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 (Afghanistan, Iran, and Turkmenistan), and the Palearctic portions of Pakistan. In this paper, we review the systematics 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, molecular, and species distribution modeling (SDM) data. Phylogenetic analyses recover *O. taeniolatus* populations from Iran and Turkmenistan in a clade with the *O. arnensis* species complex, rendering the former species paraphyletic relative to *O. taeniolatus* sensu stricto on the Indian subcontinent. To correct this, we resurrect the name *Contia transcaspica* Nikolsky, 1902 from the synonymy of *O. taeniolatus* and assign it to populations in Middle–Southwest Asia. So far, *Oligodon transcaspicus* **comb. et stat. nov.** is known only from the Köpet–Dag Mountain Range of northeast Iran and southern Turkmenistan, but SDM mapping suggests it may have a wider range. Genetic samples of *O. "arnensis"* from northern Pakistan are nested in a clade sister to the recently described

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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 complexes on the Indian subcontinent, and an updated key for both groups is provided.

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Abstract

36 The kukri snakes of the genus *Oligodon* Fitzinger, 1826 reach the westernmost limits of their
37 distribution in Middle and Southwest Asia (Afghanistan, Iran, and Turkmenistan), and the
38 Palearctic portions of Pakistan. In this paper, we review the systematics and distribution of the
39 two species native to this region, *Oligodon arnensis* (Shaw, 1802) and *Oligodon taeniolatus*
40 (Jerdon, 1853) based on an integrative approach combining morphological, molecular, and
41 species distribution modeling (SDM) data. Phylogenetic analyses recover *O. taeniolatus*
42 populations from Iran and Turkmenistan in a clade with the *O. arnensis* species complex,
43 rendering the former species paraphyletic relative to *O. taeniolatus* sensu stricto on the Indian
44 subcontinent. To correct this, we resurrect the name *Contia transcaspica* Nikolsky, 1902 from
45 the synonymy of *O. taeniolatus* and assign it to populations in Middle–Southwest Asia. So far,
46 *Oligodon transcaspicus* **comb. et stat. nov.** is known only from the Köpet–Dag Mountain Range
47 of northeast Iran and southern Turkmenistan, but SDM mapping suggests it may have a wider
48 range. Genetic samples of *O. "arnensis"* from northern Pakistan are nested in a clade sister to
49 the recently described *Oligodon churahensis* Mirza, Bhardwaj & Patel, 2021, and are
50 phylogenetically separate from *O. arnensis* sensu stricto in south India and Sri Lanka. Based on
51 morphological similarity, the Afghanistan and Pakistan populations are assigned to *Oligodon*
52 *russelius* (Daudin, 1803) and we synonymize *O. chuarhensis* with this species. Our investigation
53 leads us to remove *O. taeniolatus* from the snake fauna of Afghanistan, Iran, and Turkmenistan,
54 with the consequence that only *Oligodon transcaspicus* **comb. et stat. nov.** and *O. russelius* are
55 present in these countries. Additional studies are needed to resolve the taxonomy of the *O.*
56 *taeniolatus* and *O. arnensis* species complexes on the Indian subcontinent. An updated key to the
57 *O. arnensis* species complex and related species is provided.

Keywords

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

Introduction

62   Knowledge of the snake fauna of Middle and Southwest Asia (here considered the
63 countries of Afghanistan, Iran, western China, Mongolia and the former Soviet Middle Asian
64 republics fide Berg, 1931; Geptner, 1938; Chernov, 1949) has improved over the past decade as
65 researchers continue to contribute species descriptions, range extensions, and natural history
66 observations (Wagner et al., 2016a; Rajabizadeh, 2018; Shestopal & Rustamov, 2018a;
67 Shestopal & Rustamov, 2018b; Orlov et al., 2018; Asadi et al., 2019; Rajabizadeh et al., 2020;
68 Eskandarzadeh et al., 2020; Chen et al., 2021). Biogeographically, most snakes inhabiting
69 Middle–Southwest Asia are elements of the Palearctic; however, a few species traditionally
70 associated with the Indo-Malayan (Oriental) realm reach their westernmost distributional limits
71 in this region (Wagner et al., 2016b; Orlov et al., 2018). The kukri snakes of the genus *Oligodon*
72 Fitzinger, 1826 are one such example. Normally found across tropical portions of South and

73   Southeast Asia, two species of this diverse colubrid radiation extend into Afghanistan,
74   northeastern Iran, and southern Turkmenistan (Latifi, 1991; Green, 2010; Wagner et al., 2016b;
75   Orlov et al., 2018; Bandara et al., 2022; Uetz et al., 2023).
76   The first species, the banded kukri snake *Oligodon arnensis* (Shaw, 1802), is common
77   across the Indian subcontinent but a single specimen from Afghanistan is known (Král, 1969;
78   Wagner et al., 2016b). This species was recently divided into three taxa by Bandara et al. (2022),
79   who published a revision of *O. arnensis* sensu auctorum based largely on morphology. These
80   authors restricted *O. arnensis* sensu stricto to southern India and Sri Lanka; moreover, they
81   described a new species *Oligodon tillacki* Bandara, Ganesh, Kanishka, Danushka, Sharma,
82   Campbell, Ineich, Vogel & Amarasinghe, 2022 (Tillack's kukri snake) for *O. arnensis*
83   populations in western India, and resurrected the name *Oligodon russelius* (Daudin, 1803)
84   (Russell's kukri snake) for populations in northern/eastern India, Bangladesh (Barkat & Rabbe,
85   2022) and Nepal (Rai, Adhikari & Antón, 2022). Additionally, Mirza, Bhardwaj & Patel (2021)
86   described another species related to *O. arnensis* from the western Himalayan foothills of India,
87   *Oligodon churahensis* Mirza, Bhardwaj & Patel, 2021 (Churah Valley kukri snake). These latter
88   authors included mitochondrial DNA (mtDNA) sequences of *O. "arnensis"* from Pakistan that
89   were closely related to their new species (~3.3% genetic divergence based on the cytochrome *b*
90   gene) but were unable to examine the vouchers corresponding to these samples and tentatively
91   identified them as *O.* cf. *churahensis*. Although these studies have shed light on the taxonomic
92   nature of *O. arnensis*, they both neglected the status of specimens from Pakistan and
93   Afghanistan. We refer to these populations as *O. "arnensis"* until our clarifications in the results.
94   The second species, the streaked kukri snake *Oligodon taeniolatus* (Jerdon, 1853), also
95   inhabits the Indian subcontinent, but westward localities are known from northern Iran, southern
96   Turkmenistan, and possibly Afghanistan (Latifi, 1991; Wagner et al., 2016b; Orlov et al., 2018).
97   Like *O. "arnensis"*, *O. taeniolatus* is phenotypically variable across its range and contains
98   multiple color morphotypes that have been recognized as synonyms or subspecies by past
99   authors (Wall, 1921; Wall, 1923; Smith, 1943; Taylor, 1950). The complicated nomenclatural
100   history of *O. taeniolatus* was reviewed by Bauer (2003). In that review, Bauer (2003) designated
101   a lectotype for the species based on an illustrated specimen depicted in Russell (1796) with the
102   type locality "Vizagapatam" (now Visakhapatnam, Andhra Pradesh, India), thereby restricting
103   'true' (nominotypical) *O. taeniolatus* to eastern India. Outside of the Indian subcontinent,
104   populations of *O. taeniolatus* in Iran and Turkmenistan can be referred to the name *Contia*
105   *transcaspica* Nikolsky, 1902, described based on a single specimen collected from "Köpet–Dag,
106   Transcaspia" [=now Köpet–Dag Mountain Range, near Ashgabat, Ahal Province,
107   Turkmenistan]. Chernov (1935) considered *C. transcaspica* to be a junior synonym of *O.*
108   *taeniolatus*, owing to similarities between Turkmen and Indian specimens. Later authors would
109   follow this decision and report *Oligodon* populations from Turkmenistan and neighboring Iran as
110   *O. taeniolatus* (Terentjev & Chernov, 1949; Bogdanov, 1962; Bannikov et al., 1977; Dotsenko,
111   1984; Atayev, 1985; Szczerbak, Khomustenko & Golubev 1986; Latifi, 1991; Rustamov &
112   Sopyev, 1994; Szczerbak, 1994; Atayev, Rustamov & Shammakov, 1994). The name *Contia*

113 *transcaspica* has rarely been mentioned since and was neglected in the synonymy of *O.*
114 *taeniolatus* by Wallach, Williams & Boundy (2014). Since Chernov (1935), only a few sources
115 (Dotsenko, 1984; Latifi, 1991; Latifi, 2000; Rajabizadeh, 2018) have provided additional
116 descriptive data on *O. taeniolatus* from Iran and Turkmenistan. Though their accounts do not
117 make direct comparisons with Indian material, it is apparent that specimens from Middle and
118 Southwest Asia do not accord well with the traditional definition of *O. taeniolatus* (Wall, 1921;
119 Wall, 1923; Smith, 1943).
120   In this study, we review the taxonomy, phylogenetic relationships, and distributional
121 limits of the genus *Oligodon* at the westernmost end of its range. Our geographic focus includes
122 all Middle and Southwest Asian countries inhabited by kukri snakes, in addition to Pakistan,
123 which is traditionally part of South Asia but still encompasses part of the western Palearctic and
124 contains the same species treated here. Chiefly, we aim to clarify the status of *O. taeniolatus*
125 populations historically associated with the name *Contia transcaspica* from Iran and
126 Turkmenistan and resolve the status of *Oligodon "arnensis"* populations from Pakistan and
127 Afghanistan, which were neglected by the latest taxonomic revisors.

Materials & Methods

129 **Sampling and species delimitation**. Fieldwork which resulted in the collection of *Oligodon* in
130 Iran was conducted by RAN and MR during a field trip in May 2017 to Razavi, Khorasan
131 Province, Iran (locality 7, Figure 1). Fieldwork in Pakistan was conducted by DJ and RM during
132 a field trip in September 2018 to Punjab Province, Pakistan. Fieldwork in Sri Lanka was
133 conducted by SK and NAP during field trips between February 2018 and December 2020 to the
134 dry and wet zones of the country. Collected specimens were euthanized using a 20% solution of
135 benzocaine and fixed in formalin before being transferred into 70% ethanol for storage. Before
136 preservation, a small sample of muscle tissue was taken from each snake and stored in 95%
137 ethanol for subsampling and DNA extraction. For molecular phylogenetic analyses, we included
138 one sample of *O. taeniolatus* (referrable to *Contia transcaspica*) from Iran (ZMMU Re-16687);
139 one sample of nominotypical *O. taeniolatus* from India (CESS-180); four novel samples of *O.*
140 *arnensis* sensu stricto from India (CESS-563) and Sri Lanka (SL-Os-1, SL-Oa-2; ZMMU Re-
141 17331); two novel samples of *O. sublineatus* Duméril, Bibron & Duméril, 1854 from Sri Lanka
142 (SL-Os-2; SL-Os-3); and one novel sample morphologically resembling *Oligodon russelius* from
143 Punjab Province, Pakistan (CUHC 7904; locality 9, Figure 1). In addition, we included 53
144 publicly available sequences of other *Oligodon* species retrieved from GenBank (Table 1).
145 Bandara et al. (2022) noted that one sample (NCBS-NRC-AA-021) previously identified as *O.*
146 *"arnensis"* may represent *O. tillacki* but did not examine this specimen. As such, we re-identify
147 this specimen as *O.* cf. *tillacki* herein (see Discussion). For outgroup taxa, we chose one sample
148 each of *Oreocryptophis porphyraceus* (Cantor, 1839) (subfamily Colubrinae) and *Hebius*
149 *vibakari* (Boie, 1826) (subfamily Natricinae) due to their use in previous phylogenies of
150 *Oligodon* published in the literature (Nguyen et al., 2020; Yushchenko & Lee et al., 2023a,
151 2023b).

