kukri snake *Oligodon arnensis* (Shaw, 1802), is commonly
75   found across the Indian subcontinent, but is known from Afghanistan based on a single specimen
76   (Král, 1969; Wagner et al., 2016b). This species was recently divided into several taxa by
77   Bandara et al. (2022), who published a revision of *O. arnensis* sensu auctorum based largely on
78   morphological data. These authors restricted *O. arnensis* sensu stricto to southern India and Sri
79   Lanka, and described a new species *Oligodon tillacki* Bandara et al., 2022 (Tillack's kukri snake)
80   for *O. arnensis* populations found along the western coast of India, and the resurrected the name
81   *Oligodon russelius* (Daudin, 1803) (Russell's kukri snake) for populations in north/east India,
82   Bangladesh (Barkat & Rabbe, 2022) and Nepal (Rai, Adhikari & Antón, 2022). Additionally,
83   Mirza, Bhardwaj & Patel (2021) described a new species, the Churah Valley kukri snake *O.
84   churahensis* Mirza, Bhardwaj & Patel, 2021 from Himachal Pradesh, India, which was recovered
85   within *O. arnensis* species group based on mitochondrial DNA (mtDNA) sequences. These
86   authors included genetic samples of *O. "arnensis"* collected from Pakistan but were unable to
87   examine their specimen vouchers and tentatively identified them as *Oligodon* cf. *churahensis*.
88   While these studies have shed light on the taxonomic nature of the *O. arnensis* and related taxa,
89   both neglected the status of specimens from Pakistan and Afghanistan. We refer to these
90   populations as *O. "arnensis"* until our clarifications in the results.
91   The second species, the streaked kukri snake *Oligodon taeniolatus* (Jerdon, 1853), is also
92   widespread on the Indian subcontinent, but extends westward into northern Iran, southern
93   Turkmenistan, and possibly Afghanistan (Latifi, 1991; Wagner et al., 2016b; Orlov et al., 2018).
94   Like *O. "arnensis"*, *O. taeniolatus* exhibits substantial variation across its range, including
95   multiple color phenotypes that have invariably been recognized as synonyms or subspecies by
96   past authors (Wall, 1921; Wall, 1923; Smith, 1943; Taylor, 1950). Bauer (2003) reviewed the
97   nomenclatural history of this taxon and designated a lectotype illustrated by Russell (1796) with
98   the type locality "Vizagapatam" (=Visakhapatnam, Andhra Pradesh, India), thereby restricting
99   'true' (nominotypical) *O. taeniolatus* to eastern India. Outside of South Asia, populations of *O.
100   taeniolatus* from Iran and Turkmenistan can be referred to the name *Contia transcaspica*
101   Nikolsky, 1902, described based on a single specimen collected from "Köpet–Dag, Transcaspia"
102   [=now Köpet–Dag Mountain Range, near Ashgabat, Ahal Province, Turkmenistan]. Chernov
103   (1935) considered *C. transcaspica* to be a junior synonym of *O. taeniolatus*, owing to similarities
104   between Turkmen and Indian specimens. Later authors would follow his recommendation and
105   report these populations as *O. taeniolatus* in the subsequent literature (Terentjev & Chernov,
106   1949; Bogdanov, 1962; Bannikov et al., 1977; Dotsenko, 1984; Atayev, 1985; Szczerbak,
107   Khomustenko & Golubev 1986; Latifi, 1991; Rustamov & Sopyev, 1994; Szczerbak, 1994;
108   Atayev, Rustamov & Shammakov, 1994). The name *Contia transcaspica* has rarely been
109   mentioned since and was even neglected in the synonymy of *O. taeniolatus* by Wallach et al.
110   (2014). A few sources (Dotsenko, 1984; Latifi, 1991) would provide additional descriptive data

111 of collected specimens from this region. Their accounts showed that specimens from the Köpet–
112 Dag Mountain Range had distinct differences in coloration and scalation from Indian
113 subcontinent *O. taeniolatus* (Wall, 1921; Wall, 1923; Smith, 1943), although detailed
114 comparisons between populations were not made.
115   In this study, we review the taxonomy, phylogenetic relationships, and distributional
116 limits of the genus *Oligodon* at the westernmost end of its range. We aimed to clarify the
117 taxonomic status of *O. taeniolatus* historically associated with the name *Contia transcaspica*
118 from Iran and Turkmenistan and resolve the status of *Oligodon "arnensis"* populations from the
119 countries of Pakistan and Afghanistan, which were neglected by past taxonomic revisors.

Materials & Methods

121 **Sampling and species delimitation**. Fieldwork which resulted in the collection of *Oligodon* in
122 Iran was conducted by RAN and MR during a field trip in May 2017 to Razavi, Khorasan
123 Province, Iran (locality 7, Figure 1). Fieldwork in Pakistan was conducted by DJ and RM during
124 a field trip in September 2018 to Punjab Province, Pakistan. Fieldwork in Sri Lanka was
125 conducted by SK and NAP during field trips in February 2018 to December 2020 to dry and wet
126 zones of the country. Collected specimens were euthanized using a 20% solution of benzocaine
127 and fixed in formalin before being transferred into 70% ethanol for storage. Before preservation,
128 a small sample of muscle tissue was taken from each snake and stored in 95% ethanol for later
129 DNA analyses. For molecular analysis, we included one sample of *O. taeniolatus* (=*Contia*
130 *transcaspica*) from Iran (ZMMU Re-16687); one sample of nominotypical *O. taeniolatus* from
131 India (CESS-180); four novel samples of *O. arnensis* sensu stricto from India (CESS-563) and
132 Sri Lanka (SL-Os-1, SL-Oa-2; ZMMU Re-17331); two novel samples of *O. sublineatus*
133 Duméril, Bibron & Duméril, 1854 from Sri Lanka (SL-Os-2; SL-Os-3); and one novel sample
134 morphologically resembling *Oligodon russelius* from Punjab Province, Pakistan (CUHC 7904;
135 locality 9, Figure 1). In addition, we included 34 publicly available samples of other *Oligodon*
136 species retrieved from GenBank (Table 1). Bandara et al. (2022) noted that one sample (NCBS-
137 NRC-AA-021) previously identified as *O. "arnensis"* may represent *O. tillacki* but did not
138 examine this specimen. As such, we re-identify this specimen as *O.* cf. *tillacki* herein. For
139 outgroup taxa, we chose one sample each of *Oreocryptophis porphyraceus* (Cantor, 1839)
140 (subfamily Colubrinae) and *Hebius vibakari* (Boie, 1826) (subfamily Natricinae) due to their use
141 in previous phylogenies of *Oligodon* published in the literature (Nguyen et al., 2020).
142   We examined the morphology of seven *O. taeniolatus* specimens available to us from the
143 Iran and Turkmenistan, including the type specimen of *Contia transcaspica* (localities 1–7,
144 Figure 1). To compare these populations with typical members of the *O. arnensis* species group,
145 we examined two specimens within the range of *O. russelius* fide Bandara et al. (2022) from
146 Andhra Pradesh, India, and southern Nepal (localities 14–16, Figure 1), five specimens of *O.*
147 *arnensis* sensu stricto from southern India and Sri Lanka (localities 18–19, Figure 1) (see
148 Supplementary Material 1), and the new specimen of *O. russelius* collected from Pakistan
149 (locality 9, Figure 1). Additional morphological data for *O. taeniolatus*, the *O. arnensis* species
150 group and other taxa were derived from relevant literature sources (see Morphological analysis).

151   For aspects of species concepts and delimitation, we follow an integrative taxonomic approach
152   (Padial et al., 2010) where a species is supported by a combination of morphological and
153   molecular evidence. In addition, we follow the General Lineage Concept (De Queiroz, 2007),
154   where a species represents a single independent lineage following a separate evolutionary
155   trajectory compared to its congeners. Discrete morphological separation, substantial genetic
156   divergence using standard genetic markers, and evidence of monophyly are all used as
157   supporting evidence for evolutionary independence.
158   Abbreviations for museum collections are as following: CAS: California Academy of
159   Sciences, San Francisco, USA; CUHC: Comenius University Herpetological Collection,
160   Bratislava, Slovakia; MMB: Department of Zoology, Moravian Museum, Brno, Czech Republic;
161   USNM: National Museum of Natural History, Washington, DC, USA; ZISP: Zoological Institute
162   of Russian Academy of Sciences, St. Petersburg, Russia; ZMMU: Zoological Museum of
163   Moscow State University, Moscow, Russia. Additional abbreviations for genetic samples and
164   voucher specimens can be found in Table 1.
165   Field works, including collection of the samples and animals in the field, was performed
166   outside of any protected area, in the framework of a project contract signed by International
167   Center for Science, High Technology and Environmental Sciences, Kerman, Iran (contract
168   number 1.87, issued at 11.04.2008). The contract bears a permission to collect the reptile
169   samples outside of any protected area of Department of the Environment (specified in
170   www.doe.ir) that needed extra permissions. Specimen collection protocols and animal operations
171   followed the Institutional Ethical Committee of International Center for Science, High
172   Technology and Environmental Sciences, Kerman, Iran (certificate number 1.87-1).
173
174   **Molecular analyses.** We extracted total genomic DNA of novel samples from muscle tissue
175   preserved in 95% ethanol using a Qiagen DNAeasy Blood and Tissue Kit following
176   manufacturers protocols. We performed polymerase chain reactions (PCRs) on the extracted
177   DNA to amplify two fragments of mitochondrial DNA (mtDNA): the first fragment including
178   partial sequences of 12S ribosomal RNA (rRNA), transfer RNA (tRNA)-Valine and 16S rRNA
179   (total length up to 1930 bp), and a second fragment including the complete sequence of the gene
180   Cytochrome *b* (cyt *b*) (1,091 bp). Primers used for both PCR and sequencing are summarized in
181   Table S2. PCR protocols for 12S-16S rRNA fragments were adapted from Green et al. (2010).
182   For both primer pairs of 12S and 16S rRNA, we used the following PCR protocol: (1) initial
183   denaturation step at 94°C for 5 min; (2) 35 cycles of denaturation at 94°C for 1 min, annealing at
184   55°C for 1 min and extension at 72°C for 1 min; (3) final extension at 72°C for 10 min; and (4)
185   cooling step at 4°C for storage. For cyt *b* sequences, we used a modified PCR protocol of Chen
186   et al. (2014) with touchdown: (1) initial denaturation step at 94°C for 5 min; (2) 10 cycles of
187   denaturation at 94°C for 1 min, annealing for 1 min with temperature decreasing from 50°C to
188   45°C (with cool-down at 0.5°C per each cycle) and extension at 72°C for 1 min; (3) 24 cycles of
189   denaturation at 94°C for 1 min, annealing at 45°C for 1 min and extension at 72°C for 1 min; (4)
190   final extension at 72°C for 10 min; and (5) cooling step at 4°C for storage. All PCR products