152   We examined the morphology of seven *O. taeniolatus* specimens available to us from
153   Iran and Turkmenistan, including the name-bearing type of *Contia transcaspica* (localities 1–7,
154   Figure 1). To compare these populations with typical members of the *O. arnensis* species
155   complex (sensu Bandara et al., 2022), we examined two specimens within the range of *O.*
156   *russelius* from Andhra Pradesh, India, and southern Nepal (localities 14–16, Figure 1), five
157   specimens of *O. arnensis* sensu stricto from southern India and Sri Lanka (localities 18–19,
158   Figure 1) (see Supplementary Material 1), and a new specimen of *O. russelius* collected from
159   Pakistan (locality 9, Figure 1). Additional morphological data for *O. taeniolatus*, the *O. arnensis*
160   species complex, and other taxa were derived from relevant literature sources (see
161   Morphological analyses). For aspects of species concepts and delimitation, we act in accordance
162   with an integrative taxonomic approach (Padial et al., 2010), where the delimitation of a species
163   is supported by a combination of morphological, molecular, and ecological evidence.
164   Furthermore, we follow the General Lineage Concept (de Queiroz, 2007), where a species
165   represents a single independent lineage following a separate evolutionary trajectory compared to
166   its congeners. Criteria we used to support the existence of evolutionary independence include
167   discrete morphological separation, substantial genetic divergence based on standard genetic
168   markers, and evidence of monophyly when phylogenetically compared with other congeners.
169   The following acronyms for museum and natural history collections are used in the text:
170   CAS: California Academy of Sciences, San Francisco, USA; CUHC: Comenius University
171   Herpetological Collection, Bratislava, Slovakia; MMB: Department of Zoology,
172   Moravian Museum, Brno, Czech Republic; USNM: National Museum of Natural History,
173   Washington, DC, USA; ZISP: Zoological Institute of Russian Academy of Sciences, St.
174   Petersburg, Russia; ZMMU: Zoological Museum of Moscow State University, Moscow, Russia.
175   Additional abbreviations for genetic samples and voucher specimens can be found in Table 1.
176   Permission to conduct fieldwork in Iran, including collection of samples and animals in
177   the field, was performed outside of any protected area, in the framework of a project contract
178   signed by International Center for Science, High Technology and Environmental Sciences,
179   Kerman, Iran (contract number 1.87, issued 11.04.2008). This contract bears permission to
180   collect reptile samples outside of any protected area of the Department of the Environment
181   (specified in www.doe.ir) that require extra permissions. Specimen collection protocols and
182   animal operations followed the Institutional Ethical Committee of International Center for
183   Science, High Technology and Environmental Sciences, Kerman, Iran (certificate number 1.87-
184   1). Fieldwork to collect specimens in Pakistan was conducted under the permit of the Pakistan
185   Museum of Natural History, Islamabad, Pakistan (No. PMNH/EST-1[89]/05). In Sri Lanka,
186   permission to conduct fieldwork was granted by the Department of Wildlife Conservation and
187   Department of Forest Conservation (WL/3/2/1/14/12).
188
189   **Molecular analyses.** Methods for DNA sequencing and molecular phylogenetic analyses are
190   adapted from previous studies (Yushchenko and Lee et al., 2023a, 2023b). We extracted total
191   genomic DNA of novel samples from muscle tissue preserved in 95% ethanol using a Qiagen

192 DNAeasy Blood and Tissue Kit following manufacturer protocols. We performed polymerase
193 chain reactions (PCRs) on extracted DNA to amplify two fragments of mitochondrial DNA
194 (mtDNA): the first fragment including partial sequences of 12S ribosomal RNA (rRNA), transfer
195 RNA (tRNA)-Valine and 16S rRNA (total length up to 1,930 bp), and a second fragment
196 including the complete sequence of the gene Cytochrome *b* (cyt *b*) (1,091 bp). Primers used for
197 PCRs and sequencing are summarized in Table S2. PCR protocols for 12S–16S rRNA fragments
198 were adapted from Green et al. (2010). For both primer pairs of 12S and 16S rRNA, we used the
199 following PCR protocols: (1) initial denaturation step at 94°C for 5 min; (2) 35 cycles of
200 denaturation at 94°C for 1 min, annealing at 55°C for 1 min and extension at 72°C for 1 min; (3)
201 final extension at 72°C for 10 min; and (4) cooling step at 4°C for storage. For cyt *b* sequences,
202 we used a modified PCR protocol of Chen et al. (2014) with touchdown: (1) initial denaturation
203 step at 94°C for 5 min; (2) 10 cycles of denaturation at 94°C for 1 min, annealing for 1 min with
204 temperature decreasing from 50°C to 45°C (with cool-down at 0.5°C per each cycle) and
205 extension at 72°C for 1 min; (3) 24 cycles of denaturation at 94°C for 1 min, annealing at 45°C
206 for 1 min and extension at 72°C for 1 min; (4) final extension at 72°C for 10 min; and (5)
207 cooling step at 4°C for storage. All PCR products were sequenced in both directions by the
208 Evrogen company at the Institute of Bioorganic Chemistry, Russian Academy of Sciences
209 (Moscow, Russia) and at Macrogen Europe (Amsterdam, The Netherlands;
210 http://www.macrogen-europe.com). Sequences were assembled and checked using Sequencher
211 4.9 (GeneCodes). The obtained sequences are deposited in GenBank under the accession
212 numbers OQ092426; OQ099833–OQ099837; and OQ116816–OQ116825 (Table 1).
213   To examine the position of *O. taeniolatus* from Turkmenistan and Iran in a matrilineal
214 genealogy of the genus, we combined newly obtained sequences with all publicly available
215 GenBank sequences of *O. arnensis*, *O. churahensis*, *O. taeniolatus*, *O.* cf. *tillacki* and one
216 sequence per species of other *Oligodon* (summarized in Table 1). The morphological identities of
217 some samples remain unverified due to a lack of voucher material. In total, we analyzed mtDNA
218 sequences of 45 specimens, including 43 samples of 33 species of *Oligodon*, with outgroup
219 sequences of *Oreocryptophis porphyraceus* and *H. vibakari* from GenBank used to root the tree.
220 Nucleotide sequences were initially aligned in MAFFT v.7 (Katoh et al., 2002) with default
221 parameters, and subsequently checked by eye in BioEdit 7.0.5.2 (Hall, 1999) and slightly
222 adjusted for translation when appropriate. We used IQ-TREE web server
223 (http://iqtree.cibiv.univie.ac.at/; Trifinopoulos et al. 2016) to estimate optimal evolutionary
224 models for the data set analysis using the Akaike Information Criterion (AIC). Mean uncorrected
225 genetic distances (p-distances) were calculated in MEGA 7.0 (Kumar, Stecher & Tamura, 2016).
226 The matrilineal genealogy was inferred using Bayesian inference (BI) and Maximum Likelihood
227 (ML) approaches. The best-fitting model for both BI and ML analyses for 12S–16S rRNA
228 fragments and for the second codon partition of cyt *b* was the GTR+G+I model as of DNA
229 evolution suggested by the AIC. For the remaining portions of cyt *b*, the AIC suggested the
230 GTR+G model for the first codon partition, and the HKY+G+I for the third codon partition.

231   The ML analysis was conducted using the IQ-TREE web server (Trifinopoulos et al.,
232   2016). BI analysis was conducted in MrBayes 3.2.2 (Ronquist et al., 2012). For the BI analysis,
233   Metropolis-coupled Markov chain Monte Carlo (MCMCMC) analyses were ran with one cold
234   chain and three heated chains for one million generations and sampled every 1000 generations.
235   Two independent MCMCMC run iterations were performed and 100 trees were discarded as
236   burn-in. The convergence of the runs was checked by exploring and examining likelihood plots
237   in TRACER v1.6 (Rambaut et al., 2020), with effective sample sizes (ESS) all above 200. Nodal
238   support for the BI analysis was assessed by calculating posterior probabilities (BI PP). We *a*
239   *priori* regarded tree nodes with BI PP values over 0.95 as sufficiently resolved, whereas BI PP
240   values between 0.95 and 0.90 were regarded as tendencies. For ML analysis, confidence in nodal
241   topology was estimated via the ultrafast bootstrap approximation algorithm (UFBS; Hoang et al.,
242   2018) with 1,000 bootstrap pseudoreplicates. Nodes having ML UFBS values of 95 and above
243   were *a priori* considered highly supported, nodes with values of 90–94 were considered well-
244   supported, and nodes with values of 70–89 were considered as tendencies. Lower values were
245   regarded as indicating unresolved nodes (Huelsenbeck & Hillis, 1993).
246
247   **Morphological analysis**. Coloration and pattern were recorded during examination of preserved
248   specimens. For some specimens, live coloration was also recorded from digital images taken
249   before preservation. No statistical analyses were performed between species due to the low
250   sample size of comparative material. All body measurements, except body and tail lengths, were
251   taken under a dissecting microscope using a digital slide-caliper to the nearest 0.1 mm. Body and
252   tail lengths were measured to the nearest millimeter by straightening snakes along a flexible
253   ruler. Methodology for counting ventral and subcaudal scales follow Dowling (1951). The tail tip
254   was not included in the number of subcaudals. Head scale suture angle protocols follows that of
255   Kaiser, O'Shea & Kaiser (2019). Maxillary teeth were counted by examination of the dissected
256   maxillary bone when available, or by carefully removing the gum layer of the maxilla. Sex was
257   determined by ventral incision below the vent to detect the presence or absence of hemipenes.
258   Our data on specimens referrable to *Contia transcaspica* were compared and reviewed with
259   relevant literature on *O. taeniolatus* across its distribution (Nikolsky, 1902; Nikolsky, 1903a;
260   Wall, 1921; Wall, 1923; Chernov, 1935; Smith, 1943; Minton, 1966; Dotsenko, 1984; Latifi,
261   1991; Khan, 2002).
262   Linear morphometric data of examined specimens were collected as previously described
263   by Nguyen et al. (2020) and Yushchenko and Lee et al. (2023a, 2023b). Specifically, the
264   following linear measurements (all in mm) were taken: snout to vent length (SVL) ─ measured
265   from the tip of the snout to the vent; tail length (TailL) ─ measured from the vent to the tip of
266   the tail; total length (TotalL) ─ sum of SVL and TailL; relative tail length to total length
267   (TailLR) calculated as tail length to total length ratio; head length (HeadL) from the tip of the
268   snout to the posterior margin of the mandible; head width (HeadW) measured at the widest part
269   of the head immediately posterior to the eye; snout length (SnoutL) ─ distance between the tip
270   of the snout and anterior edge of eye; eye diameter (EyeD) ─ maximal horizontal length of the