191 were sequenced in both directions by the Evrogen company at the Institute of Bioorganic
192 Chemistry, Russian Academy of Sciences (Moscow, Russia) and at Macrogen Europe
193 (Amsterdam, The Netherlands; http://www. macrogen-europe.com). Sequences were assembled
194 and checked using Sequencher 4.9 (GeneCodes). The obtained sequences are deposited in
195 GenBank under the accession numbers OQ092426; OQ099833–OQ099837; and OQ116816–
196 OQ116825 (Table 1).
197   To examine the position of *O. taeniolatus* from Turkmenistan and Iran in a matrilineal
198 genealogy of the genus, we combined newly obtained sequences with all publicly available
199 GenBank sequences of *O. arnensis*, *O. churahensis*, *O. taeniolatus*, *O.* cf. *tillacki* and one
200 sequence per species of other *Oligodon* (summarized in Table 1). In total, we analyzed mtDNA
201 sequences of 45 specimens, including 43 samples of 33 species of *Oligodon*, with outgroup
202 sequences of *O. porphyraceus* and *H. vibakari* used to root the tree. Nucleotide sequences were
203 initially aligned in MAFFT v.7 (Katoh et al., 2002) with default parameters, and subsequently
204 checked by eye in BioEdit 7.0.5.2 (Hall, 1999) and slightly adjusted for translation when
205 appropriate. We used IQ-TREE web server (http://iqtree.cibiv.univie.ac.at/; Trifinopoulos et al.
206 2016) to estimate optimal evolutionary models for the data set analysis using the Akaike
207 Information Criterion (AIC). Mean uncorrected genetic distances (p-distances) were calculated
208 in MEGA 7.0 (Kumar, Stecher & Tamura, 2016). The matrilineal genealogy was inferred using
209 Bayesian inference (BI) and Maximum Likelihood (ML) approaches. The best-fitting model for
210 both BI and ML analyses for 12S–16S rRNA fragments and for the second codon partition of cyt
211 *b* was the GTR+G+I model as of DNA evolution suggested by the AIC. For the remaining
212 portions of cyt *b*, the AIC suggested the GTR+G model for the first codon partition, and the
213 HKY+G+I for the third codon partition.
214   ML was conducted using the IQ-TREE web server (Trifinopoulos et al., 2016). BI was
215 conducted in MrBayes 3.2.2 (Ronquist et al., 2012); Metropolis-coupled Markov chain Monte
216 Carlo (MCMCMC) analyses were run with one cold chain and three heated chains for one
217 million generations and sampled every 1000 generations. Two independent MCMCMC run
218 iterations were performed and 100 trees were discarded as burn-in. The convergence of the runs
219 was checked by exploring and examining likelihood plots in TRACER v1.6 (Rambaut et al.,
220 2020), with effective sample sizes (ESS) all above 200. Nodal support for BI was assessed by
221 calculating posterior probabilities (BI PP). We *a priori* regarded tree nodes with BI PP values
222 over 0.95 as sufficiently resolved, while BI PP values between 0.95 and 0.90 were regarded as
223 tendencies. For ML, confidence in nodal topology was estimated via the ultrafast bootstrap
224 approximation algorithm (UFBS; Hoang et al., 2018) with 1,000 bootstrap pseudoreplicates.
225 Nodes having ML UFBS values of 95 and above were *a priori* considered highly supported,
226 while nodes with values of 90–94 were considered well-supported, and nodes with values of 70–
227 89 were considered as tendencies. Lower values were regarded as indicating unresolved nodes
228 (Huelsenbeck & Hillis, 1993).
229

230 **Morphological analysis**. Coloration and pattern were recorded during examination of preserved
231 specimens. For some specimens, live coloration was also recorded from digital images taken
232 before preservation. No statistical analyses were performed between species due to the low
233 sample size of comparative material. All body measurements, except body and tail lengths, were
234 taken under a dissecting microscope using a digital slide-caliper to the nearest 0.1 mm. Body and
235 tail lengths were measured to the nearest millimeter by straightening snakes along a flexible
236 ruler. Methodology for counting ventral and subcaudal scales follow Dowling (1951). The tail tip
237 was not included in the number of subcaudals. Head scale suture angle terminology follows that
238 of Kaiser, O'Shea & Kaiser (2019). Maxillary teeth were counted by examination of the
239 dissected maxillary bone when available, or by carefully removing the gum layer of the maxilla.
240 Sex was determined by ventral incision below the vent to detect the presence or absence of
241 hemipenes. Our data on specimens referrable to *Contia transcaspica* were compared and
242 reviewed with relevant literature on *O. taeniolatus* across its distribution (Nikolsky, 1902;
243 Nikolsky, 1903a; Wall, 1921; Wall 1923; Chernov, 1935; Smith, 1943; Minton, 1966; Dotsenko,
244 1984; Latifi, 1991; Khan, 2002).
245   The following linear measurements (all in mm) were taken: snout to vent length (SVL)
246 — measured from the tip of the snout to the vent; tail length (TailL) — measured from the vent
247 to the tip of the tail; total length (TotalL) — sum of SVL and TailL; relative tail length to total
248 length (TailLR) calculated as tail length to total length ratio; head length (HeadL) from the tip of
249 the snout to the posterior margin of the mandible; head width (HeadW) measured at the widest
250 part of the head immediately posterior to the eye; snout length (SnoutL) — distance between the
251 tip of the snout and anterior edge of eye; eye diameter (EyeD) — maximal horizontal length of
252 the eye; frontal scale length (FrontalL); frontal scale width (FrontalW); distance (IOD) — the
253 shortest distance between the eyes; and internarial distance (IND) — distance between the
254 nostrils. Additional morphological characters examined include the number of maxillary teeth
255 (MT); anterior scale rows (ASR) — namely number of scale rows at one head length behind the
256 head; midbody scale rows (MSR) — the number of scale rows at midbody; posterior scale rows
257 (PSR) — number of dorsal scale rows at one head length prior to the vent; dorsal scale row
258 formula (DSR) — a given acronym summarizing the three dorsal scale row counts (i.e., ASR–
259 MSR–PSR); ventral scales (VEN) — the number of belly scales starting from the scale
260 contacting the first dorsal scale row to the vent, excluding the cloacal plate; subcaudal scales
261 (SC) — the number of paired subcaudal scales excluding the terminal scute; total body scales
262 (TOTAL) — the sum of ventral, subcaudal scales and the cloacal plate (included as one scale
263 regardless of whether the plate is single or divided); subcaudal ratio (SCR) — namely the ratio
264 between the number of subcaudal scales and the number of total body scales given as a decimal
265 value; cloacal plate (CP) — the number of terminal ventral scales immediately anterior to vent
266 (given as single for one scale, and divided for two scales); condition of nasal scale (NASAL) —
267 given as either vertically divided, entire, or partially divided; condition of loreal scale
268 (LOREAL) — given as present or absent; supralabials (SL) — the number of scales on upper lip;
269 number of supralabials in contact with the eye (SL-Eye); infralabials (IL) — the number of

270   scales on lower lip; infralabials contacting each other (IL-contact) — the number of pairs of
271   infralabial scales in contact; infralabials contacting the anterior chin shields (IL-CS) — the
272   number of infralabial scales contacting the anterior chin shields; number of preocular scales
273   (PrO); number of presubocular scales (PrsO); number of postocular scales (PtO); number of
274   anterior temporals (Ate) — the number of temporal scales in contact with the postocular scales;
275   number of posterior temporals (Pte) — the number of temporal scales immediately contacting
276   the anterior temporal scales. We also describe and abbreviate certain color pattern characteristics
277   found in specimens, including the number of body blotches or crossbars from nape to vent (B-
278   Blotch); the number of blotches or crossbars from vent to tail tip (T-Blotch); the width in
279   vertebral (dorsal) scales of each blotch at midbody (BlotchW); and the distance between each
280   blotch at midbody counted using vertebral (dorsal) scales (BlotchD). Abbreviations for these
281   characters are used in Tables 3–4. Symmetric characters are given in left/right order.
282
283   **Species distribution modeling**. We used MaxEnt 3.3.3 (Phillips, Anderson & Schapire, 2006)
284   and modelled the potential distribution of *Oligodon* population in Central Asia in the present as
285   well as three previous historical epochs: the mid-Pliocene (ca 3.2 Mya), the Last Glacial
286   Maximum (ca 21 Kya), and the mid-Holocene (ca 6 Kya). We used 23 unique georeferenced
287   data points (Table S1), 23 bioclimatic and four landscape layers. Data were filtered and
288   correlated variables were excluded using ENMTools 1.3. (Warren et al., 2010) and models
289   assessed by computing the area under the CURVE (AUC). Further, we estimated the relative
290   contribution of variables to the model. For the current climate projection, we used the CHELSA
291   database (Karger et al., 2017). The PaleoCLIM database was used for the past conditions, the
292   mid-Pliocene, the Last Glacial Maximum (LGM) and the Mid-Holocene (Fordham et al., 2017;
293   Brown et al., 2018), at 5 km pixel size. The final maps were designed in QGIS Desktop 3.28
294   software (QGIS Development Team, 2021).

Results

295 **Results**
296   **Molecular analyses.** The final concatenated alignment of the 12S–16S rRNA and cyt *b* gene
297   sequences contained 3019 base pairs with 1812 conserved sites, 1191 variable sites, and 833
298   parsimony informative sites. The transition-transversion bias (R) was estimated as 1.2.
299   Nucleotide frequencies were 36.7% (A), 23.0% (T), 25.7% (C), and 14.6% (G) (all data given for
300   ingroups only). The uncorrected pairwise genetic distances (hereafter p-distances; given for the
301   cyt *b* mtRNA gene fragment) between and within examined *Oligodon* species are presented in
302   Table 4. Intraspecific genetic distances varied from $p = 0\%$ (in *O. sublineatus*) to $p = 2.2\%$ (*O.*
303   *churahensis*, including samples of *O.* cf. *churahensis* and *O. russelius*). The interspecific genetic
304   distances within examined *Oligodon* varied from $p = 3.3\%$ (between *O. arnensis* sensu stricto
305   and *O. churahensis*) to $p = 21.0\%$ (between *O. sublineatus* and *O. churahensis*).
306   In general, our mtDNA-based genealogy of *Oligodon* (Figure 2) correlates well with the
307   set of phylogenetic relationships obtained from previous authors (Green et al., 2010; Nguyen et
308   al., 2020; Mirza, Bhardwaj & Patel, 2021; Das et al., 2022; Yushchenko & Lee et al., *in press*).
309   Both ML and BI topologies of our mtDNA-genealogy of *Oligodon* support the specimen of *O.*

310   *taeniolatus* from Iran as a separate lineage sister to *Oligodon melaneus* Wall, 1909, the newly
311   described species *O. churahensis*, and Pakistani specimens *O. russelius* and *O.* cf. *churahensis*,
312   with strong support from both analyses (0.97/92). Genetic p-distances in this clade varied from
313   7.8% (between *O. taeniolatus* and *O. melaneus*), 6.3% (between *O. taeniolatus* and *O. russelius*),
314   and 5.7% (between *O. taeniolatus* and *O. churahensis*) based on cyt *b*. Together with *O. arnensis*
315   they form the most basal clade (1/100), while the three samples of *O. taeniolatus* from India and
316   Sri Lanka form a distinct clade together with *O. sublineatus* and *Oligodon calamarius* (Linnaeus,
317   1758) also with strong support (1.0/100). This topology renders *O. taeniolatus* sensu lato as
318   paraphyletic. Notably, the sample of *O. taeniolatus* from Sri Lanka is divergent (2.2% p-distance
319   based on 16S rRNA) from the Indian sample, which suggests additional undescribed diversity is
320   present in *O. taeniolatus* outside of Middle and Southwest Asia. Distances of such a percentage
321   based on 16S rRNA are more significant than the cyt *b* gene as 12S–16S rRNA evolves at a
322   slower rate (Mueller, 2006). The newly collected Pakistan sample (CUHC 7904) identified by us
323   as *O. russelius* is recovered within a clade containing two other Pakistan samples from Genbank
324   that were identified as *O.* cf. *churahensis* by Mirza, Bhardwaj & Patel (2021) with high support
325   (1.0/99). Low genetic divergence ($p = 2.2\%$) exists between the three samples, suggesting they
326   are conspecific. Additionally, the divergence between the Pakistan samples and the type series of
327   *O. churahensis* from Himachal Pradesh, India is only 3.3% in cyt *b* gene (Table 5). The genetic
328   distance between the sample re-identified as *O.* cf. *tillacki* and samples of *O. arnensis* sensu
329   stricto was also low ($p = 3.6\%$).
330
331   **Species distribution modeling.** The species distribution model (SDM) maps based on
332   geolocation points of *Oligodon* from Iran and Turkmenistan is shown in Figure 3. Variables that
333   mostly account for the species presence are landscape uniformity, mean temperature of coldest
334   quarter (Bio 11), slope, and precipitation seasonality (coefficient of variation) (Bio 15). The
335   average test AUCs for the replicate runs was estimated as 0.988. The predicted distribution of
336   *Oligodon* during past and present epochs expanded and contracted across the Plio-Pleistocene
337   and Holocene and suggests that the current distribution of *Oligodon* in Middle/Southwest Asia is
338   significantly different. The most suitable habitat for *Oligodon* mostly occurred during the last
339   glacial maximum (LGM) period, with the range including more expansive areas of current day
340   Turkmenistan, Afghanistan, and the southern edge of the Caspian Sea. Subsequent range
341   reduction is visible since the mid-Holocene, with the model prediction expecting the most
342   suitable habitat for this species in Köpet-Dag Mountain Range of northeast Iran and southwest
343   Turkmenistan, and small parts of Afghanistan, Azerbaijan, and western Iran (Figure 3).
344
345   **Resurrection and revalidation of *Contia transcaspica* Nikolsky, 1902.** Re-examination of
346   Turkmen and Iranian *O. taeniolatus* as well as past literature descriptions *O. taeniolatus* from
347   this region by Dotsenko (1984) and Latifi (1991) revealed that individuals from these localities
348   are morphologically identical to the type specimen of *Contia transcaspica* (ZISP 9868). These
349   specimens differ from Indian subcontinent *O. taeniolatus* in several features, the most obvious