271   eye; frontal scale length (FrontalL); frontal scale width (FrontalW); distance (IOD) — the
272   shortest distance between the eyes; and internarial distance (IND) — distance between the
273   nostrils. Morphological characters examined also follow past descriptions of Yushchenko and
274   Lee et al. (2023a, 2023b), and include the number of maxillary teeth (MT); anterior scale rows
275   (ASR) — namely number of scale rows at one head length behind the head; midbody scale rows
276   (MSR) — the number of scale rows at midbody (namely halfway between the measured snout-
277   vent length); posterior scale rows (PSR) — number of dorsal scale rows at one head length prior
278   to the vent; dorsal scale row formula (DSR) — a given acronym summarizing the three dorsal
279   scale row counts (i.e., ASR–MSR–PSR); ventral scales (VEN) — the number of ventral scales
280   starting from the scale contacting the first dorsal scale row to the vent, excluding the cloacal
281   plate; subcaudal scales (SC) — the number of paired subcaudal scales excluding the terminal
282   scute; total body scales (TOTAL) — the sum of ventral, subcaudal scales and the cloacal plate
283   (included as one scale regardless of whether the plate is single or divided); subcaudal ratio (SCR)
284   — namely the ratio between the number of subcaudal scales and the number of total body scales
285   given as a decimal value; cloacal plate (CP) — the number of terminal ventral scales
286   immediately anterior to vent (given as single for one scale, and divided for two scales); condition
287   of nasal scale (NASAL) — given as either vertically divided, entire, or partially divided;
288   condition of loreal scale (LOREAL) — given as present or absent; supralabials (SL) — the
289   number of scales on upper lip; number of supralabials in contact with the eye (SL-Eye);
290   infralabials (IL) — the number of scales on lower lip; infralabials contacting each other (IL-
291   contact) — the number of pairs of infralabial scales in contact; infralabials contacting the
292   anterior chin shields (IL-CS) — the number of infralabial scales contacting the anterior chin
293   shields; number of preocular scales (PrO); number of presubocular scales (PrsO); number of
294   postocular scales (PtO); number of anterior temporals (Ate) — the number of temporal scales in
295   contact with the postocular scales; number of posterior temporals (Pte) — the number of
296   temporal scales immediately contacting the anterior temporal scales. Besides these data, we
297   quantified color pattern features found in examined *Oligodon*, including the number of body
298   blotches or crossbars counted from nape to vent (B-Blotch); the number of blotches or crossbars
299   counted from vent to tail tip (T-Blotch); the width in vertebral (dorsal) scales of each
300   blotch/crossbar at midbody (BlotchW); and the distance between each blotch/crossbar at
301   midbody counted using vertebral (dorsal) scales (BlotchD). Incomplete blotches/crossbars were
302   counted as a single element, and partially fused blotches were counted as two elements. If a
303   blotch/crossbar overlapped with the cloacal plate, it was counted as part of the number of body
304   blotches. Abbreviations for these characters are used in Tables 2–4. Symmetric characters are
305   given in left/right order.
306
307   **Species distribution modeling (SDM)**. We used the program MaxEnt 3.3.3 (Phillips, Anderson
308   & Schapire, 2006) to model the potential distribution of *O. taeniolatus* populations in Middle and
309   Southwest Asia during current conditions and three previous historical epochs, namely the mid-
310   Pliocene (ca 3.2 Mya), the Last Glacial Maximum (ca 21 Kya), and the mid-Holocene (ca 6

311   Kya). A total of 23 unique georeferenced data points (Table S1), 23 bioclimatic variables, and
312   four landscape layers were used to generate the model. We used the CHELSA database (Karger
313   et al., 2017) to obtain current climatic conditions, and the PaleoCLIM database for past
314   conditions during the mid-Pliocene, the Last Glacial Maximum (LGM) and the Mid-Holocene
315   (Fordham et al., 2017; Brown et al., 2018), at 5 km pixel size. The program ENMTools 1.3
316   (Warren et al., 2010) was used to filter SDM data and exclude correlated variables. Models were
317   assessed by computing the area under the curve (AUC), which was used to estimate the relative
318   contribution of variables for each model. The final maps were designed using the QGIS Desktop
319   3.28 software (QGIS Development Team, 2021).

Results
320

321   **Molecular analyses.** The final concatenated alignment comprised of 12S–16S rRNA and cyt *b*
322   gene sequences contained 3,019 base pairs with 1,812 conserved sites, 1,191 variable sites, and
323   833 parsimony informative sites. The transition-transversion bias (R) was estimated to be 1.2.
324   Nucleotide frequencies were 36.7% (A), 23.0% (T), 25.7% (C), and 14.6% (G) (all data given for
325   ingroups only). Uncorrected pairwise genetic distances (hereafter p-distances; given for cyt *b*)
326   between and within examined *Oligodon* species are presented in Table 4. Intraspecific genetic
327   distances varied from $p = 0\%$ (in *O. sublineatus*) to $p = 2.2\%$ (*O. churahensis*, including samples
328   of *O.* cf. *churahensis* and *O. russelius*). Interspecific genetic distances within examined *Oligodon*
329   varied from $p = 3.3\%$ (between *O. arnensis* sensu stricto and *O. churahensis*) to $p = 21.0\%$
330   (between *O. sublineatus* and *O. churahensis*).
331   In general, our mtDNA-based tree topology of *Oligodon* (Figure 2) corresponds well with
332   the set of phylogenetic relationships obtained from previous studies (Green et al., 2010; Nguyen
333   et al., 2020; Mirza, Bhardwaj & Patel, 2021; Das et al., 2022; Yushchenko & Lee et al., 2023a,
334   2023b). Both ML and BI topologies support the specimen of *O. taeniolatus* from Iran as a
335   separate lineage sister to *Oligodon melaneus* Wall, 1909, *O. churahensis*, and Pakistani
336   specimens *O. russelius* and *O.* cf. *churahensis*, with strong support from both analyses (0.97/92).
337   Genetic p-distances in this clade varied from 7.8% (between *O. taeniolatus* and *O. melaneus*),
338   6.3% (between *O. taeniolatus* and *O. russelius*), and 5.7% (between *O. taeniolatus* and *O.*
339   *churahensis*) based on cyt *b*. Together with *O. arnensis* they form the most basal clade (1/100),
340   while the three samples of *O. taeniolatus* from India and Sri Lanka form a distinct clade together
341   with *O. sublineatus* and *Oligodon calamarius* (Linnaeus, 1758) also with strong support
342   (1.0/100). This topology renders *O. taeniolatus* sensu lato as paraphyletic. Notably, the sample of
343   *O. taeniolatus* from Sri Lanka is divergent (2.2% p-distance based on 16S rRNA) from the
344   Indian sample, which suggests additional undescribed diversity is present in *O. taeniolatus*
345   outside of Middle and Southwest Asia. Distances of such a percentage based on 16S rRNA are
346   more significant than the cyt *b* gene because 12S–16S rRNA evolves at a slower rate (Mueller,
347   2006). The newly collected Pakistan sample (CUHC 7904) identified by us as *O. russelius* is
348   nested in a clade with two other Pakistan samples from GenBank identified as *O.* cf. *churahensis*
349   by Mirza, Bhardwaj & Patel (2021) with high support (1.0/99). Low genetic divergence ($p =$
350   2.2%) exists between the three samples, suggesting they are conspecific. Additionally, the

351 divergence between the Pakistani samples and the type series of *O. churahensis* from Himachal
352 Pradesh, India is only 3.3% in cyt *b* gene (Table 4). The genetic distance between the sample re-
353 identified as *O.* cf. *tillacki* and samples of *O. arnensis* sensu stricto was also low ($p = 3.6\%$).
354
355 **Species distribution modeling.** SDM maps based on geolocation points of *O. taeniolatus* from
356 Iran and Turkmenistan are shown in Figure 3. Variables that primarily account for species
357 presence include landscape uniformity, mean temperature of the coldest quarter (Bio 11), slope,
358 and precipitation seasonality (coefficient of variation) (Bio 15). The average performance of the
359 MaxEnt SDMs for the replicate runs was estimated at AUC = 0.988. The predicted distribution
360 of Middle and Southwest Asian *O. taeniolatus* experienced expansions and contractions across
361 the Plio-Pleistocene and Holocene, indicating the species probably had a much wider range
362 during historical times. The largest expansion of suitable habitat for the species mostly occurred
363 during the last glacial maximum (LGM), with the distribution during this period including large
364 portions of present-day Turkmenistan, Afghanistan, and Iran (near the southern portion of the
365 Caspian Sea). Range reductions of *O. taeniolatus* started in the mid-Holocene, with the SDM
366 maps predicting the most suitable habitat in the Köpet-Dag Mountain Range of northeast Iran
367 and southwest Turkmenistan, and adjacent parts of Afghanistan, Azerbaijan, and western Iran
368 (Figure 3).
369
370 **Resurrection and revalidation of *Contia transcaspica* Nikolsky, 1902.** Phylogenetically, the
371 sample of *O. taeniolatus* from northern Iran is monophyletic and recovered in a separate clade
372 within the broader *O. arnensis* species complex (defined here as *O. arnensis*, *O. churahensis*, *O.*
373 *melaneus, O. russelius,* and *O. tillacki* per Bandara et al., 2022 and Das et al., 2022). Genetic
374 distances between its closest relatives, *O. churahensis, O. melaneus,* and *O. russelius* range from
375 5.7%–7.8% (based on cyt *b*) and are typical of species-level divergences within *Oligodon* and
376 other colubrid snakes. Based on morphology, all Iranian and Turkmen *O. taeniolatus* we
377 examined are identical to the type specimen of *Contia transcaspica* (ZISP 9868), as well as past
378 literature descriptions by Dotsenko (1984) and Latifi (1991). These specimens are distinct from
379 Indian subcontinent *O. taeniolatus* in several features, the most obvious being the presence of
380 only 5 (rarely 6) supralabial scales with only the 3rd supralabial contacting the orbit, 3 (rarely 2)
381 posterior temporal scales, narrow contact between the 4th and 5th supralabials, and the presence
382 of brown transverse crossbars on the dorsal surface. Iranian and Turkmen *O. taeniolatus* are also
383 distinct from members of the *O. arnensis* species complex based on several coloration and
384 scalation features, especially the presence of 15 dorsal scale rows throughout the body (*vs.* 17–
385 17–15). Since the combination of molecular and morphological evidence support the distinct
386 status of Iranian and Turkmen *O.* "*taeniolatus*", we resurrect the name *Contia transcaspica* from
387 the subjective junior synonymy of this species. This decision maintains the monophyly of *O.*
388 *taeniolatus* sensu stricto and restricts its range to the Indian Subcontinent. The Iranian and
389 Turkmen populations from the Köpet–Dag Mountain Range should now be referred to as

390 *Oligodon transcaspicus* **comb. et. stat. nov.** and a detailed redescription, including the holotype
391 of *Contia transcaspica*, is provided below.
392
393 ***Oligodon transcaspicus* (Nikolsky, 1902) comb. et stat. nov.**
394 (Figures 4–6; Table 2)
395