350 being the presence of only 5 (rarely 6) supralabial scales, and narrow contact between the 4th and
351 5th supralabials due to the bottommost posterior temporal scale. These specimens can also be
352 diagnosed from all members of its sister clade, the *O. arnensis* species group (*O. arnensis*, *O.*
353 *churahensis*, *O. melaneus*, *O. russelius*, and *O. tillacki*), based on several coloration and
354 scalation features, namely the presence of 15 dorsal scale rows throughout the body (*versus* 17–
355 17–15). In terms of color pattern, these specimens also differ from typical *O. taeniolatus* (and
356 most *Oligodon* species across Asia) by the presence of brown transverse crossbars across the
357 dorsal surface. Phylogenetically, the sample of *O. taeniolatus* from northern Iran is monophyletic
358 and separate from all other congeners in the *O. arnensis* species group. Genetic distances
359 between its closest relatives, *O. churahensis, O. melaneus, O. russelius* are also substantial
360 (5.7%–7.8% based on cyt *b*) are also substantial. Since the combination of molecular and
361 morphological evidence support the distinct status of Iranian and Turkmen *O. taeniolatus*, we
362 resurrect the name *Contia transcaspica* from the subjective junior synonymy of this species. *O.*
363 *taeniolatus* sensu stricto is no longer paraphyletic and is now restricted to the Indian
364 Subcontinent in Bangladesh, India, Sri Lanka, and Pakistan. The Iranian and Turkmen
365 populations from the Köpet–Dag Mountain Range shall now be referred to as *Oligodon*
366 *transcaspicus* **comb. et. stat. nov.** and a detailed redescription, including the holotype of *Contia*
367 *transcaspica*, is provided below.
368
369 ***Oligodon transcaspicus* comb. et stat. nov. (Nikolsky, 1902)**
370 (Figures 4–6; Table 2)
371
372   *Contia transcaspica*: Nikolsky (1902: 839–840). *Holotype*: "Köpet–Dag, Transcaspia" [=
373   now Köpet–Dag Mountain Range, near Ashgabat, Ahal Province, Turkmenistan],
374   Nikolsky (1903a: 11–13), Bobrinskoy (1923: 8), Chernov (1935: 351) (in part), Welch
375   (1983: 77) (in part), Green (2010: 139) (in part), Bandara et al. (2022: 68) (in part), Uetz
376   et al. (2022) (in part)
377   *Oligodon taeniolatus* (in part): Chernov (1935: 351), Filippov (1947), Terentjev & Chernov
378   (1949), Bogdanov (1962), Brück (1968: 201), Nurgeldyev, Shammakov & Atayev (1970:
379   187–190), Rustamov & Atayev (1976: 47–53), Bannikov et al. (1977) Atayev, Gorelov &
380   Shammakov (1978), Szczerbak (1979: 68–70), Welch (1983: 77), Dotsenko (1984: 23–
381   26), Atayev (1985), Szczerbak, Khomustenko & Golubev (1986: 68–70), Latifi (1991: pl.
382   52 & 117), Rustamov & Sopyev (1994: 224), Atayev, Rustamov & Shammakov (1994:
383   337), Szczerbak (1994: 312), Ananjeva et al. (2006: 175), Green (2010: 139), Rustamow
384   (2011), Safaei-Mahroo et al. (2015: 280), Shestopal & Rustamov (2018a: 40), Orlov et al.
385   (2018: 58–67), Rajabizadeh (2018: 242).
386
387 **Holotype.** ZISP 9868, adult female from "Köpet–Dag, Transcaspia" [= now Köpet–Dag
388 Mountain Range, near Ashgabat, Ahal Province, Turkmenistan] collected by N. Kinschin in
389 1901 (Figure 4).

390   **Referred Specimens. Turkmenistan:** Ahal Province. CAS 180042, adult female from
391   "the Iran border south of Goalon, Ashkabad (Ashkhabad) Region" collected in May 1989 by
392   Soviet Border Patrol (obtained by J. R. Macey); ZMMU Re-5589, subadult female from
393   "Karanki", collected on 1 May 1979; ZMMU Re-6155, juvenile male from "Aidere" unknown
394   collection date; ZMMU Re-7318, adult female from "Chuli, Geok-Tepe" collected on 20 June
395   1990; ZISP 18334, juvenile of undetermined sex from "Geok-Tepe", collected on May 1971;
396   ZISP 18976, subadult male from "Geok-Tepe", collected on 05 August 1968. **Iran:** Khorasan
397   Province. ZMMU Re-16687 (field number RAN-3264), adult male from Bazangan Lake, Razavi
398   (36.3044ºN, 60.4751ºE, WGS 84; 900–950 meters a.s.l.) collected by Roman A. Nazarov and
399   Mehdi Radjabizadeh on 27 May 2017. See Table S1 for more details.
400   **Diagnosis.** A Kukri Snake in the genus *Oligodon* that is distinguished from all other
401   congeners by the following combination of morphological characters: 1) 7–9 maxillary teeth,
402   with posterior two teeth enlarged and blade-like; 2) dorsal scales in 15–15–15 rows; 3) cloacal
403   plate divided; 4) ventral scales 179–188 in males, 193–214 in females; 5) subcaudals 48–52 in
404   males, 44–51 in females; 6) total body scales 232–240 in males, 240–266 in females (232–266
405   scales combined); 7) subcaudal ratio 0.203–0.224 in males, 0.177–192 in females; 8) almost
406   always 5 supralabials (sometimes 6 according to Latifi, 1991), with 3rd supralabial in contact
407   with orbit; 9) loreal and preocular scales present, presubocular sometimes present; 10) posterior
408   temporal scales 3 (rarely 2), with lowest temporal causing 4th and 5th supralabial to contact
409   narrowly; 11) dorsal color pattern beige or light brown with of 42–57 dark transverse crossbands
410   on body and 12-17 crossbands on the tail; 12) dorsal color pattern on tail similar to rest of body,
411   with no vertebral stripe along tail.
412   **Comparisons.** We compare *Oligodon transcaspicus* **comb. et stat. nov.** to all species of
413   *Oligodon* found in Middle and Southwest Asia, which may be confused with this species,
414   particularly *O. taeniolatus* sensu stricto, with which it was previously confused with, and
415   members of its sister clade in the *O. arnensis* species group. We base our comparisons primarily
416   on data from the following literature sources (Wall, 1921; Wall, 1923; Smith, 1943; Khan, 2002;
417   Mirza, Bhardwaj & Patel, 2021; Bandara et al., 2022) as well as data from our own examined
418   specimens (Supplementary Material 1). *Oligodon transcaspicus* **comb. et stat. nov.** can be
419   morphologically assigned to the genus *Oligodon* by having a subcylindrical body, enlarged
420   blade-like maxillary teeth, two prefrontals and internasals present, a blunt and subterminal-
421   shaped rostral scale, length of rostral scale visible from above two times as long as the internasal
422   suture, two temporal scales bordering edge of parietals (generic diagnosis modified from Wall
423   1923).
424   The closest relatives of *O. transcaspicus* **comb. et stat. nov.** include members of the *O.*
425   *arnensis* species group. Of these, *O. transcaspicus* **comb. et stat. nov.** can be distinguished from
426   *O. arnensis* sensu stricto by having 15 dorsal scale rows (*versus* 17–17–15), 179–202 ventrals in
427   both sexes (*versus* 164–188 in both sexes), loreal scale present (*versus* loreal absent), 5–6
428   supralabials (*versus* 7–8, rarely 6), usually 3 posterior temporal scales (*versus* always 2), 7–9
429   maxillary teeth (*versus* 12–16), and irregular dorsal mottling with 47–57 transverse body

430 blotches (*versus* dorsum immaculate, less than 20 black body bands). *O. transcaspicus* **comb. et**
431 **stat. nov.** can be distinguished from *O. churahensis* (later synonymized with *O. russelius*) by
432 having 15 dorsal scale rows (*versus* 17–17–15), 179–202 ventrals in both sexes (*versus* 170–175
433 in both sexes), 5–6 supralabials (*versus* 7–8), usually 3 posterior temporal scales (*versus* always
434 2), and irregular dorsal mottling with 42–57 transverse body blotches 1.5–3.0 dorsal scales wide
435 and 12–16 tail blotches (*versus* 37–45 broad black body crossbars, all edged with a cream color,
436 1.0–2.0 dorsal scales wide and 9–11 tail bars). *O. transcaspicus* **comb. et stat. nov.** is
437 distinguished from *O. melaneus* by having 15 dorsal scale rows (*versus* 17–15–15), 5–6
438 supralabials (*versus* usually 7, rarely 6), usually 3 posterior temporal scales (*versus* always 2),
439 and irregular dorsal mottling with 42–57 transverse body blotches 1.5–3.0 dorsal scales wide and
440 12–16 tail blotches (versus black dorsum without conspicuous blotches or markings and a
441 distinct blue ventral coloration in life). *O. transcaspicus* **comb. et stat. nov.** can be distinguished
442 from *O. russelius* by having 15 dorsal scale rows (*versus* 17–17–15), 5–6 supralabials (*versus* 7–
443 8, rarely 6), usually 3 posterior temporal scales (*versus* always 2), and irregular dorsal mottling
444 with 42–57 transverse body blotches 1.5–3.0 dorsal scales wide (*versus* dorsum immaculate with
445 narrow black body bands or crossbars usually edged with white, 1.0–2.0 dorsal scales wide). *O.*
446 *transcaspicus* **comb. et stat. nov.** can be distinguished from *O. tillacki* by having 15 dorsal scale
447 rows (*versus* 17–17–15), 5–6 supralabials (*versus* 7–8), usually 3 posterior temporal scales
448 (*versus* always 2), and irregular dorsal mottling with 42–57 transverse body blotches 1.5–3.0
449 dorsal scales wide (*versus* dorsum immaculate with 25–35 broad black body bands 4.0–6.0
450 dorsal scales wide).
451   In addition, *O. transcaspicus* **comb. et stat. nov.** can be distinguished from *O.*
452 *taeniolatus*, which it was previously confused with, by having 5 (rarely 6) supralabials (*versus*
453 always 7–8) with only the 3rd supralabial contacting the orbit (*versus* usually the 3rd and 4th in
454 contact with orbit), two posterior supralabials (4th and 5th) in narrow contact due to the lowest
455 posterior temporal scale abutting the two scales (*versus* all supralabials in broad contact),
456 temporal scale formula 1+3 (*versus* temporals 1+2), and a dorsal color pattern with irregular
457 transverse crossbars and no distinct vertebral stripe on the body or tail (*versus* dorsal color
458 pattern variable, but usually with irregular non-transverse crossbars or body blotches, and a small
459 thin vertebral stripe on the body and tail).
460   **Redescription of the Holotype (ZISP 9868).** Adult female specimen in good condition
461 after 118 years of preservation. Small portion of midbody in slightly poor condition, large ventral
462 incision posteriorly until vent (Figure 4). SVL 304 mm, TailL 53 mm (TotalL 357 mm). HeadL
463 9.6 mm, HeadW 5.6 mm, SnL 2.6 mm, EyeL 1.4 mm, FrontalL 3.2 mm. TailLR 0.148,
464 HeadW/HeadL 0.58, SnL/HeadL 0.29, EyeL/SnL 0.54, EyeL/HeadL 0.15. Body elongated and
465 cylindrical in cross section; head ovoid, slightly distinct from neck; snout narrowing in dorsal
466 view, depressed very slightly towards the tip with rostral appearing rounded in lateral profile;
467 snout tip subterminal near mouth; eyes moderately sized compared to head, with a round pupil;
468 nostrils small and subelliptical, pointed in lateral view; mouth flat with lips curving upwards
469 posteriorly along last supralabial; tail gradually tapering to a sharp terminal scute.