396   *Contia transcaspica*: Nikolsky (1902: 839–840). *Holotype*: ZISP 9868 collected from
397   "Kopet-Dag, Transcaspia" [now Köpet–Dag Mountain Range, near Ashgabat, Ahal
398   Province, Turkmenistan] by N. Kinsohin in 1901, Nikolsky (1903a: 11–13), Bobrinskoy
399   (1923: 8), Chernov (1935: 351) (in part), Welch (1983: 77) (in part), Green (2010: 139)
400   (in part), Bandara et al. (2022: 68) (in part), Uetz et al. (2022) (in part)
401   *Oligodon taeniolatus* (in part): Chernov (1935: 351), Filippov (1947), Terentjev & Chernov
402   (1949), Bogdanov (1962), Brück (1968: 201), Nurgeldyev, Shammakov & Atayev (1970:
403   187–190), Rustamov & Atayev (1976: 47–53), Bannikov et al. (1977) Atayev, Gorelov &
404   Shammakov (1978), Szczerbak (1979: 68–70), Welch (1983: 77), Dotsenko (1984: 23–
405   26), Atayev (1985), Szczerbak, Khomustenko & Golubev (1986: 68–70), Latifi (1991: pl.
406   52 & 117), Rustamov & Sopyev (1994: 224), Atayev, Rustamov & Shammakov (1994:
407   337), Szczerbak (1994: 312), Latifi (2000), Ananjeva et al. (2006: 175), Green (2010:
408   139), Rustamow (2011), Safaei-Mahroo et al. (2015: 280), Shestopal & Rustamov
409   (2018a: 40), Orlov et al. (2018: 58–67), Rajabizadeh (2018: 242).
410
411 **Holotype.** ZISP 9868, adult female from "Köpet–Dag, Transcaspia" [= now Köpet–Dag
412 Mountain Range, near Ashgabat, Ahal Province, Turkmenistan] collected by N. Kinschin in
413 1901 (Figure 4).
414   **Referred Specimens. Turkmenistan:** Ahal Province. CAS 180042, adult female from
415 "the Iran border south of Goalon, Ashkabad (Ashkhabad) Region" collected in May 1989 by
416 Soviet Border Patrol (obtained by J. R. Macey); ZMMU Re-5589, subadult female from
417 "Karanki", collected on 1 May 1979; ZMMU Re-6155, juvenile male from "Aidere" unknown
418 collection date; ZMMU Re-7318, adult female from "Chuli, Geok-Tepe" collected on 20 June
419 1990; ZISP 18334, juvenile of undetermined sex from "Geok-Tepe", collected on May 1971;
420 ZISP 18976, subadult male from "Geok-Tepe", collected on 05 August 1968. **Iran:** Khorasan
421 Province. ZMMU Re-16687 (field number RAN-3264), adult male from Bazangan Lake, Razavi
422 (36.3044ºN, 60.4751ºE, WGS 84; 900–950 meters a.s.l.) collected by Roman A. Nazarov and
423 Mahdi Rajabizadeh on 27 May 2017. See Table S1 for more details.
424   **Diagnosis.** A kukri snake in the genus *Oligodon* that is distinguished from all other
425 congeners by the following combination of morphological characters: 1) 7–9 maxillary teeth,
426 with the posterior two teeth enlarged and blade-like; 2) dorsal scales in 15–15–15 rows; 3)
427 cloacal plate divided; 4) ventral scales 179–188 in males, 193–214 in females; 5) subcaudals 48–
428 52 in males, 44–51 in females; 6) total body scales 232–240 in males, 240–266 in females (232–
429 266 scales combined); 7) subcaudal ratio 0.203–0.224 in males, 0.177–192 in females; 8) almost

430   always 5 supralabials (sometimes 6 according to Latifi, 1991), with only the 3rd supralabial
431   contacting the orbit; 9) loreal and preocular scales present, presubocular sometimes present; 10)
432   posterior temporal scales 3 (rarely 2), with the lowest temporal causing 4th and 5th supralabial to
433   contact narrowly; 11) dorsal color pattern beige or light brown with of 42–57 dark transverse
434   crossbands on body and 12–17 crossbands on the tail; 12) dorsal color pattern on tail resembling
435   the rest of the body, with no vertebral stripe along the tail.
436   **Comparisons.** We compare *Oligodon transcaspicus* **comb. et stat. nov.** to all species of
437   *Oligodon* found in Middle and Southwest Asia, which may be confused with this species,
438   particularly *O. taeniolatus* sensu stricto, with which it was previously confused with, and
439   members of its sister clade in the *O. arnensis* species complex. We base our comparisons
440   primarily on data from the following literature sources (Wall, 1921; Wall, 1923; Smith, 1943;
441   Khan, 2002; Mirza, Bhardwaj & Patel, 2021; Bandara et al., 2022) as well as data from our own
442   examined specimens (Supplementary Material 1). *Oligodon transcaspicus* **comb. et stat. nov.**
443   can be morphologically assigned to the genus *Oligodon* by having a subcylindrical body,
444   enlarged blade-like maxillary teeth, two prefrontals and internasals present, a blunt and
445   subterminal shaped rostral scale, length of rostral scale visible from above two times as long as
446   the internasal suture, and two temporal scales bordering the edge of the parietals (generic
447   diagnosis modified from Wall, 1923).
448   The closest relatives of *O. transcaspicus* **comb. et stat. nov.** include members of the *O.*
449   *arnensis* species complex. *O. transcaspicus* **comb. et stat. nov.** can be distinguished from *O.*
450   *arnensis* sensu stricto by having 15 dorsal scale rows (*vs.* 17–17–15), 179–202 ventrals in both
451   sexes (*vs.* 164–188 in both sexes), loreal scale present (*vs.* absent), 5–6 supralabials (*vs.* 7–8,
452   rarely 6), usually 3 posterior temporal scales (*vs.* always 2), 7–9 maxillary teeth (*vs.* 12–16), and
453   irregular dorsal mottling with 47–57 transverse body blotches (*vs.* dorsum immaculate, less than
454   20 black body bands). *O. transcaspicus* **comb. et stat. nov.** can be distinguished from *O.*
455   *churahensis* (later synonymized with *O. russelius*) by having 15 dorsal scale rows (*vs.* 17–17–
456   15), 179–202 ventrals in both sexes (*vs.* 170–175 in both sexes), 5–6 supralabials (*vs.* 7–8),
457   usually 3 posterior temporal scales (*vs.* always 2), and irregular dorsal mottling with 42–57
458   transverse body blotches 1.5–3.0 dorsal scales wide and 12–16 tail blotches (*vs.* 37–45 broad
459   black body crossbars, all edged with a cream color, 1.0–2.0 dorsal scales wide and 9–11 tail
460   bars). *O. transcaspicus* **comb. et stat. nov.** is distinguished from *O. melaneus* by having 15
461   dorsal scale rows (*vs.* 17–15–15), 5–6 supralabials (*vs.* usually 7, rarely 6), usually 3 posterior
462   temporal scales (*vs.* always 2), and irregular dorsal mottling with 42–57 transverse body blotches
463   1.5–3.0 dorsal scales wide and 12–16 tail blotches (vs. black dorsum without conspicuous
464   blotches or markings and a distinct blue ventral coloration in life). *O. transcaspicus* **comb. et**
465   **stat. nov.** can be distinguished from *O. russelius* by having 15 dorsal scale rows (*vs.* 17–17–15),
466   5–6 supralabials (*vs.* 7–8, rarely 6), usually 3 posterior temporal scales (*vs.* always 2), and
467   irregular dorsal mottling with 42–57 transverse body blotches 1.5–3.0 dorsal scales wide (*vs.*
468   dorsum immaculate with narrow black body bands or crossbars usually edged with white, 1.0–
469   2.0 dorsal scales wide). *O. transcaspicus* **comb. et stat. nov.** can be distinguished from *O.*

470   *tillacki* by having 15 dorsal scale rows (*vs.* 17–17–15), 5–6 supralabials (*vs.* 7–8), usually 3
471   posterior temporal scales (*vs.* always 2), and irregular dorsal mottling with 42–57 transverse
472   body blotches 1.5–3.0 dorsal scales wide (*vs.* dorsum immaculate with 25–35 broad black body
473   bands 4.0–6.0 dorsal scales wide).

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

483   **Redescription of the Holotype (ZISP 9868; Figure 4).** Adult female specimen in good
484   condition after 121 years of preservation. Small portion of midbody in fair condition, large
485   ventral incision on the posterior third of the body, ending at the vent (Figure 4). SVL 304 mm,
486   TailL 53 mm (TotalL 357 mm). HeadL 9.6 mm, HeadW 5.6 mm, SnL 2.6 mm, EyeL 1.4 mm,
487   FrontalL 3.2 mm. TailLR 0.148, HeadW/HeadL 0.58, SnL/HeadL 0.29, EyeL/SnL 0.54,
488   EyeL/HeadL 0.15. Body elongated and cylindrical; head ovoid, slightly distinct from neck; snout
489   narrowing in dorsal view, slightly depressed towards the tip, rostral round and slightly protruding
490   in lateral profile; snout tip subterminal near mouth; eyes moderately sized compared to head,
491   pupil round; nostrils small and subelliptical, pointed in lateral view; mouth flat with lips curled
492   upwards posteriorly relative to the last supralabial; tail gradually tapering to a sharp terminal
493   scute.

494   Rostral distinctly enlarged, wider than high, triangular in dorsal view, partially separating
495   anterior half of internasals; posterior scale suture of rostral bordering internasals "deep-V"
496   shaped, posterior vertex of rostral in-line with nostrils narrowly obtuse angled (~99º); internasals
497   subpentagonal, wider than long, internasal suture equal in length compared to prefrontal suture;
498   prefrontals subhexagonal, wider than long, wider and longer than internasals; frontal
499   subpentagonal, shield shaped, anterior suture with prefrontals concave; frontal longer than
500   prefrontals; eyes placed posterior relative to the anterior edge of the frontal; angle formed by
501   posterior sutures producing the vertex of the frontal a right angle, almost acute (~90);
502   supraoculars subrectangular, longer than wide, shorter in length than frontal; parietals
503   subpentagonal, longer than wide, wider than parietal suture, posterior sutures bordering occipital
504   region strongly concave; length of parietals roughly equal to length of frontal; parietal suture
505   shorter than frontal; parietal suture shorter than length of frontal; anterior parietal angle formed
506   by the sutures between the parietal/frontal and the suture between the supraocular/parietal a
507   broad obtuse angle (~130º) with its lateral ray pointing posterolaterally. Nasal scale rectangular,
508   longer than wide, fully divided; loreal 1/1, small and square shaped, slightly wider than than
509   long, less than half the size of the nasal; supralabials 5/5; 3rd supralabial in contact with orbit; 5th

510   supralabial largest, first supralabial smallest; all supralabials in broad contact, except for
511   supralabials 4–5, which are in narrow contact due to abutting posterior temporal; preoculars 1/1,
512   wider than long; presubocular 1/1, smaller than preocular; postoculars 2/2, uppermost postocular
513   largest; anterior temporal 1/1; posterior temporals 3/3, bottommost temporal large and
514   subpentagonal in shape, blocking the 4th and 5th supralabial from broadly contacting each other;
515   infralabials 7/7 in all specimens, first in contact with each other, 4/4 infralabials in contact with
516   anterior chin shields; mental subtriangular, wider than long; small mental groove present, starting
517   from border of 1st infralabial and mental terminating at the posterior chin shields; length and
518   width of both chin shields equal in size.
519   Dorsal scale rows 15–15–15, smooth throughout without apical pits; ventral scales 202;
520   subcaudals 47, paired; total body scales 250; subcaudal ratio 0.19; cloacal plate divided; tail tip a
521   sharp pointed scute. Maxillary teeth 7, posterior two teeth enlarged and blade-like.
522   **Coloration in Preservation.** After 121 years in preservation fluid, dorsal ground color
523   cream, margins of dorsal scales brown forming indistinct and irregular mottling most heavily
524   concentrated along the flanks; 47 indistinct transverse bars across the dorsum, broadest
525   vertebrally, narrowing laterally, around 1.5–2.0 dorsal scales at their widest; along tail 12 more
526   transverse bands of similar color. Dorsal portion of head cream with an indistinct beige ocular-
527   bar edged with brown starting along 3rd and 4th supralabial scale, crossing through each eye and
528   covering the first half of the supraocular, prefrontals and anterior frontal suture; a second beige
529   and brown-edged temporal bar originating near the gulars and first dorsal scales, extending
530   through the posterior portion of the fifth supralabial before meeting medially at the parietals and
531   frontal forming a "V" shaped marking; brown nuchal chevron present starting at the parietal
532   suture as a small lanceolate tip, broadening along the nape as a thick tripartite shaped blotch,
533   extending laterally on each side of the flanks before ending near the edge of the ventral scales.
534   Ventral surface immaculate cream, faint beige spotting and mottling along the edge of each
535   ventral scale, more prominent along the tail.
536   **General Description and Variation (Figures 5–6).** The additional six specimens
537   examined agree with the description of the holotype in most aspects of coloration, scalation and
538   morphometric characteristics. SVL 145–312 mm in male, 267–361 mm in females; TailL 27–70
539   mm in male, 42–64 mm in females; TotalL in male 195–382 mm, 309–425 mm in females. The
540   largest specimen is an adult female (ZMMU Re-7318) with a SVL of 361 mm and TailL of 64
541   mm. HeadL 5.9–9.6 mm; HeadW 3.6–6.0 mm, SnL 2.3–3.5 mm, EyeL 0.8–1.4 mm, FrontalL
542   1.4–3.2 mm. TailLR 0.157–0.183 in males, 0.136–0.159 in females, HeadW/HeadL 0.53–0.72,
543   SnL/HeadL 0.27–0.42, EyeL/SnL 0.34–0.54, EyeL/HeadL 0.12–0.15. Body elongated and
544   cylindrical, slightly robust along midbody in some specimens; head ovoid, slightly distinct from
545   neck; snout narrowing in dorsal view, slightly depressed in lateral view; head oblong in lateral
546   profile; snout tip subterminal near mouth; eyes moderately sized when compared to the head;
547   nostrils pointed in lateral view; mouth flat, lips slightly curled posteriorly relative to the last
548   supralabial; tail tapering to a sharp terminal scute.

549   Rostral distinctly enlarged, wider than high, triangular in dorsal view, extending
550 posteriorly and separating the first half of the internasals from contacting; posterior suture of
551 rostral bordering the internasals "deep-V" shaped, posterior vertex of rostral in-line with nostrils
552 obtuse angled (95º–115º); internasals subpentagonal, wider than long, internasal suture slightly
553 longer or equal to prefrontal suture; prefrontals subhexagonal, wider than long, larger than
554 internasals; frontal subhexagonal, shield shaped, anterior suture usually concave; the posterior
555 suture of the frontal of one specimen (ZMMU Re-16687) has a pair of pores near the border of
556 the parietals and at the center of the scale; frontal roughly twice the length of prefrontals;
557 supraoculars subrectangular, longer than wide, shorter in length and width than frontal; eyes
558 placed posterior relative to the anterior edge of the frontal; angle formed by sutures producing
559 the posterior vertex of the frontal right or acute-angled (80º–90º), making the posterior portion of
560 the frontal appear acuminate in dorsal view; parietals subpentagonal, posterior portion concave,
561 occasionally squared; parietals slightly longer than wide, wider than parietal suture; length of
562 parietals equal or slightly longer than length of frontal; parietal suture shorter than frontal length;
563 anterior parietal angle formed by the sutures between the parietal/frontal and the suture between
564 the supraocular/parietal a broadly obtuse (120º–130º), with the lateral ray pointing
565 posterolaterally. Nasal scale rectangular to square shaped, fully divided, longer than wide; loreal
566 1/1, square, around one fourth or half the size of the nasal; supralabials 5/5 in all examined
567 specimens, although Latifi (1991) mentions specimens with 6 supralabials; 3rd supralabial always
568 in contact with orbit; 5th supralabial largest, 1st supralabial smallest; all supralabials in broad
569 contact with each other except for supralabials 4–5, which contact narrowly due to abutting
570 posterior temporal; preoculars 1/1, uppermost preocular larger; presubocular 1/1 present in four
571 specimens (including holotype), absent in other three specimens; postoculars 2/2, uppermost
572 postocular largest; anterior temporal 1/1; posterior temporals 3/3 (in one specimen, CAS 180042,
573 3/2), bottommost temporal largest , subpentagonal, blocking the 4th and 5th supralabial from
574 broad contact; infralabials 7/7 in all specimens, the first pair in contact with each other, 4/4
575 infralabials in contact with anterior chin shields; mental subtriangular, wider than long; a small
576 mental groove present, starting at the border of the 1st infralabial and terminating at the posterior
577 chin shields; length and width of both chin shields equal in size.
578   Dorsal scale rows 15–15–15, smooth throughout and without apical pits; ventral scales
579 179–188 in males, 193–202 in females; subcaudals 48–52 in male, 44–51 in females; total body
580 scales 232–240 in male, 240–266 in females; subcaudal ratio 0.203–0.224 in males, 0.177–192 in
581 females; anal plate divided; tail tip tapers to a sharp tip. Maxillary teeth 7 in two specimens
582 (including the holotype) and 9 in one specimen (CAS 180042), posterior two teeth enlarged and
583 blade-like. Teeth unavailable for examination in other specimens. We did not examine the
584 hemipenis of any specimens as all organs were retracted. The structure of hemipenes is a rather
585 conservative feature. Therefore, despite the lack of any information about hemipenial
586 morphology of *O. transcaspicus* **comb. et stat. nov.**, we expect that the fully everted and
587 expanded hemipenes of this species will likely share the same structure with its closest relatives
588 in the *O. arnensis* species complex, namely a short and slightly bilobed hemipenes with spinous

589 calyces and a simple sulcus spermaticus. Our sample size is too low to make statistical
590 comparisons between sexes, however a few instances of putative sexual dimorphism are noted.
591 First, the number of ventral scales appear to be higher in the single male specimen. The male
592 specimens also have a higher number of subcaudals, TailLR ratio and subcaudal ratio than the
593 females. The number of total body scales appears to be higher in females.
594   The dorsum of all specimens in preservative is cream or beige with well-defined brown
595 mottling concentrated along the flanks; white mottling is also present on the vertebral region in
596 some specimens; 47–57 light brown transverse crossbars on the body, each bar weakly edged
597 with white; all crossbars more well-defined compared to the holotype, 1.5–3.0 vertebral dorsal
598 scales in length, broadest vertebrally and narrowest laterally; margins of the dorsal scales near
599 each crossbar dark brown or black; 12–16 crossbars present on the tail, similar in coloration. No
600 sexual dimorphism was noted in the number of body or tail crossbars. Dorsal surface of the head
601 tan to cream, anteroventral portions of the snout gray-brown in some specimens; gray-brown
602 mottling occasionally present along the supralabials and underside of head; the position of the
603 ocular and temporal bars are consistent amongst all specimens, but vary in coloration from
604 brown to dark-brown and are usually edged with black; the nuchal chevron in some specimens is
605 lanceolate-shaped at its anterior origin along the parietals, but in two specimens it is blunt or
606 obtuse, terminating before the ventral surface along the nape as a thick triangular shaped blotch.
607 No vertebral stripe is present along the tail in preserved specimens. The ventral surface is tan to
608 cream and usually immaculate, however in three specimens the dorsal crossbars extend onto the
609 lateral sides of the ventral scales. The color in life based on ZMMU Re-16687 (Figure 5) and two
610 specimens photographed in Turkmenistan by A. V. Pavlenko (Figure 6) resembles the coloration
611 in preservative, but the dorsal patterning and blotching are more pronounced. In these specimens,
612 the dorsum is brown to reddish-brown with white mottling concentrated on the vertebral region
613 and dark-brown mottling concentrated on the flanks; the transverse bars are brown and have
614 small dark-brown edges on the dorsal scales of each bar; the nuchal chevron and ocular bars are
615 darker than the crossbars on the dorsum; the eyes have a gold-brown iris, pupils black; ventral
616 surface and areas between head markings plain white.
617   **Distribution and Natural History.** The known distribution of *Oligodon transcaspicus*
618 **comb. et stat. nov.** is summarized in Figure 1 and Table S1. This species is currently known
619 from the Köpet–Dag region of northern Iran and southern Turkmenistan. In Turkmenistan, it is
620 known from the present-day Balkan, Ahal and Mary provinces. The distribution of the species in
621 Turkmenistan was recently reviewed by Orlov et al. (2018). They report *O. transcaspicus* **comb.**
622 **et stat. nov.** from ten localities in the foothills of the Köpet–Dag Mountains: Balkan and Ahal
623 Provinces (Danata spring; Eldere Gorge north from Kara–Kala; Chandyr Valley; Makhmumkala
624 village; Kara–Elchi and Eishem gorges; Aidere, Kurygol; Arvaz Valley; 7 km northwards from
625 Saivan; Firuza and Chuli villages; Shamly, near Babazo) and from two localities in Mary
626 Province (Dana–Germab spring, and Nardyvanly spring; environs of Badkhyz). In Iran,
627 *Oligodon transcaspicus* **comb. et stat. nov.** is known definitively from Razavi Khorasan
628 Province from two localities (ZMMU Re-16687 from Bazangan Lake; and another sight record

629 we confirm from ~5 km SW of Mashahd), and Golestan Province (town of Dashliburun [Dashil
630 Borun]). The Golestan Province records originates from Latifi (1991), who reported the locality
631 as "Mazandaran Province (Ghonbad Kavoos) … in Dashley Boron region". At the time of
632 Latifi's writings, the locality "Ghonbad Kavoos… Dashley Boron" (the romanized spelling of
633 Gonbad-e Kavus county) was included within Mazandaran Province before being separated into
634 Golestan Province in 1997. We here confirm this locality in Golestan Province as "Dashliburun"
635 (sometimes spelled as "Dashil Boron"), close to the Turkmenistan border. Rajabizadeh (2018)
636 reported the species in Northeastern Iran close to border of Turkmenistan from eastern Golestan
637 Province to north of Khorasan Razavi Province. Latifi (2000) and Safaei-Mahroo et al. (2015)
638 also reported this species from North Khorasan, and from Zanjan and West Azarbaijan
639 Provinces, although the occurrences in western Iran require further verification (see Discussion).
640   Several authors have provided insights on the natural history of *O. transcaspicus* **comb.
641 et stat. nov.** (Dotsenko, 1984; Atayev, 1985; Szczerbak, Khomustenko & Golubev, 1986;
642 Rustamov & Sopyev, 1994; Szczerbak, 1994; Atayev, Rustamov & Shammakov, 1994; Orlov et
643 al., 2018). Two individuals photographed by A. Pavlenko (pers. comm.) were found in the
644 daytime amongst rocky outcrops (Figure 6); however, Orlov et al. (2018) noted specimens were
645 predominately nocturnal. These authors report that *O. transcaspicus* **comb. et stat. nov.** was
646 most abundant between elevations of 400–700 meters and note a few specimens which were
647 found at higher altitudes up to 1,000 meters. Most of the specimens recorded were found on the
648 surface or under rocks at the base of gradually sloping mountain gorges, mudstone channels,
649 riverbeds and open habitats with shrubs and tree vegetation that maintain enough moisture.
650 Based on this, Orlov et al. (2018) posited that the activity period of *O. transcaspicus* **comb. et
651 stat. nov.** is highly dependent on recent precipitation and relative humidity. Ananjeva et al.
652 (2006) noted that *O. transcaspicus* **comb. et stat. nov.** was a rare species in Turkmenistan,
653 although the summary of observations by Orlov et al. (2018) may indicate it is more common
654 than currently ascertained and may be difficult to observe in the field unless specific seasonal
655 and weather conditions are met. Like other *Oligodon*, this species probably feeds on reptile and
656 bird eggs, and may also consume small lizards, frogs, and small mammals. Atayev, Rustamov &
657 Shammakov (1994) and sources therein record this species laying one to two eggs between the
658 months of May and June, suggesting the reproductive season is in the spring and early summer.
659   **Remarks.** Most sources that mention *O. transcaspicus* **comb. et stat. nov.** have cited
660 Nikolsky (1903a) as the source of original description. However, we have discovered an earlier
661 book that was also authored by Nikolsky describing *Contia transcaspica* dated to 1902. Thus, the
662 year of original description and its publication source should be fixed, and we do so here in the
663 present paper.
664   **Etymology.** The species epithet "*transcaspicus*" is a latinized toponymic adjective in
665 genitive singular and given in reference to the type locality of this species, which during the time
666 of its description, was called the Transcaspian Region (Zakaspiyskaya Oblast or Zakaspiyskiy
667 Krai) and was part of the Turkestan Governor–Generalship of the Russian Empire. The
668 Transcaspian Region later became known as Turkmenistan during its time as a constituent