470   Rostral distinctly enlarged, wider than high, triangular in dorsal view, partially separating
471   the anterior half of internasals; posterior scale suture of rostral with internasals "deep-V" shaped,
472   with vertex of rostral in-line with nostrils as a narrow obtuse angle (~99º); internasals
473   subpentagonal, wider than long, internasal suture equal in length compared to prefrontal suture;
474   prefrontals subhexagonal, wider than long, wider and longer than internasals; frontal
475   subpentagonal, shield shaped, anterior suture with prefrontals concave and angled; frontal longer
476   than prefrontals; eyes placed posterior relative to the anterior edge of the frontal; angle formed
477   by sutures producing the posterior vertex of the frontal a right angle, almost acute (~90);
478   supraoculars subrectangular, longer than wide, shorter in length than frontal; parietals
479   subpentagonal, longer than wide, width of scale wider than parietal suture, posterior sutures
480   bordering occipital region strongly concave and curved; length of parietals approximately equal
481   in length of frontal; parietal suture shorter than frontal; parietal suture shorter than length of
482   frontal; anterior parietal angle formed by the sutures between the parietal/frontal and the suture
483   between the supraocular/parietal a broad obtuse angle (~130º) with lateral ray of angle pointing
484   posterolaterally. Nasal scale rectangular-shaped, longer than wide, fully divided; loreal 1/1, small
485   and square shaped, slightly wider than than long, less than half the size of the nasal; supralabials
486   5/5; 3rd supralabial in contact with orbit; 5th supralabial largest, first supralabial smallest; all
487   supralabials in broad contact, except for supralabials 4–5, which are in narrow contact due to
488   abutting posterior temporal; preoculars 1/1, wider than long; presubocular 1/1, smaller than
489   preocular; postoculars 2/2, uppermost postocular largest; anterior temporal 1/1; posterior
490   temporals 3/3, bottommost temporal large and subpentagonal in shape, blocking the 4th and 5th
491   supralabial from broadly contacting each other; infralabials 7/7 in all specimens, first in contact
492   with each other, 4/4 infralabials in contact with anterior chin shields; mental subtriangular, wider
493   than long; small mental groove present, starting from border of 1st infralabial and mental
494   terminating at the posterior chin shields; length and width of both chin shields equal in size.
495   Dorsal scale rows 15–15–15, smooth throughout without apical pits; ventral scales 202;
496   subcaudals 47, paired; total body scales 250; subcaudal ratio 0.19; cloacal plate divided; tail tip a
497   sharp pointed scute. Maxillary teeth 7, posterior two teeth enlarged and blade-like.
498   **Coloration in Preservation.** After 121 years in preservation fluids, dorsal ground color
499   cream, margins of some dorsal scales brown forming indistinct and irregular mottling along
500   flanks; 47 indistinct transverse bars along dorsum, broadest vertebrally and slightly narrowing
501   laterally, around 1.5–2.0 dorsal scales at their widest; along tail 12 transverse bands of similar
502   color with any additional markings. Dorsal portion of head is cream, indistinct beige ocular-bar
503   edged with brown starting along 3rd and 4th supralabial scale, past eye covering first half of
504   supraocular, prefrontals and anterior suture of frontal; a second beige and brown-edged temporal
505   bar starting near gulars and first dorsal scales, extending across posterior portion of the fifth
506   supralabial before meeting medially at the parietals and frontal forming a "V" shaped mark;
507   brown nuchal chevron present medially starting at the parietal suture as a small lanceolate tip
508   broadening along the nape as a thick tripartite-shaped blotch, extending laterally on each side of

509 the flanks, ending before reaching the ventral surface. Ventral surface an immaculate cream,
510 faint beige spotting or mottling along edge of ventral scales, more prominent along the tail.
511   **General Description and Variation.** The additional six specimens examined agree with
512 the description of the holotype in most aspects of coloration, scalation and morphometric
513 characteristics. SVL 145–312 mm in male, 267–361 mm in females; TailL 27–70 mm in male,
514 42–64 mm in females; TotalL in male 195–382 mm, 309–425 mm in females. The largest
515 specimen is an adult female (ZMMU Re-7318) with a SVL of 361 mm and TailL of 64 mm.
516 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
517 mm. TailLR 0.157–0.183 in males, 0.136–0.159 in females, HeadL/HeadW 0.53–0.72,
518 SnL/HeadL 0.27–0.42, EyeL/SnL 0.34–0.54, EyeL/HeadL 0.12–0.15. Body elongated and
519 cylindrical, slightly robust along midbody in some specimens; head ovoid, slightly distinct from
520 neck; snout narrowing in dorsal view, depressed only slightly towards the tip in dorsolateral
521 view; head oblong in lateral profile; snout tip subterminal near mouth; eyes moderately sized
522 compared to head; nostrils pointed in lateral view; mouth flat, lips slightly curved posteriorly;
523 tail tapering to a sharp terminal scute.
524   Rostral distinctly enlarged, wider than high, triangular in dorsal view, extending
525 posteriorly partially separating internasals; posterior scale suture of rostral with internasals
526 "deep-V" shaped, with vertex of rostral in-line with nostrils obtuse angled (95º–115º); internasals
527 subpentagonal, wider than long, suture roughly equal or slightly longer than prefrontal suture;
528 prefrontals subhexagonal, wider than long, longer and wider than internasals; frontal
529 subhexagonal, shield shaped, anterior margin of scale clearly angled in most specimens but
530 sometimes more concave; the posterior border of the frontal of one specimen (ZMMU Re-
531 16687) is slightly notched with two pores near the border of the parietals and two similar notched
532 "pores" in the center of the scale (Figure 5); frontal around twice the length of prefrontals;
533 supraoculars subrectangular, longer than wide, shorter in length and width than frontal; eyes
534 placed posterior relative to the anterior edge of the frontal; angle formed by sutures producing
535 the posterior vertex of the frontal right or acute-angled (80º–90º); oftentimes the posterior
536 portion of the frontal truncates, giving the vertex a notched appearance in dorsal profile; parietals
537 subpentagonal, posterior portion concave and usually curved, occasionally straight; parietals
538 slightly longer than wide, width of scale wider than parietal suture; length of parietals equal or
539 slightly longer than length of frontal; parietal suture shorter than frontal length; anterior parietal
540 angle formed by the sutures between the parietal/frontal and the suture between the
541 supraocular/parietal a broad obtuse angle (120º–130º) with lateral ray of angle pointing
542 posterolaterally. Nasal scale rectangular to square shaped, fully divided and usually longer than
543 wide; loreal 1/1, square-shaped, around a quarter or half the size of nasal; supralabials 5/5 in all
544 examined specimens, although Latifi (1991) mentions specimens with 6 supralabials; 3rd
545 supralabial always in contact with orbit; 5th supralabial largest, 1st supralabial smallest; all
546 supralabials in broad contact, except for supralabials 4–5, which contact narrowly due to abutting
547 posterior temporal; preoculars 1/1, uppermost preocular slightly larger; presubocular 1/1 present
548 in four specimens (including holotype), absent in rest; postoculars 2/2, uppermost postocular

549 largest; anterior temporal 1/1; posterior temporals 3/3 (in one specimen, CAS 180042, 3/2),
550 bottommost temporal large and subpentagonal in shape, blocking the 4th and 5th supralabial from
551 broadly contacting each other; infralabials 7/7 in all specimens, first in contact with eachother,
552 4/4 infralabials in contact with anterior chin shields; mental subtriangular, wider than long; small
553 mental groove present, starting from border of 1st infralabial and mental terminating at the
554 posterior chin shields; length and width of both chin shields equal in size.
555   Dorsal scale rows 15–15–15, smooth throughout and without apical pits; ventral scales
556 179–188 in males, 193–202 in females; subcaudals 48–52 in male, 44–51 in females; total body
557 scales 232–240 in male, 240–266 in females; subcaudal ratio 0.203–0.224 in males, 0.177–192 in
558 females; anal plate divided; tail tip tapers to a sharp tip. Maxillary teeth 7 in two specimens
559 (including the holotype) and 9 in one specimen (CAS 180042), posterior two teeth enlarged and
560 blade-like. Teeth unavailable for examination in other specimens. We did not examine the
561 hemipenis of any specimens as all organs were retracted. The structure of hemipenes is a rather
562 conservative feature. Therefore, despite the lack of any information about hemipenial
563 morphology of *O. transcaspicus* **comb. et stat. nov.**, we expect that the fully everted and
564 expanded hemipenes of this species will likely share the same structure with its closest relatives
565 in the *O. arnensis* species group, namely a short and slightly bilobed hemipenes with spinous
566 calyces and a simple sulcus spermaticus. Our sample size is too low to make statistical
567 comparisons between sexes, however a few instances of putative sexual dimorphism are noted.
568 First, the number of ventral scales appear to be higher in the single male specimen. The male
569 specimens also have a higher number of subcaudals, TailLR ratio and subcaudal ratio than the
570 females. The number of total body scales appears to be higher in females.
571   All specimens in preservative have a cream to beige colored dorsum, with brown
572 mottling mostly well-defined and restricted across the flanks, some vertebral portions of dorsum
573 also with white mottling; 47–57 transverse crossbars, usually light brown with the margins of
574 dorsal scales along bars dark-brown or black and the edges of each bar surrounded weakly edged
575 by white; all crossbars more well-defined compared to the holotype, widest in the vertebral
576 region and are narrower laterally, at widest between 1.5–3.0 dorsal scales in length; crossbar
577 counts on body are not sexually dimorphic; tail blotches range from 12–16 and are similar in
578 coloration. Dorsal surface of the head tan to cream, lower portions of snout sometimes grayish-
579 brown; occasional vermiculations present along supralabials and underside of head; the position
580 of the ocular and temporal bars are consistent amongst all specimens, but are usually brown or
581 dark-brown and edged with black; the nuchal chevron in some specimens is lanceolate-shaped at
582 its anterior origin along the parietals, but in two specimens it is blunt or obtuse-pointed,
583 terminating before the ventral surface along the nape as a thick tripartite or triangular-shaped
584 blotch. No vertebral stripe is present along the tail in preserved specimens. The ventral surface is
585 tan to cream, with three specimens bearing irregular margins of dorsal cross-bands visible on
586 lateral sides of the ventral scales, but in other specimens the ventral surface is immaculate. The
587 color in life based on ZMMU Re-16687 (Figure 5) and two specimens photographed in
588 Turkmenistan by A. V. Pavlenko (Figure 6) resembles the coloration in preservative, but its