669 republic of the Soviet Union (Turkmen S.S.R.) and now as an independent nation. The epithet is
670 fixed to agree with the gender of the generic name *Oligodon*, which is masculine. We
671 recommend the English common name "Köpet–Dag kukri snake" for this species, followed by
672 the Russian, Farsi, and Turkmen common names "Zakaspiyskiy oligodon", "داغ کپه مار لوس"
673 [*Loos Mār-e Kopet Dagh*], and "Goňurja ýylanjyk", respectively (see Rustamow, 2011;
674 Rajabizadeh, 2018).
675

676 **The taxonomic status of *Oligodon "arnensis"* in Pakistan.** Because the revision of *O. arnensis*
677 sensu auctorum by Bandara et al. (2022) only focused on material from India and Sri Lanka, we
678 use this section to review the status of populations in neighboring Pakistan. We examined one
679 specimen of *O.* "*arnensis*" (CUHC 7904) recently collected by DJ and RM on 16 September
680 2018 from Kallar Kahar, Punjab Province, Pakistan (32.7695ºN, 72.7065ºE, 613 m a.s.l.). Based
681 on the presented mtDNA phylogeny, this specimen was recovered in a clade with two additional
682 samples from Pakistan that were previously identified as *O.* cf. *churahensis* by Mirza, Bhardwaj
683 & Patel (2021). A brief description of CUHC 7904 is provided here (Figure 7): adult male, SVL
684 345 mm, TailL 65 mm (TotalL 410 mm; TailLR 0.159) 16–17–15 dorsal scale rows, 183
685 ventrals, 49 subcaudals (233 total body scales), subcaudal ratio of 0.21, 1/1 loreal present, 1/1
686 divided nasal, 7/7 supralabials with the third and fourth in contact with the eye, 7/7 infralabials,
687 and an immaculate brown dorsum with 37 black crossbands across the body and 13 tail bands
688 approximately 1.0–1.5 dorsal scales wide at midbody and interspaces between each band
689 approximately 4.0 dorsal scales long. In addition to this specimen, past authors have also
690 recorded *O.* "*arnensis*" specimens from Pakistan (Minton, 1962; Minton, 1966; Mertens, 1969;
691 Khan, 2002). Both Minton (1962) and Khan (2002) figure an *O.* "*arnensis*" (with Khan, 2002
692 swapping the images of *O.* "*arnensis*" and *O. taeniolatus* by mistake) bearing small narrow
693 black crossbars with white edges. Based on these characteristics, along with other scalation
694 features (see Table 3), the literature descriptions of Pakistani *O.* "*arnensis*" are very similar to
695 CUHC 7904 and specimens *O. russelius* sensu Bandara et al. (2022). Therefore, based on our
696 specimen and previous reports of *O.* "*arnensis*", we refer the northern Pakistan populations of
697 *O.* "*arnensis*" to *O. russelius*.
698

699 **Records of *Oligodon* in Afghanistan.** Literature reports of *O.* "*arnensis*" and *O. taeniolatus*
700 from Afghanistan are sparse but have been the subject of confusion for decades. Brück (1968)
701 first reported a juvenile kukri snake he identified as *O. taeniolatus* from "dem Gebiete um
702 Djelalabad" [= vicinity of Jalalabad]. This record was plotted by Sindaco et al. (2013) but
703 rejected due to imprecision by Wagner et al. (2016b). Although Brück (1968) identified this
704 specimen as *O. taeniolatus*, data he provided for this specimen indicates it bears 17 dorsal scale
705 rows, contra the 15 dorsal scales normally observed in *O. taeniolatus*. This was noticed quickly
706 by Král (1969), who subsequently corrected its identification to *O. arnensis*. Nevertheless, both
707 Sindaco, Venchi & Grieco (2013) and Wagner et al. (2016b) record *O. arnensis* and *O.*
708 *taeniolatus* as inhabitants of Afghanistan, unaware that the records refer to the same specimen

709   (MMB 28497). Brück (1968)'s account provided additional morphological data that allow us to
710   confirm its identification. He notes that the specimen bears the following features: juvenile
711   (unsexed, but based on relative tail length and subcaudal ratio, possibly an immature female),
712   SVL 153 mm, TailL 24 mm (TotalL 177 mm, TailLR 0.136), dorsal scales in 17 rows, 198
713   ventrals, 44 subcaudals, (243 total body scales, subcaudal ratio 0.181), 7/7 supralabials (3–5
714   contacting eye), 6/6 infralabials, 1 preocular, 2 postocular, 1+2 temporals, and 49 dark crossbars
715   across the body and tail. These characteristics confirm that the specimen should not be identified
716   as *O. taeniolatus* and that Král's re-identification as *O. "arnensis"* was correct (see Table 3 for
717   more comparisons). A second *Oligodon* record from Afghanistan was recently documented on
718   the citizen science platform iNaturalist (2022). This specimen (obs. 110932106, user
719   mohammadfarooq) was observed from Dara–i–Pech district, Kunar Province, Afghanistan
720   (35.0553ºN, 70.9561ºE; 1,700–1,800 meters a.s.l.) on 9 April 2022. While photographs of the
721   specimen are too poor in quality to discern any scalation features, its color pattern consisting of
722   approximately 51 black crossbars and 13 tail bars (64 total crossbars) greatly resembles *O.*
723   *"arnensis"*, specifically *O. russelius* (and to some extent *O. churahensis*, but see Discussion). In
724   conjunction with our re-identification of Pakistani populations, we conclude that the Afghanistan
725   populations previously recorded as *O. arnensis* (Brück, 1968; Král, 1969; Khan, 2002; Wagner
726   et al., 2016b) should also represent *O. russelius*. All records of this species from the country are
727   restricted to the western foothills of the Hindu Kush.
728   The only other report of an Afghan *Oligodon* is a record of *O. taeniolatus* from
729   Afghanistan noted by Wagner et al. (2016b) from "Kars, Kandahar Province" based on specimen
730   USNM 194971. We attempted to trace the voucher of this specimen and discovered that the
731   museum catalog number USNM 194971 actually refers to a scincid lizard *Eurylepis taeniolatus*
732   Blyth, 1854a, and not a kukri snake. No collection records of *Oligodon* from Afghanistan have
733   been found within the USNM collections ledger (E. Langan, 2022, pers. comm.), so the
734   Kandahar Province record of *O. taeniolatus* must be considered erroneous. The similar species
735   epithets between *E. taeniolatus* and *O. taeniolatus* may have caused Wagner et al. (2016b) to
736   mistake its identity, resulting in a *lapsus calami*. As a result, we formally remove *O. taeniolatus*
737   from the herpetofauna of Afghanistan, Iran, and Turkmenistan. However, we note that the
738   presence of *O. transcaspicus* **comb. et stat. nov.** in Afghanistan is still possible, particularly in
739   northwestern provinces bordering with Iran and Turkmenistan (suggested also by the SDM
740   analysis).

Discussion

742
743   **Distribution and conservation of *Oligodon transcaspicus* comb. et stat. nov.** The phylogenetic
744   analysis of 12S–16S rRNA, cyt *b* fragments, morphological data and SDM mapping data support
745   the resurrection of *Contia transcaspica* as *Oligodon transcaspicus* **comb. et stat. nov.** for Iranian
746   and Turkmen populations previously ranked under *O. taeniolatus*. This analysis also revealed
747   substantial genetic differentiation between populations of *O. taeniolatus* on the Indian
748   subcontinent warranting additional revisionary work from future authors. We cannot provide a

749   valid description for the deeply divergent lineages in Sri Lanka and mainland India due to a lack
750   of broad morphological and genetic sampling. However, we note that the names *Oligodon*
751   *fasciatus* Günther, 1864 (now considered a subspecies of *O. taeniolatus*) and *Oligodon*
752   *taeniolatus* var. *ceylonicus* Wall, 1921 are both available names for Sri Lankan populations if
753   they indeed prove to be distinct from others on the island, and/or the remainder of the Indian
754   subcontinent. While the taxonomy of *O. taeniolatus* remains unresolved, the position of *O.*
755   *transcaspicus* **comb. et stat. nov.** outside of this clade justifies its separation as a distinct
756   species. The distribution of *O. transcaspicus* **comb. et stat. nov.** is probably more expansive
757   than currently ascertained, and we expect that this species will eventually be found in additional
758   localities across the Köpet–Dag Mountain region. The SDM models identified some patches of
759   suitable habitat across the Western Caspian region and Central Iranian Desert in areas where
760   Latifi (1991, 2000) and Safaei-Mahroo et al. (2015) reported its presence. Unfortunately, we
761   could not trace any specimen vouchers of Latifi's collection in the Razi Vaccine and Serum
762   Research Institute associated with these Iranian records. Since Latifi's specimens come from
763   snake hunters of the institute (and were not collected by Latifi himself), and the locality data is
764   given only at province level, these locality records should be treated with caution. Only
765   subsequent fieldwork in these areas might verify such reports, particularly in adjacent Iranian
766   provinces bordering Turkmenistan.
767   Verified records of *O. transcaspicus* **comb. et stat. nov.** also exist close to the border of
768   Afghanistan in Mary Province, Turkmenistan. Since SDM modelling also predicts suitable
769   habitat in this region, it is possible that this species persists in the northwestern portion of
770   Afghanistan (specifically Herat, Badghis, Faryab and Jowzan provinces), but remains
771   unconfirmed there due to ongoing security concerns (see Jablonski et al., 2021). The
772   conservation of *O. transcaspicus* **comb. et stat. nov.** does not seem to be under any significant
773   threats, however habitat degradation and human encroachment could pose a threat to some
774   populations. Climate projections across the southern portions of Turkmenistan predict an
775   increase in aridification and a reduction of river runoff over the following decades (Lioubimtseva
776   et al., 2012; Duan et al., 2019). Because the SDM mapping analyses indicated temperature and
777   precipitation seasonality were major factors influencing the distribution of *O. transcaspicus*
778   **comb. et stat. nov.**, climate change could negatively impact populations. Under listings provided
779   by the International Union for Conservation of Nature (IUCN) we would recommend classifying
780   this species as "Least Concern". Continued monitoring of existing populations and additional
781   field surveys across the Köpet–Dag Mountain Range would improve our understanding of the
782   ecology and conservation of this species.
783
784   **Taxonomic comments on the *Oligodon arnensis* species complex.** Although our sampling is
785   limited, the results from our study suggest the three-taxon statement of *O. arnensis* sensu
786   auctorum by Bandara et al. (2022) requires additional scrutiny. Specimens we examined from
787   Ganjam district, Odisha, India (CAS 17224–225) are well within the distribution of *O. russelius*
788   (fide Bandara et al., 2022) but morphologically resemble *O. arnensis* sensu stricto, bearing no