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

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

618   The natural history of *Oligodon transcaspicus* **comb. et stat. nov.** is somewhat well-
619 known in the literature (Dotsenko, 1984; Atayev, 1985; Szczerbak, Khomustenko & Golubev,
620 1986; Rustamov & Sopyev, 1994; Szczerbak, 1994; Atayev, Rustamov & Shammakov, 1994;
621 Orlov et al., 2018) and several additional specimens have been recorded. Two specimens
622 photographed by A. Pavlenko (pers. comm.) were found in the daytime amongst rocky outcrops
623 (Figure 6); however, Orlov et al. (2018) noted most specimens were strictly nocturnal or
624 crepuscular. These authors found *Oligodon transcaspicus* **comb. et stat. nov.** was most abundant
625 between elevations of 400–700 meters, but also noted a few specimens that were found at lower
626 and higher altitudes. Most animals were captured at the base of gradually sloping mountain
627 gorges, riverbeds and open habitats with shrubs and tree vegetation that maintain enough surface
628 moisture. Based on this, Orlov et al. (2018) posited that the activity period of *Oligodon*

629 *transcaspicus* **comb. et stat. nov.** is highly dependent on high moisture and relative humidity
630 and will only come up on the surface when these conditions are met. Like other *Oligodon*, this
631 species probably feeds on reptile and bird eggs. Atayev, Rustamov & Shammakov (1994) and
632 sources therein record this species laying one to two eggs between the months of May and June,
633 suggesting the reproductive season is in the spring and early summer. It is assumed like other
634 *Oligodon* that its diet primarily consists of reptile eggs.
635   **Remarks.** Most sources that mention *O. transcaspicus* **comb. et stat. nov.** have cited
636 Nikolsky (1903a) as the source of original description. However, we have discovered an earlier
637 book that was also authored by Nikolsky describing *Contia transcaspica* dated to 1902. Thus, the
638 year of original description and its publication source should be fixed, and we do so here in the
639 present paper.
640   **Etymology.** The species epithet "*transcaspicus*" is a latinized toponymic adjective in
641 genitive singular and given in reference to the type locality of this species, which during the time
642 of its description, was called the Transcaspian Region (Zakaspiyskaya Oblast or Zakaspiyskiy
643 Krai) and was part of the Turkestan Governor–Generalship of the Russian Empire. The
644 Transcaspian Region later became known as Turkmenistan during its time as a constituent
645 republic of the Soviet Union (Turkmen S.S.R.) and now as an independent nation. The epithet is
646 fixed to agree with the gender of the generic name *Oligodon*, which is masculine. We
647 recommend the English common name "Köpet–Dag Kukri Snake" for this species, followed by
648 the Russian, Farsi, and Turkmen common names "Zakaspiyskiy oligodon", "داغ کپه مار لوس"
649 [*Loos Mār-e Kopet Dagh*], and "Goňurja ýylanjyk", respectively (see Rustamow, 2011;
650 Rajabizadeh, 2018).
651
652 **The taxonomic status of *Oligodon "arnensis"* in Pakistan.** Because the revision of *O. arnensis*
653 sensu auctorum by Bandara et al. (2022) only focused on material from India and Sri Lanka, we
654 use this section to review the status of these snakes in neighboring Pakistan. We examined one
655 specimen of *O.* "*arnensis*" (CUHC 7904) recently collected by DJ and RM on 16 September
656 2018 from Kallar Kahar, Punjab Province, Pakistan (32.7695ºN, 72.7065ºE, 613 m a.s.l.). Based
657 on the presented mtDNA phylogeny, this specimen was recovered in a clade with two additional
658 samples from Pakistan that were previously identified as *O.* cf. *churahensis* by Mirza, Bhardwaj
659 & Patel (2021). These authors only briefly commented on the status of these genetic samples and
660 could not examine voucher specimens from Pakistan in their study. A brief description of CUHC
661 7904 is as follows (Figure 7): adult male, SVL 345 mm, TailL 65 mm (TotalL 410 mm; TailLR
662 0.159) 16–17–15 dorsal scale rows, 183 ventrals, 49 subcaudals (233 total body scales),
663 subcaudal ratio of 0.21, 1/1 loreal present, 1/1 divided nasal, 7/7 supralabials with the third and
664 fourth in contact with the eye, 7/7 infralabials, and an immaculate brown dorsum with 37 black
665 crossbands across the body and 13 tail bands approximately 1.0–1.5 dorsal scales wide at
666 midbody and interspaces between each band approximately 4.0 dorsal scales long. In addition to
667 this specimen, multiple authors who have conducted fieldwork in Pakistan (Minton, 1962;
668 Minton, 1966; Mertens, 1969; Khan, 2002) have recorded *O. "arnensis"* specimens. Both

669 Minton (1962) and Khan (2002) figure an *O. "arnensis"* (with Khan, 2002 swapping the images
670 of *O. "arnensis"* and *O. taeniolatus* by mistake) bearing small narrow black crossbars with white
671 edges. Based on these characteristics, along with other scalation features (see Table 3), the
672 literature descriptions of Pakistani *O. "arnensis"* are very similar to CUHC 7904 and specimens
673 *O. russelius* fide Bandara et al. (2022). Therefore, based on our specimen and previous reports of
674 *O. "arnensis"*, we refer the northern Pakistan populations of *O. "arnensis"* to *O. russelius*.
675
676 **Records of *Oligodon* in Afghanistan.** Literature reports of *O. "arnensis"* and *O. taeniolatus*
677 from Afghanistan are sparse but have been the subject of confusion for decades. Brück (1968)
678 first reported a juvenile Kukri Snake he identified as *O. taeniolatus* from "dem Gebiete um
679 Djelalabad" [= vicinity of Jalalabad]. This record was plotted by Sindaco et al. (2013) but
680 rejected due to imprecision by Wagner et al. (2016b). Although Brück (1968) identified this
681 specimen as *O. taeniolatus*, data he provided for this specimen indicates it bears 17 dorsal scale
682 rows, contra the 15 dorsal scales normally observed in *O. taeniolatus*. This was noticed quickly
683 by Král (1969), who subsequently corrected its identification to *O. arnensis*. Nevertheless, both
684 Sindaco, Venchi & Grieco (2013) and Wagner et al. (2016b) recorded both *O. arnensis* and *O.*
685 *taeniolatus* as inhabitants of Afghanistan, failing to realize that their records refer to the same
686 specimen (MMB 28497). Brück (1968)'s account provided additional morphological data that
687 allow us to confirm its identification. He notes that the specimen bears the following features:
688 juvenile (unsexed, but based on relative tail length and subcaudal ratio, possibly an immature
689 female), SVL 153 mm, TailL 24 mm (TotalL 177 mm, TailLR 0.136), dorsal scales in 17 rows,
690 198 ventrals, 44 subcaudals, (243 total body scales, subcaudal ratio 0.181), 7/7 supralabials (3–5
691 contacting eye), 6/6 infralabials, 1 preocular, 2 postocular, 1+2 temporals, and 49 dark crossbars
692 across the body and tail. These characteristics confirm that the specimen should not be identified
693 as *O. taeniolatus* and that Král's re-identification as *O. "arnensis"* was correct (see Table 3 for
694 more comparisons). A second *Oligodon* record from Afghanistan was recently documented on
695 the citizen science platform iNaturalist (2022). This specimen (obs. 110932106, user
696 mohammadfarooq) was observed from Dara–i–Pech district, Kunar Province, Afghanistan
697 (35.0553ºN, 70.9561ºE; 1,700–1,800 meters a.s.l.) on 9 April 2022. While photographs of the
698 specimen are too poor in quality to discern any scalation features, its color pattern consisting of
699 approximately 51 black crossbars and 13 tail bars (64 total crossbars) greatly resembles *O.*
700 *"arnensis"*, specifically *O. russelius* (and to some extends *O. churahensis* but see Discussion).
701 Because of this, we conclude that the Afghanistan populations previously recorded as *O.*
702 *arnensis* (Khan, 2002; Wagner et al., 2016b) should also represent *O. russelius*. All records of
703 this species from the country are restricted to the western portion of the Hindu Kush.
704   The only other report of an Afghan *Oligodon* is a record of *O. taeniolatus* from
705 Afghanistan noted by Wagner et al. (2016b) from "Kars, Kandahar Province" based on specimen
706 USNM 194971. We attempted to trace the voucher of this specimen and discovered that the
707 museum catalog number USNM 194971 refers to a scincid lizard *Eurylepis taeniolatus* Blyth,
708 1854a, and not a kukri snake. No collection records of *Oligodon* from Afghanistan have been

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

Discussion

717   The phylogenetic analysis of 12S–16S rRNA, cyt *b* fragments, morphological data and
718 SDM mapping data support the resurrection of *Contia transcaspica* as *Oligodon transcaspicus*
719 **comb. et stat. nov.** for Iranian and Turkmen populations previously ranked under *O. taeniolatus*.
720 This analysis also revealed substantial genetic differentiation between populations of *O.*
721 *taeniolatus* on the Indian subcontinent warranting additional revisionary work from future
722 authors. We cannot provide a valid description for the deeply divergent lineages in Sri Lanka and
723 mainland India due to a lack of broad morphological and genetic sampling. However, we note
724 that the names *Oligodon fasciatus* Günther, 1864 (now considered a subspecies of *O.*
725 *taeniolatus*) and *Oligodon taeniolatus* var. *ceylonicus* Wall, 1921 are both available names for
726 Sri Lankan populations if they indeed prove to be distinct from others on the island, and/or the
727 remainder of the Indian subcontinent. While the taxonomy of *O. taeniolatus* remains unresolved,
728 the position of *O. transcaspicus* **comb. et stat. nov.** outside of this clade in the *O. arnensis*
729 species group justifies its separation as a distinct species. The distribution of *O. transcaspicus*
730 **comb. et stat. nov.** is probably more expansive than currently ascertained, and we expect that
731 this species will eventually be found in additional localities across the Köpet–Dag Mountain
732 region.
733 The SDM models identified some patches of suitable habitat across the Western Caspian region
734 and Central Iranian Desert in areas where Latifi (1991, 2000) and Safaei-Mahroo et al. (2015)
735 reported its presence. Unfortunately, we could not trace any specimen vouchers of Latifi's
736 collection in the Razi Vaccine and Serum Research Institute associated with these Iranian
737 records. Since these Latifi's specimens come from snake hunters of the institute (and were not
738 collected by Latifi himself) and the locality data is given only at province level, researchers must
739 be very cautious about them. Only subsequent fieldwork in these areas might verify such reports,
740 particularly in adjacent Iranian provinces bordering Turkmenistan.
741 Verified vouchers specimens of *O. transcaspicus* **comb. et stat. nov.** also exist close to the
742 border of Afghanistan in Mary Province, Turkmenistan. Since SDM modelling also predicts
743 suitable habitat in this region, it is possible that this species also persists in the northwestern
744 portion of Afghanistan (specifically Herat, Badghis, Faryab and Jowzan provinces), but a lack of
745 survey effort due to security concerns makes it difficult to ascertain whether this species will be
746 found here anytime soon (see Jablonski et al., 2021). The conservation of *O. transcaspicus*
747 **comb. et stat. nov.** does not seem to be under any significant threats, although factors such as
748 habitat degradation and human encroachment could pose a threat to some populations. Climate

749 projections also state that aridification and a reduction of river runoff is expected across the
750 southern portion of Turkmenistan over the following decades (Lioubimtseva et al., 2012; Duan et
751 al., 2019). Because the SDM mapping analyses indicated temperature and precipitation
752 seasonality were major factors influencing the distribution of *O. transcaspicus* **comb. et stat.**
753 **nov.**, climate change may also negatively impact populations. Under listings provided by the
754 International Union for Conservation of Nature (IUCN) we would recommend classifying this
755 species as "Least Concern". Continued monitoring of existing populations and additional field
756 surveys across the Köpet–Dag Mountain Range would improve our understanding of the ecology
757 and conservation of this species.
758 Although our sampling is very limited, the results from our study suggest the three-taxon
759 statement of the *O. arnensis* sensu auctorum by Bandara et al. (2022) requires additional
760 scrutiny. Specimens we included from Ganjam district, Odisha, India (CAS 17224–225) are well
761 within the distribution of *O. russelius* (fide Bandara et al., 2022) and both morphologically
762 resemble *O. arnensis* sensu stricto, bearing 18–20 dark black body bands that are 2.0–3.0 dorsal
763 scales wide. Another specimen collected near Rajamahendravaram, Andhra Province, India
764 (CAS 94375) is close to the type locality of *O. russelius* but has 22 dorsal body bands that are
765 1.5–2.0 dorsal scales wide (band count resembling the species diagnosis of *O. arnensis* sensu
766 stricto fide Bandara et al., 2022). Either the ranges of *O. arnensis* sensu stricto and *O. russelius*
767 are sympatric in parts eastern India, or a broad contact zone between the two species may exist.
768 This could explain why some specimens we examined have more variable color pattern
769 conditions than previously described. The distribution map of *O. arnensis, O. russelius* and *O.*
770 *tillacki* in Bandara et al. (2022)'s clearly separates the three taxa on the Indian subcontinent;
771 however, we note that the collection localities in their map combine collection localities with
772 observations identified from iNaturalist. We agree that such citizen scientist databases have great
773 utility in documenting rare and understudied herpetofauna, but they still can suffer from data
774 quality issues (i.e., limited number of visible morphological features, misidentification errors). It
775 is difficult to discern which locations in Bandara et al. (2022)'s map are voucher specimens or
776 iNaturalist observations because the authors do not provide a geolocation appendix in their paper
777 and do not denote a distinction between their location datapoints. Furthermore, we note that the
778 p-distance (based on cyt *b*) between Sri Lankan *O. arnensis* samples and the GenBank sample
779 identified as *O.* cf. *tillacki* is only 3.6%, lower than most normal p-distances separating species-
780 level lineages of *Oligodon*. We conservatively retain the species status of *O. tillacki* as we have
781 not directly examined the voucher specimen of this sample to verify its identity. Subsequent
782 treatments of *O. arnensis* sensu stricto, *O. russelius*, and *O. tillacki* should emphasize increased
783 specimen and tissue collection for an integrative taxonomic approach.
784 Our analysis also confirmed the taxonomic identity of *O. "arnensis"* populations in
785 northern Pakistan and Afghanistan as *O. russelius*. Nevertheless, several authors (Minton, 1966;
786 Mertens, 1969; Khan, 2002) note the distribution of *O. "arnensis"* extends into central and
787 southern Pakistan close to the border of western India. These locations come close to the known
788 distribution of *O. tillacki*, especially near Gujarat State, India. However, Minton (1966) noted

789   that all his specimens have black bars with white edges, a phenotypic trait that Khan (2002) also
790   described. Both illustrations by these authors show a "V-shaped" marking on the nape, although
791   it is not a thick triangular blotch that is observed in *O. tillacki*. We believe there is little
792   indication that *O.* "*arnensis*" populations in southern and central Pakistan match the description
793   *O. tillacki* and we maintain the identity these populations as *O. russelius* for the time being. It is
794   still possible that *O. tillacki* could range into this part of the country due to the continuity of
795   habitat within this region, and we suggest future herpetological survey work and the examination
796   of additional material to confirm this. Such a discovery could align with recent studies that have
797   denoted a biogeographic break between the right and left banks of the Indus River seen in several
798   Pakistani amphibians and reptiles (Gowande et al., 2021; Agarwal et al., 2022; Dufresnes et al.,
799   2022).
800   Our study has taxonomic implications for the recently described *O. churahensis*, as
801   Mirza, Bhardwaj & Patel (2021) tentatively associated Pakistani samples of *O.* "*arnensis*" with
802   this species. Like the genetic distances between *O.* cf. *tillacki* and *O. arnensis* sensu stricto, the
803   cyt *b* p-distance between the Pakistani clade of *O. russelius* (= *O.* cf. *churahensis*) and the clade
804   containing the type series of *O. churahensis* is low for species-level divergence, standing at only
805   3.3%. *Oligodon churahensis* was described by Mirza, Bhardwaj & Patel (2021) based on two
806   specimens collected at the foothills of the western Himalayas in Himachal Pradesh, India.
807   Bandara et al. (2022) correctly noted that literature descriptions of kukri snakes similar to *O.*
808   *churahensis* were reported as *O. arnensis* sensu lato (= now *O. russelius*) by past authors (Wall,
809   1921; Deraniyagala, 1936; Constable, 1949; Deraniyagala, 1955). However, because Bandara et
810   al. (2022) include data from these historical sources into their conception of *O. churahensis* (as
811   seen in their supplementary material), diagnosing this species from *O. russelius* becomes
812   puzzling. In the comparisons section of *O. russelius*, Bandara et al. (2022) separated this species
813   from *O. churahensis* by the presence of 30–45 crossbars (*versus* 48–54 in *O. churahensis*) the
814   distance between each crossbar measured in vertebral dorsal scales (4–6 scales *versus* 2–4 in *O.*
815   *churahensis*), and by a different head shape marking (inverted Y-shaped marking *versus* heart-
816   shaped symbol in *O. churahensis*). However, the authors note that *O. churahensis* has 56–62
817   crossbars in the remaining text, especially in Table 1, where it is again compared to the 30–45
818   crossbars of *O. russelius*. It appears that the authors confused the true number of crossbars found
819   in *O. churahensis* and *O. russelius*, failed to specify between "total crossbars" (including body
820   and tail bars) and "body crossbars" (restricted from nape to vent) and did not completely
821   summarize the color pattern traits observed in all of the sources they believe comprise *O.*
822   *churahensis* (Wall, 1921; Deraniyagala, 1936; Constable, 1949; Deraniyagala, 1955; Mirza,
823   Bhardwaj & Patel 2021). Per the original description (Mirza, Bhardwaj & Patel 2021), the actual
824   number of body crossbars in *O. churahensis* is 37–45, with the total crossbars noted as 48–54.
825   Furthermore, Bandara et al. (2022) state in the written description that *O. russelius* has 30–45
826   body crossbars and 6–10 tail bars. This indicates that the supposed differences in crossbar
827   numbers are a lot less significant than previously considered. As argued by Mahony & Kamei

828 (2021), errors and inconsistencies in taxonomic articles are inevitable, but authors should
829 practice great care to make sure data inputted into descriptions and tables is consistent.
830   When we combine our own data on *O. russelius* from Afghanistan, Pakistan with the
831 clarified characters of Bandara et al. (2022) and existing data in the literature (Wall, 1921;
832 Constable, 1949), most color pattern and scalation traits between this taxon and *O. churahensis*
833 overlap (Table 3). Combined with the low genetic divergence revealed by our molecular data,
834 our study does not support the species-rank status of *O. churahensis*. It is plausible that
835 specimens identified as *O. churahensis* represent the high-end of a geographic cline of cross-
836 banded phenotypes found within *O. russelius* across its range, as suggested in part by Wall
837 (1921). Alternatively, it is possible that the *O. churahensis* and *O. russelius* clades could
838 maintain their reciprocal monophyly, albeit with low genetic divergence that would support the
839 existence of two lineages at the subspecies level. In the absence of additional samples from the
840 type locality of *O. churahensis* and adjacent regions of northern India and Pakistan, we believe
841 the most appropriate decision is to relegate the species to the junior synonymy of *O. russelius*,
842 which we do so here.
843   Our resurrection of *O. transcaspicus* **comb. et stat. nov.** and the clarification of *O.*
844 "*arnensis*" and *O. taeniolatus* records from Middle and Southwest Asia represents a small step of
845 a long journey in our goal of understanding the evolutionary history of snakes and other
846 herpetofauna of this region. Interestingly, several reptiles found in Middle and Southwest Asian
847 countries that are Oriental realm elements of the region's herpetofauna are recognized as
848 separate taxa. Such examples include *Boiga trigonata melanocephala* (Annandale, 1904),
849 *Lycodon striatus bicolor* Nikolsky, 1903b and *Ptyas mucosa nigriceps* Terentjev & Chernov,
850 1949. Other reptile taxa found in Middle/Southwest Asia whose close relatives are of Oriental
851 realm origin include *Naja oxiana* Eichwald, 1831 and *Eublepharis macularius* Blyth, 1854b. For
852 these latter species, phylogeographic evidence indicates minimal genetic differentiation between
853 populations opposite of the Hindu Kush suggesting rapid range expansion from the Indian
854 subcontinent into Middle/Southwest Asia due to suitable environmental conditions formed by
855 steppe habitats west of the Hindu Kush mountains (Kazemi et al., 2021; Agarwal et al., 2022).
856 The uniqueness of the evolutionary lineage representing *O. transcaspicus* **comb. et stat. nov.**
857 paints a different picture, as the presented molecular, morphological and SDM evidence implies
858 that the divergence of its common ancestor into present-day Iran and Turkmenistan occurred
859 much earlier. The high topography surrounding the Hindu Kush and the south-adjacent Registan-
860 North Pakistan sandy deserts present formidable biogeographic barriers, and probably limited
861 dispersal opportunities periods when climatic and habitat conditions were suitable. The diversity
862 and cladogenesis of other Oriental-affiliated elements of Middle and Southwest Asia's
863 amphibians and reptiles are still poorly understood by herpetologists, and present numerous
864 intriguing questions for future research. The acquisition of new material along with more
865 comprehensive phylogeographic analyses will undoubtedly shed light on these unique animals
866 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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939 ### Author Contributions
940 **Justin L. Lee** collected data, conceived and designed the experiments, analyzed the data,
941 prepared figures and tables, prepared the drafts of the paper, reviewed drafts of the paper, and
942 approved the final draft.

943 **Platon V. Yushchenko** collected data, conceived and designed the experiments, analyzed the
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946 **Konstantin D. Milto** collected data, prepared figures, reviewed drafts of the paper, discussion of
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952 **Daniel Jablonski** collected data, contributed analysis tools, prepared figures, prepared the drafts
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954 **Rafaqat Masroor** collected data for the paper, contributed analysis tools, reviewed drafts of the
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960 **Princia Dsouza** collected data for the paper, reviewed drafts of the paper, approved the final
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962 **Nikolai L. Orlov** analyzed the data, reviewed drafts of the paper, discussion of the results
963 **Roman A. Nazarov** collected data, prepared figures, reviewed drafts of the paper, discussion of
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965 **Nikolay A. Poyarkov** conceived and designed the experiments, analyzed the data, prepared the
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968 ## Animal Ethics

969 The following information was supplied relating to ethical approvals (i.e., approving body and
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971 Specimen collection protocols and animal operations followed the Institutional Ethical
972 Committee of International Center for Science, High Technology and Environmental Sciences,
973 Kerman, Iran (Certificate #1.87-1).
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975 ## Field Study Permissions

976 The following information was supplied relating to field study approvals (i.e., approving
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978 Field works, including collection of the samples and animals in the field, was performed outside
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981 issued at 11.04.2008). The contract bears a permission to collect the reptile samples outside of
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983   extra permissions. Specimen collection protocols and animal operations followed the
984   Institutional Ethical Committee of International Center for Science, High Technology and
985   Environmental Sciences, Kerman, Iran (certificate number 1.87-1).
986

DNA Deposition

988   The following information was supplied regarding the deposition of DNA sequences:
989   Sequences of 12S–16S rRNA and cyt *b* genes presented here are accessible via GenBank
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991

Data Availability

993   The following information was supplied regarding data availability:
994   Specimens examined in this study are deposited in herpetological collections of the following
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996   1. CAS: California Academy of Sciences, San Francisco, USA;
997   2. CUHC: Comenius University Herpetological Collection, Bratislava, Slovakia;
998   3. MMB: Department of Zoology, Moravian Museum, Brno, Czech Republic;
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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

1419 Table Legends:

1420

1421 **Table 1. Sequences and voucher specimens of *Oligodon* and outgroup taxa used in**
1422 **molecular analyses of this study.**
1423 Note that the numbers (column one) included in this table are not the same as those found in
1424 other tables or figures. Acronyms present here that are not noted in the materials and methods
1425 include the following: CHS, unknown field tag series; KIZ, Kunming Institute of Zoology,
1426 Chinese Academy of Sciences, Kunming, China; NCBS, National Center for Biological
1427 Sciences, Bangalore, India; RAP, field tags of R. Alexander Pyron; ROM, Royal Ontario
1428 Museum, Toronto, Canada; RS, field tags of Ruchira Somaweera; SIEZC, Department of
1429 Zoology, Southern Institute of Ecology, Ho Chi Minh City, Vietnam; SYNU, Shenyang Normal
1430 University, Shenyang, China; TNHC, Texas Natural History Collections, Austin, USA; UMMZ,
1431 University of Michigan Museum of Zoology, Ann Arbor, USA; ZMUVAS, Zoological Museum
1432 of the University of Veterinary and Animal Sciences, Punjab, Pakistan. Additional abbreviations
1433 include NP: National Park, NR: Nature Reserve, and WS: Wildlife Sanctuary.