789   loreal scale, and 18–20 dark black body bands that are 2.0–3.0 dorsal scales wide. Another
790   specimen collected near Rajamahendravaram, Andhra Province, India (CAS 94375) is close to
791   the type locality of *O. russelius* but has 22 dorsal body bands that are 1.5–2.0 dorsal scales wide
792   and also lacks a loreal scale, thus resembling the species diagnosis of *O. arnensis* sensu stricto.
793   Either *O. arnensis* and *O. russelius* are sympatric in parts eastern India, or a broad contact zone
794   between the two species exists, which could explain why these specimens we examined have
795   more variable color pattern conditions than previously described. There are also issues with the
796   distribution map of *O. arnensis, O. russelius* and *O. tillacki* in Bandara et al. (2022; figure 10
797   therein). The map clearly separates the three taxa in India, but the figured collection localities
798   represent a combination of specimen vouchers and observations from iNaturalist, with no
799   meaningful way to distinguish between these lines of data. While we agree that citizen scientist
800   databases like iNaturalist have great utility in documenting rare and understudied herpetofauna
801   (as exemplified here by the Afghan record of *O. russelius*), they can still suffer from data quality
802   issues (namely, limited number of visible morphological features, inaccurate locality data and
803   misidentification errors). It is impossible to discern whether the locations in Bandara et al.
804   (2022)'s map represent voucher specimens or iNaturalist observations, and the distribution map
805   is not scientifically repeatable because the authors failed to provide a geolocation appendix for
806   the iNaturalist records. Besides issues related to species distribution, we note that the p-distance
807   (based on cyt *b*) between Sri Lankan *O. arnensis* samples and the GenBank sample Bandara et
808   al. (2022) identified as *O.* cf. *tillacki* is only 3.6%, lower than normal p-distances separating
809   species-level lineages of *Oligodon*. We conservatively retain the species status of *O. tillacki*
810   because we have not directly examined the voucher specimen of this sample to verify its identity.
811   Overall, we recommend that subsequent treatments of *O. arnensis* sensu stricto, *O. russelius*, and
812   *O. tillacki* emphasize increased specimen and tissue collection for an integrative taxonomic
813   approach.
814   Our analysis also confirmed the taxonomic identity of *O. "arnensis"* populations in
815   northern Pakistan and Afghanistan as *O. russelius*. Nevertheless, several authors (Minton, 1966;
816   Mertens, 1969; Khan, 2002) note the distribution of *O. "arnensis"* extends into central and
817   southern Pakistan close to the border of western India. These locations come close to the known
818   distribution of *O. tillacki*, especially near Gujarat State, India. However, Minton (1966) noted
819   that all his specimens have black bars with white edges, a phenotypic trait that Khan (2002) also
820   described. Both illustrations by these authors show a "V-shaped" marking on the nape, although
821   it is not a thick triangular blotch that is observed in *O. tillacki*. We believe there is little
822   indication that *O. "arnensis"* populations in southern and central Pakistan match the description
823   *O. tillacki* and we maintain the identity these populations as *O. russelius* for the time being. It is
824   still possible that *O. tillacki* could range into this part of the country due to the continuity of
825   habitat within this region, and we suggest future herpetological survey work and the examination
826   of additional material to confirm this. Such a discovery could align with recent studies that have
827   documented a biogeographic break between the right and left banks of the Indus River seen in

828   several Pakistani amphibians and reptiles (Gowande et al., 2021; Agarwal et al., 2022; Dufresnes
829   et al., 2022).
830   Additionally, our study has taxonomic implications for the recently described *O.*
831   *churahensis*, as Mirza, Bhardwaj & Patel (2021) tentatively associated Pakistani samples of *O.*
832   "*arnensis*" with this species. Like the genetic distances between *O.* cf. *tillacki* and *O. arnensis*
833   sensu stricto, the cyt *b* p-distance between the Pakistani clade of *O. russelius* (= *O.* cf.
834   *churahensis*) and the clade containing the type series of *O. churahensis* is low for species-level
835   divergence, standing at only 3.3%. *Oligodon churahensis* was described by Mirza, Bhardwaj &
836   Patel (2021) based on two specimens collected at the foothills of the western Himalayas in
837   Himachal Pradesh, India. Bandara et al. (2022) correctly noted that literature descriptions of
838   kukri snakes similar to *O. churahensis* were reported as *O. arnensis* sensu lato (= now *O.*
839   *russelius*) by past authors (Wall, 1921; Deraniyagala, 1936; Constable, 1949; Deraniyagala,
840   1955). However, because Bandara et al. (2022) include data from these historical sources into
841   their conception of *O. churahensis* (as seen in their supplementary material), diagnosing this
842   species from *O. russelius* becomes puzzling. In the comparisons section of *O. russelius*, Bandara
843   et al. (2022) separated this species from *O. churahensis* by the presence of 30–45 crossbars (*vs.*
844   48–54 in *O. churahensis*) the distance between each crossbar measured in vertebral dorsal scales
845   (4–6 scales *vs.* 2–4 in *O. churahensis*), and by a different head shape marking (inverted Y-shaped
846   marking *vs.* heart-shaped symbol in *O. churahensis*). However, the authors note that *O.*
847   *churahensis* has 56–62 crossbars in the remaining text, especially in Table 1, where it is again
848   compared to the 30–45 crossbars of *O. russelius*. It appears that the authors confused the true
849   number of crossbars found in *O. churahensis* and *O. russelius*, failed to specify between "total
850   crossbars" (including body and tail bars) and "body crossbars" (restricted from nape to vent) and
851   did not completely summarize the color pattern traits observed in all of the sources they believe
852   comprise *O. churahensis* (Wall, 1921; Deraniyagala, 1936; Constable, 1949; Deraniyagala,
853   1955; Mirza, Bhardwaj & Patel 2021). Per the original description (Mirza, Bhardwaj & Patel
854   2021), the actual number of body crossbars found in *O. churahensis* is 37–45, with the number
855   of total crossbars noted as 48–54. Furthermore, Bandara et al. (2022) stated in their written
856   description that *O. russelius* has 30–45 body crossbars and 6–10 tail bars. This indicates that the
857   supposed differences in crossbar numbers are a lot less significant than previously considered.
858   As argued by Mahony & Kamei (2021), errors and inconsistencies in taxonomic articles are
859   inevitable, but authors should practice great care to make sure data inputted into descriptions and
860   tables is consistent.
861   When we combine our own data on *O. russelius* from Afghanistan, Pakistan with the
862   clarified characters of Bandara et al. (2022) and existing data in the literature (Wall, 1921;
863   Constable, 1949), most color pattern and scalation traits between this taxon and *O. churahensis*
864   overlap (Table 3). Combined with the low genetic divergence revealed by our molecular data,
865   our study does not support the species-rank status of *O. churahensis*. It is plausible that
866   specimens identified as *O. churahensis* represent the high-end of a geographic cline of cross-
867   banded phenotypes found within *O. russelius* across its range, as suggested in part by Wall

868   (1921). Alternatively, it is possible that the *O. churahensis* and *O. russelius* clades could
869   maintain their reciprocal monophyly, albeit with low genetic divergence that would support the
870   existence of two lineages at the subspecies level. In the absence of additional samples from the
871   type locality of *O. churahensis* and adjacent regions of northern India and Pakistan, we believe
872   the most appropriate decision is to relegate the species to the junior synonymy of *O. russelius*,
873   which we do so here. A key to the *O. arnensis* species complex and related species is provided
874   below to summarize our taxonomic changes (see Conclusions).
875
876   **Biogeographic implications.** Our resurrection of *O. transcaspicus* **comb. et stat. nov.** and the
877   clarification of *O.* "*arnensis*" and *O. taeniolatus* records from Middle and Southwest Asia (along
878   with Pakistan) represents a small step in understanding the evolutionary history of the region's
879   herpetofauna. Interestingly, several Indo-Malayan reptiles found in Middle and Southwest Asia
880   are recognized as separate taxa. Examples include *Boiga trigonata melanocephala* (Annandale,
881   1904), *Lycodon bicolor* (Nikolsky, 1903) and *Ptyas mucosa nigriceps* Terentjev & Chernov,
882   1949 (Orlov et al., 2018; Amarasinghe et al., 2023). Other species found in Middle/Southwest
883   Asia whose close relatives originate from the Indo-Malayan realm include *Naja oxiana*
884   Eichwald, 1831 and *Eublepharis macularius* Blyth, 1854b. For the latter species,
885   phylogeographic studies show there is low genetic differentiation between populations opposite
886   of the Hindu Kush, implying that these species experienced recent and rapid range expansions
887   into Middle/Southwest Asia (Kazemi et al., 2021; Agarwal et al., 2022). The uniqueness of the
888   evolutionary lineage representing *O. transcaspicus* **comb. et stat. nov.** paints a different picture,
889   because the presented molecular, morphological and SDM evidence implies that the divergence
890   of its common ancestor into present-day Iran and Turkmenistan occurred much earlier. Though it
891   is difficult to hypothesize the exact timing of divergence for *O. transcaspicus* **comb. et stat.**
892   **nov.**, the high topography surrounding the Hindu Kush and the arid Registan-North Pakistan
893   sandy deserts to its south probably reduced opportunities for range expansion to periods in the
894   late Miocene and the Plio-Pleistocene, when climatic conditions promoted the growth of more
895   suitable semi-arid steppes and shrublands (Hoorn et al., 2000; Merceron et al., 2004; Modarres et
896   al., 2019). The diversity and cladogenesis of Indo-Malayan-affiliated elements of Middle and
897   Southwest Asia's amphibians and reptiles remain poorly understood, presenting intriguing
898   questions for future research. The acquisition of new material along with more comprehensive
899   phylogeographic analyses will undoubtedly shed light on these unique animals and their
900   taxonomic and evolutionary status.

Conclusions

902   We carefully reviewed the status of the two kukri snake species found in Middle and
903   Southwestern Asia, the banded kukri snake *O.* "*arnensis*" and the streaked kukri snake *O.*
904   *taeniolatus*, leading to several taxonomic and distributional clarifications. For *O. taeniolatus*, we
905   found that specimens from the Köpet-Dag Mountain Range of northern Iran and southern
906   Turkmenistan were phylogenetically nested in a different intrageneric grouping compared to
907   nominotypical *O. taeniolatus* on the Indian subcontinent. To fix the paraphyly recovered by

908   these analyses, we resurrected the junior synonym *Contia transcaspica* and provided a thorough

909   morphological redescription supplemented with SDM mapping to explore its potential range. We

910   also found that Afghanistan and northern Pakistan records of kukri snakes previously recognized

911   as *O. arnensis* should in fact be assigned to the species *O. russelius*. This latter species forms a

912   sister clade to the recently described *O. churahensis* from northern India, but is only separated by

913   a small genetic divergence of 3.3% based on cytochrome *b*. Because the morphology between *O.*

914   *russelius* and *O. churahensis* overlaps, we consider both species to be conspecific, and relegate

915   *O. churahensis* to the junior synonymy of *O. russelius*. Our investigation further revealed that

916   there are no records of *O. taeniolatus* from Afghanistan, as the two past reports from the

917   literature refer to a misidentified specimen of *O. russelius*, and a misidentified scincid lizard,

918   respectively. As a consequence, we remove *O. taeniolatus* from the snake fauna of Afghanistan,

919   Iran, and Turkmenistan. The two kukri snakes found in Middle and Southwestern Asia are *O.*

920   *transcaspicus* **comb. et stat. nov.** and *O. russelius*. These two species represent key Indo-

921   Malayan herpetofaunal elements in a region that primarily consists of Palearctic amphibians and

922   reptiles. Their ranges in Middle and Southwest Asia appear to be influenced by past climate

923   change across the Hindu Kush Mountain range, in addition to past biotic and abiotic fluctuations

924   that occurred during the Plio-Pleistocene. Future studies that explore the biogeographic origins

925   of these animals are recommended. We also suggest that additional taxonomic work on *O.*

926   *arnensis* and *O. taeniolatus* are needed on Indian subcontinent populations. The number of

927   recognized species in *Oligodon* remains at 88 (fide Yushchenko & Lee, 2023a, 2023b).