1434

1435 **Table 2. Selected morphological characters of *Oligodon transcaspicus* comb. et stat. nov.**
1436 **based on examined specimens.**
1437 Abbreviations for males and females are denoted by (m) or (f) respectively. For abbreviations of
1438 characters, see materials and methods section for details.

1439

1440 **Table 3. Morphological comparisons of *Oligodon russelius* specimens from Afghanistan,**
1441 **northern India, and Pakistan hitherto recognized as *Oligodon* "arnensis" or *Oligodon***
1442 **churahensis.**
1443 Data from the literature are combined from multiple authors unless denoted with an asterisk (*),
1444 which indicates that only a single source was used. Abbreviations for males and females are
1445 denoted by (m) or (f) respectively and (total) is used to indicate that the data combines both
1446 sexes or combines the total number of body and tail blotches.

1447

1448 **Table 4. Pairwise matrix of genetic distances between and within *Oligodon* species sampled**
1449 **in this study.**
1450 Uncorrected p-distances (given as percentages) are based on sequences of the cytochrome *b*
1451 mtDNA gene are shown below the diagonal. Intraspecific genetic p-distances are shown along
1452 the diagonal and are highlighted in bold. See Table 1 for the list of samples used to create this
1453 matrix.

1454

1455   Figure Legends:

1456

1457   **Figure 1. Approximate distribution and location of samples utilized in this study for**

1458   **molecular and morphological analyses (A); and approximate distribution of *Oligodon***

1459   ***transcaspicus* comb. et stat. nov in the Köpet–Dag Mountain range of Iran and**

1460   **Turkmenistan (B).**

1461   Triangle icons denote specimens with only molecular data; square icons denote specimens with

1462   only morphological data; rhombic icons denote specimens without molecular and morphological

1463   data (only locality is known); round icons denote specimens with both molecular and

1464   morphological data. Stars/asterisks next to numbers indicate type localities. Localities: (1)

1465   Ashgabat, Ahal Prov., Turkmenistan (type locality of *Oligodon transcaspicus* **comb. et stat.**

1466   **nov**); (2) Chuli, Ahal Prov., Turkmenistan; (3) Geok-Tepe, Ahal Prov., Turkmenistan; (4)

1467   Karanki, Ahal Prov., Turkmenistan; (5) "Goalon" (Goudan), Ahal Prov., Turkmenistan; (6)

1468   Aidere, Ahal Prov., Turkmenistan; (7) Bazangan Lake, Razavi Khorasan Prov., Iran; (8) Punjab

1469   Prov., Pakistan; (9) Kallar Kahar, Punjab Prov., Pakistan; (10) Chamba Distr., Himachal

1470   Pradesh, India (type locality of *Oligodon churahensis*); (11) Jalalabad, Nangarhar Prov.,

1471   Afghanistan; (12) Dara-i-Pech district, Kunar Prov., Afghanistan; (13) Maharashtra, India; (14)

1472   Chitwan NP, Bagmati Prov., Nepal; (15) Ganjam, Odisha, India; (16) 24.1 km SW of

1473   Rajamahendravaram, Andhra Pradesh, India; (17) Bangalore, Karnataka, India; (18) Tamil Nadu,

1474   India; (19) Puttalam Distr., North Western Prov., Sri Lanka; (20) Udawalawe National Park, Uva

1475   Prov.; (21) Monargala Distr., Southern Prov., Sri Lanka; (22) Hambantota Distr., Southern Prov.,

1476   Sri Lanka; (23) Gampaha Distr., Western Prov., Sri Lanka; (24) Polonnaruwa Distr., North

1477   Central Prov., Sri Lanka; (25) Paramikulam, Kerala, India; (26) Barengabari, Assam, India.

1478

1479   **Figure 2. Phylogenetic tree of *Oligodon* derived from the analysis of 3,019 bp of 12S rRNA,**

1480   **16S rRNA and cyt *b* mitochondrial DNA gene sequences.**

1481   For voucher specimen information and GenBank accession numbers see Table 1. Numbers at

1482   tree nodes correspond to BI PP/ML BS support values, respectively; n-dash denotes no support.

1483   Outgroup taxa are not shown. Colors of clades and locality numbers correspond to Figure 1.

1484

1485   **Figure 3. Species distribution model (SDM) map based on geolocation points of *Oligodon***

1486   ***transcaspicus* comb. et stat. nov. from Iran and Turkmenistan.**

1487   Darker red coloration indicates more suitable habitat, whereas lighter colors indicate less suitable

1488   habitat.

1489

1490   **Figure 4. Photographs of the preserved holotype specimen of *Contia transcaspica* (ZISP**

1491   **9868) now *Oligodon transcaspicus* comb. et stat. nov. from "Köpet–Dag, Transcaspica".**

1492   Scale bars equal 10 millimeters. Photos by Konstantin D. Milto.

1493

1494 **Figure 5. Live photographs of *Oligodon transcaspicus* comb. et stat. nov. (ZMMU Re-**
1495 **16687; field number RAN-3264) from Khorasan Province, Iran.**
1496 (a) Right lateral, (b) left lateral, (c) ventral, (d) ventral views of the head, and (e) general habitus.
1497 Photographs by Roman A. Nazarov.
1498
1499 **Figure 6. Two unvouchered specimens of *Oligodon transcaspicus* comb. et stat. nov.**
1500 Specimens photographed from (a) Podere, Sumbar Valley, Turkmenistan and (b) Seqiz-Khan
1501 Gorge, Turkmenistan. Photographs taken by Alexander V. Pavlenko.
1502
1503 **Figure 7. Photographs of *Oligodon russelius* from Pakistan (a–e) and Afghanistan (f).**
1504 Shown in a–e is specimen CUHC 7904 from Kallar Kahar, Punjab Province, Pakistan, showing
1505 (a) general habitus in life, (b) right lateral, (c) left lateral, (d) dorsal, and (e) ventral views of the
1506 head in preservative. Shown in (f) is a cropped image of *O. russelius* from Kunar Province,
1507 Afghanistan observed on iNaturalist (obs. 110932106, user mohammadfarooq). Photographs a–e
1508 by Daniel Jablonski, photograph f taken by Mohammad Farooq from iNaturalist.org.
1509
1510
1511

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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5 field tags of R. Alexander Pyron; ROM, Royal Ontario Museum, Toronto, Canada; RS, field tags of Ruchira Somaweera; SIEZC,

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7 China; TNHC, Texas Natural History Collections, Austin, USA; UMMZ, University of Michigan Museum of Zoology, Ann Arbor,

8 USA; ZMUVAS, Zoological Museum of the University of Veterinary and Animal Sciences, Punjab, Pakistan. Additional

9 abbreviations include NP: National Park, NR: Nature Reserve, and WS: Wildlife Sanctuary.

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

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

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. 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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2 **northern India, and Pakistan hitherto recognized as *Oligodon* "*arnensis*" or *Oligodon***
3 ***churahensis*.**
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5 which indicates that only a single source was used. Abbreviations for males and females are
6 denoted by (m) or (f) respectively and (total) is used to indicate that the data combines both
7 sexes or combines the total number of body and tail blotches.

Morphology	CUHC 7904	MMB 28497	*O. churahensis*	*O. russelius*	Pakistan *O.* "*arnensis*"	West Himalayan *O.* "*arnensis*"
Location	Kallar Kahar, Punjab Province, Pakistan	Jalalabad, Nangarhar, Afghanistan	Churah Valley, Himachal Pradesh, India	Northern and Eastern India	Northern and Southern Pakistsan	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*)

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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.

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

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4 used to create this matrix.

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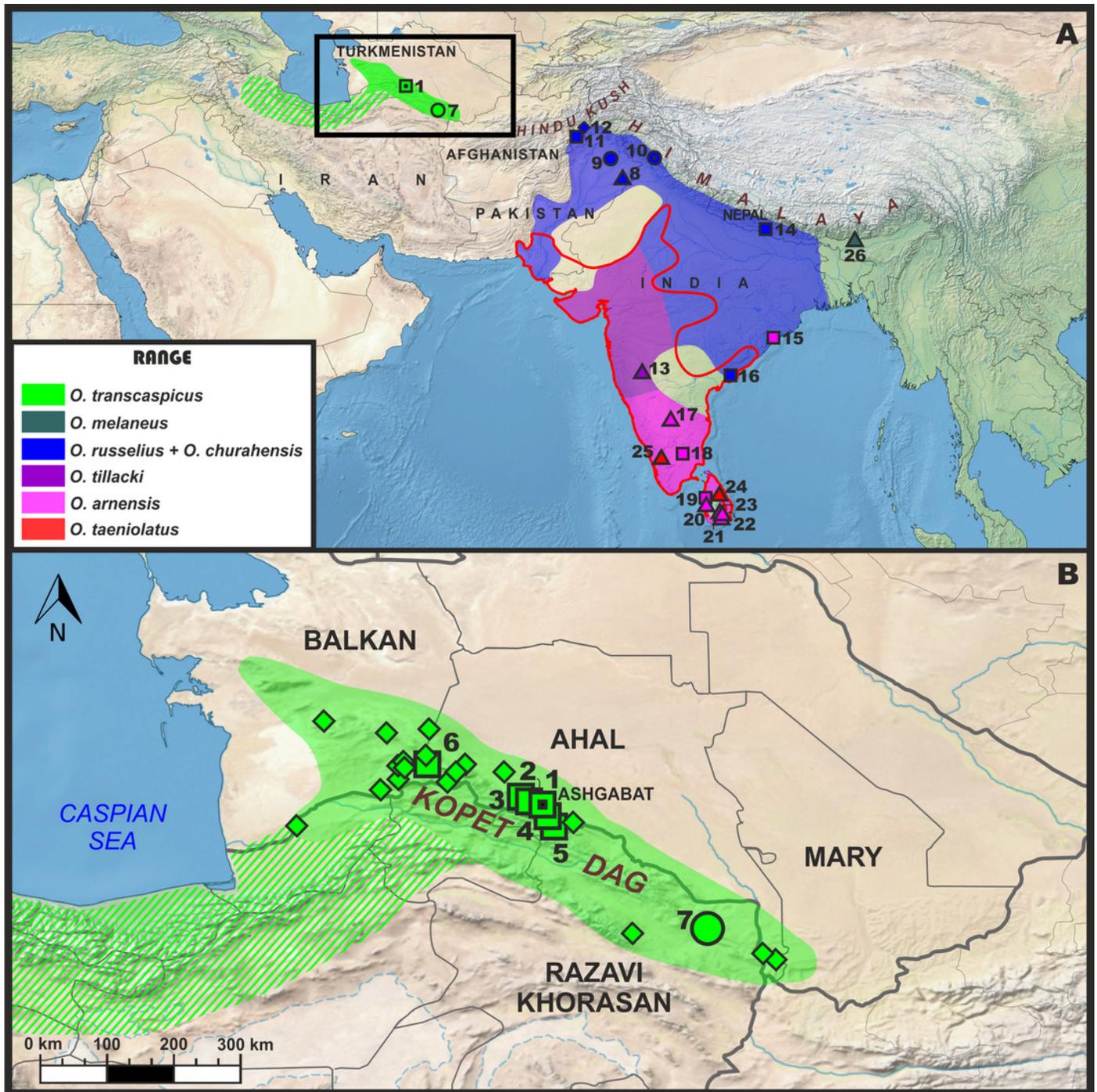
Figure 2

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.
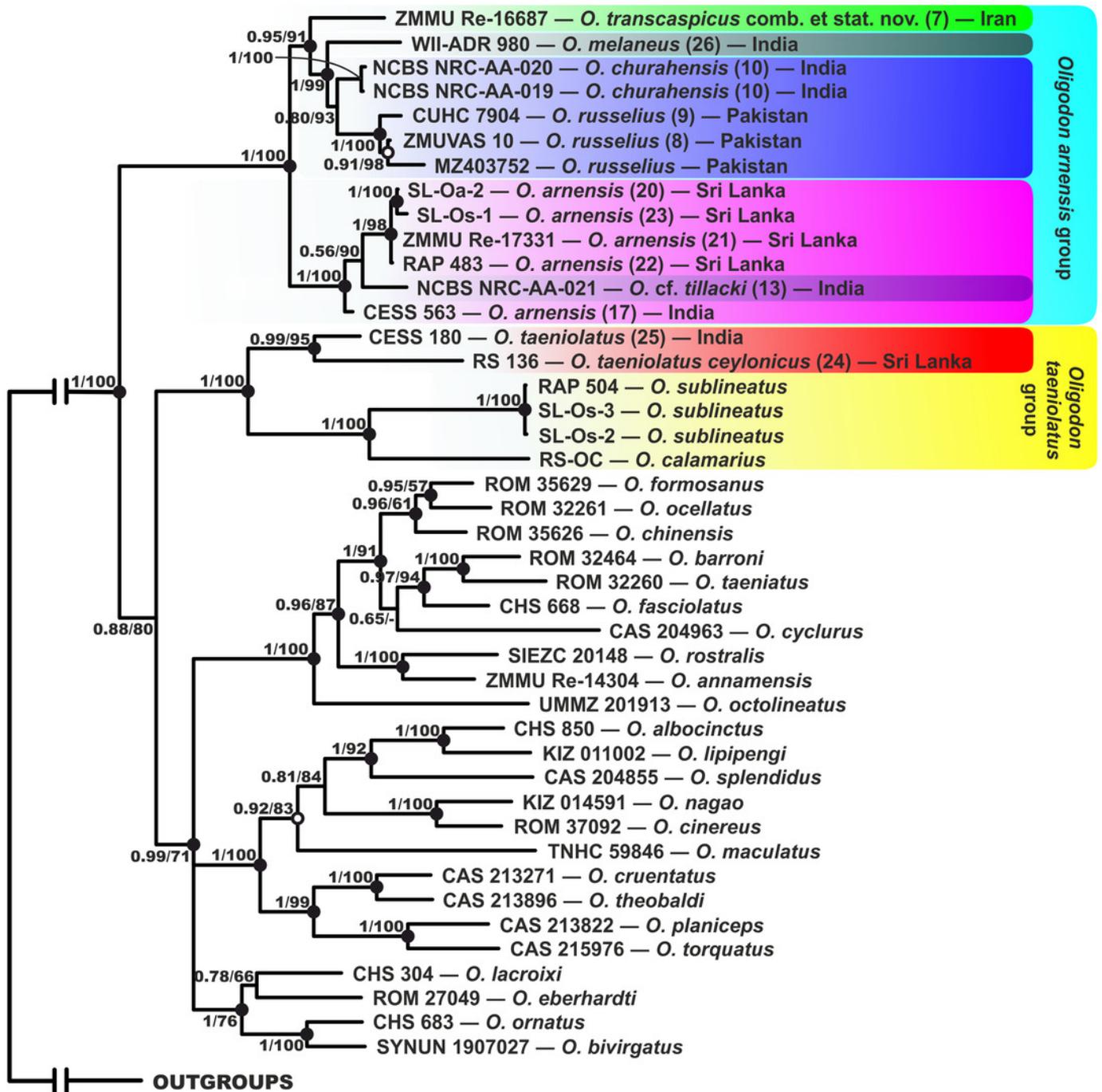
Figure 3

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.
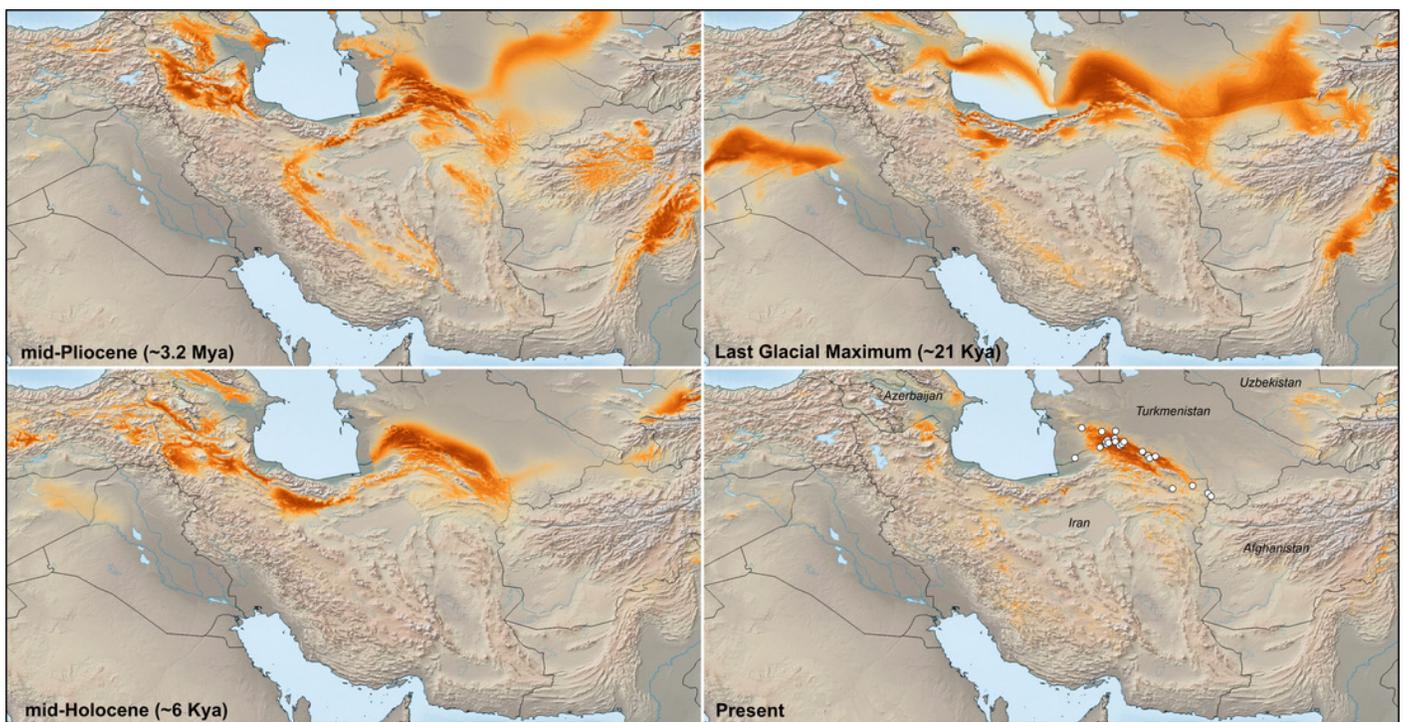
Figure 4

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.
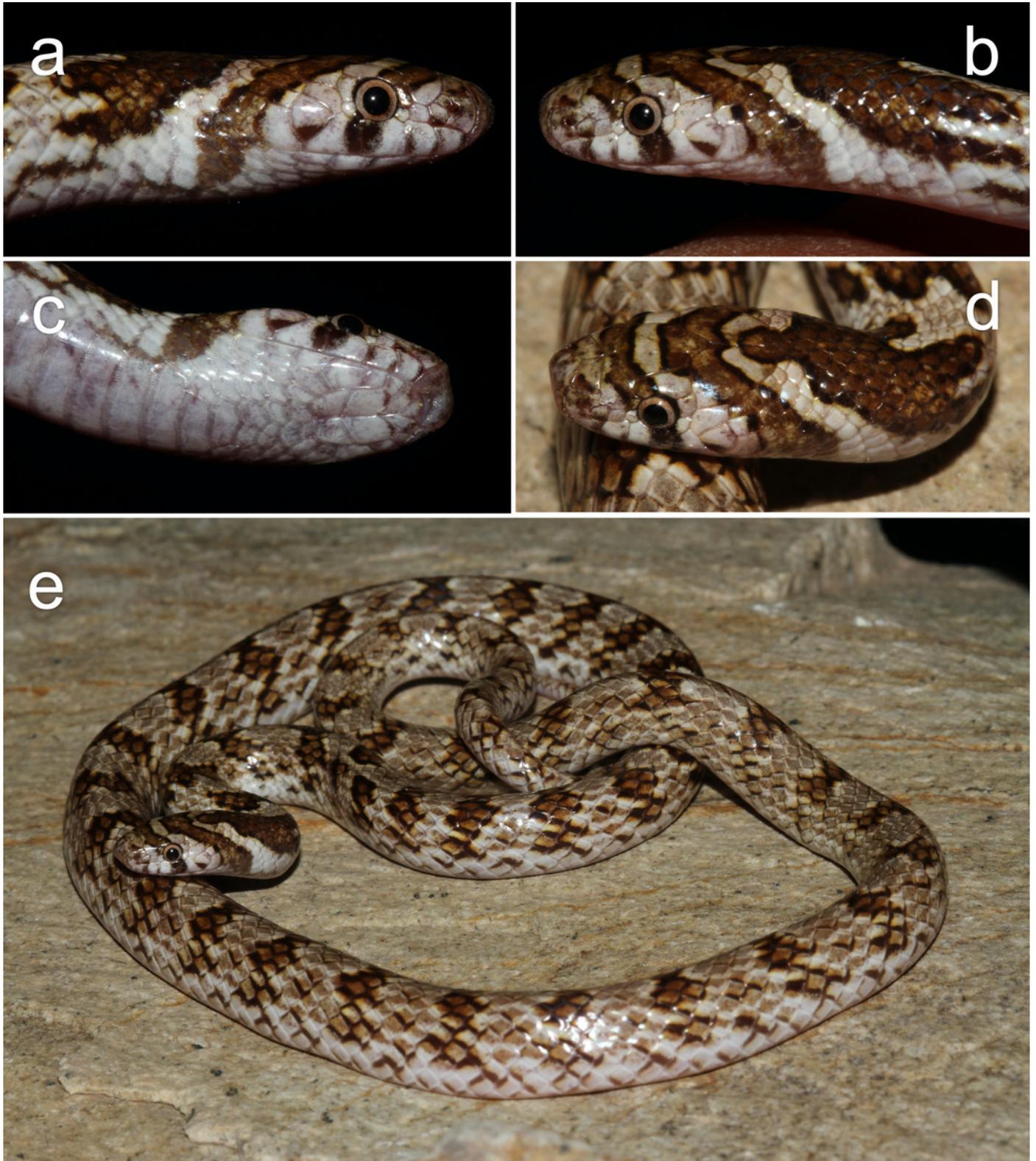
Figure 6

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.