928

929   **Key to members of the *Oligodon arnensis* species complex and related species.** We provide a

930   new key summarizing the taxonomic changes of our study. Our phylogenetic results separate *O.*

931   *arnensis* sensu auctorum and *O. taeniolatus* sensu auctorum into two separate clades, however

932   we note that Smith (1943) originally included both taxa in the same morphological species

933   grouping. We tentatively follow Smith's classification for this key and include *Oligodon affinis*

934   Günther, 1862, *Oligodon brevicauda* Günther, 1862, *O. calamarius*, *Oligodon erythrorhachis*

935   Wall, 1910, *O. sublineatus* and *O. taeniolatus*, in addition to members currently assigned to the

936   *O. arnensis* species complex, acknowledging that this does not reflect the phylogenetic results of

937   our study. Data used to create this key originate from Wall (1923), Smith (1943), Bandara et al.

938   (2022), Das et al. (2022) and our own examined material.

939

940   1a. Anterior dorsal scale rows in 15 rows (2)

941   1b. Anterior dorsal scale rows in 17 rows (7)

942   2a. Internasals and prefrontals fused, loreal absent, dorsal color pattern red in life consisting of

943   reddish brown and dark brown longitudinal stripes with occasional interspaced spots (*Oligodon*

944   *brevicauda*)

945   2b. Internasals and prefrontals separate, loreal condition variable, dorsal pattern not consisting of

946   longitudinal series of stripes (3)

947   3a. 5–6 supralabials with only the 3rd supralabial in contact with the orbit, and narrow contact
948   between the 4th and 5th supralabial, usually 3 posterior temporal scales, restricted to the Köpet-
949   Dag Mountain range of Iran and Turkmenistan (*Oligodon transcaspicus* **comb. et stat. nov.**)
950   3b. More than 6 supralabials with more than one scale contacting the orbit and broad contact
951   between all supralabials (4)
952   4a. Loreal present, dorsal color pattern variable but always without a red vertebral stripe and
953   lacking narrow black crossbars (5)
954   4b. Loreal absent, dorsal color pattern dark gray consisting of a bright red vertebral stripe and
955   approximately 29 black, narrow crossbars on the body, 7 on the tail, all crossbars black with
956   white edges. Known only from northeast India (*Oligodon erythrorhachis*)
957   5a. Usually more than 160 ventral scales, color pattern with conspicuous broad crossbars or
958   blotches that maintain the same size across the body, a narrow vertebral stripe present, two-fifths
959   of the retracted hemipenis bilobed and spinose (*Oligodon taeniolatus*)
960   5b. Usually less than 160 ventral scales, color pattern consisting of irregularly shaped crossbars
961   that mostly concentrated on the anterior half of body and decrease in size posteriorly, retracted
962   hemipenis unilobed or only bilobed at the apex (6)
963   6a. Light vertebral stripe present, crossbars dark brown and narrow, concentrated on the anterior
964   half of the body, ventral surface with separate equally arranged rectangular spots, retracted
965   hemipenis unilobed (*Oligodon calamarius*)
966   6b. Light vertebral stripe absent, crossbars broad and irregular, restricted to the anterior third of
967   the body, ventral surface with longitudinal rows of spots forming three distinct rows of stripes,
968   retracted hemipenis bilobed at apex (*Oligodon sublineatus*)
969   7a. Less than 160 ventrals, dorsum grayish brown to brown with small reticulations, crossbars
970   present or absent (8)
971   7b. More than 160 ventrals, dorsum olive brown with dark crossbars (9)
972   8a. Ventral surface white below with dark square spots, dorsal scales 17 at midbody, 129–145
973   ventrals (*Oligodon affinis*)
974   8b. Ventral surface distinctively gray blue in life, dorsal scales 15 at midbody, 144–159 ventrals
975   (*Oligodon melaneus*)
976   9a. Loreal always absent, 164–188 ventrals in both sexes, 15–20 dark body crossbars that are 2–3
977   vertebral dorsal scales wide, 7–12 vertebral dorsal scales between each crossbar (*Oligodon*
978   *arnensis*)
979   9b. Loreal present, 169–207 ventrals in both sexes, 30–54 dark body crossbars that are less than
980   2 vertebral dorsal scales wide, 3–6 vertebral dorsal scales between each crossbar (*Oligodon*
981   *russelius*)
982   9c. Loreal present (rarely absent), 180–201 ventrals in both sexes, 25–35 dark body crossbars
983   with the first 5–8 distinctly enlarged, 4–6 vertebral dorsal scales wide and 2–4 vertebral dorsal
984   scales between each crossbar (*Oligodon tillacki*).

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Author Contributions

1032 **Justin L. Lee** collected data, conceived and designed the experiments, analyzed the data,
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References

1097 Agarwal I, Bauer AM, Gamble T, Giri VB, Jablonski D, Khandekar A, Mohapatra PP, Masroor
1098   R, Mishra A, Ramakrishnan U (2022) The evolutionary history of an accidental model
1099   organism, the leopard gecko *Eublepharis macularius* (Squamata: Eublepharidae). Molecular
1100   Phylogenetics and Evolution 168: 107414.
1101   https://doi.org/10.1016/j.ympev.2022.107414

1102

1103 Amarasinghe TT, Masroor R, Lalremsanga HT, Weerakkody S, Ananjeva NB, Campbell PD,
1104   Kennedy-Gold SR, Bandara SK, Bragin AM, Anusha Gayan AK, Sharma VR, Sayyed A,
1105   Biakzuala L, Suneth Kanishka A, Ganesh SR, Ineich I, de Silva A, Mendis Wickramasinghe
1106   LJ, Seneviratne SS, Poyarkov NA, Vogel G, Jablonski D (2023) Integrative approach
1107   resolves the systematics of barred wolf snakes in *Lycodon striatus* complex (Reptilia,
1108   Colubridae). Zoologica Scripta: accepted
1109
1110 Ananjeva NB, Orlov NL, Khalikov RG, Darevsky IS, Ryabov SA, Barabanov A (2006) The
1111   Reptiles of Northern Eurasia. Taxonomic Diversity, Distribution, Conservation Status.
1112   Pensoft Series Faunistica, Sofia, 250 pp.
1113
1114 Annandale N (1904) Additions to the Collection of Oriental Snakes in the Indian Museum.
1115   Journal of the Asiatic Society of Bengal 73(2): 207–211 + pl. ix.
1116
1117 Asadi A, Montgelard C, Nazarizadeh M, Moghaddasi A, Fatemizadeh F, Simonov E, Kami HG,
1118   Kaboli M (2019) Evolutionary history and postglacial colonization of an Asian pit viper
1119   (*Gloydius halys caucasicus*) into Transcaucasia revealed by phylogenetic and
1120   phylogeographic analyses. Scientific Reports 9: 1224.
1121   https://doi.org/10.1038/s41598-018-37558-8
1122
1123 Atayev Ch (1985) Reptiles of the Mountains of Turkmenistan. Ylym Press, Ashkhabad, 344 pp.
1124   (in Russian)
1125
1126 Atayev Ch, Gorelov YK, Shammakov S (1978) Data on rare and endangered species of reptiles
1127   of the Turkmenistan fauna. Proceedings of the Academy of Sciences of the Turkmen SSR.
1128   Series of Biological Sciences 4: 81–83. (in Russian)
1129
1130 Atayev Ch, Rustamov AK, Shammakov S (1994) Reptiles of Kopetdagh. In: V. Fet and K. I.
1131   Atamuradov (Eds) Biogeography and Ecology of Turkmenistan. Monographiae Biologicae.
1132   Springer, Dordrecht, 329–350.
1133
1134 Bandara SK, Ganesh SR, Kanishka AS, Danushka AD, Sharma VR, Campbell PD, Ineich I,
1135   Vogel G, Amarasinghe AAT (2022) Taxonomic Composition of the *Oligodon arnensis*
1136   (Shaw 1802) Species Complex (Squamata: Colubridae) with the Description of a New
1137   Species from India. Herpetologica 78(1): 51–73.
1138   https://doi.org/10.1655/Herpetologica-D-21-00026.1
1139
1140 Bannikov AG, Darevsky IS, Ischenko VG, Rustamov EA, Scherbak NN (1977) Opredelitel'
1141   zemnovodnykh I presmykayuschikhsya SSSR (The guide to amphibians and reptiles of the
1142   USSR). Prosveschenie, Moscow, 414 pp. (in Russian)

1143

1144   Barkat AI, Rabbe MF (2022) A confirmed record of Russell's kukri (*Oligodon russelius*) from
1145   Bangladesh. Taprobanica 11(1): 44.
1146   https://doi.org/10.47605/tapro.v11i1.280

1147

1148   Bauer AM (2003) On the status of the name *Oligodon taeniolatus* (Jerdon, 1853) and its long-
1149   ignored senior synonym and secondary homonym, *Oligodon taeniolatus* (Daudin, 1803).
1150   Hamadryad 27(2): 205–213.

1151

1152   Berg LS (1931) Landscape and geographical zones of the USSR. Izdaniye Instituta
1153   Rastenievodstva, Leningrad (St. Petersburg), 401 pp. (in Russian)

1154

1155   Blyth E (1854a) Notices and descriptions of various reptiles, new or little known [part 2]. Journal
1156   of the Asiatic Society of Bengal 23(3): 287–302.

1157

1158   Blyth E (1854b) Proceedings of the Society. Report of the Curator, Zoological Department.
1159   Journal of the Asiatic Society of Bengal 23(7): 737–740.

1160

1161   Bobrinskoy NA (1923) Guide to snakes of the Turkestan Territory (Russian Turkestan,
1162   Semirechye, Khiva and Transcaspian Region). Middle Asian State University, Tashkent, 14
1163   pp. (in Russian)

1164

1165   Bogdanov OP (1962) Reptiles of Turkmenia. Izdatelstvo Akademii Nauk Turkmenskoi S.S.R.,
1166   Ashkhabad, 260 pp. (in Russian)

1167

1168   Boie, H. (1826) Merkmale einiger japanischen Lurche. Isis von Oken 19(2): cols. 203–216.

1169

1170   Brown JL, Hill DJ, Dolan AM, Carnaval AC, Haywood AM (2018) PaleoClim, high spatial
1171   resolution paleoclimate surfaces for global land areas. Scientific Data 5: 180254.
1172   https://doi.org/10.1038/sdata.2018.254

1173

1174   Brück G (1968) Zur Herpetofauna Afghanistans. Věstník Československé Společnosti
1175   Zoologické, Acta Societatis Zoologicae Bohemoslovenicae 32: 201–208.

1176

1177   Cantor T (1839) Spicilegium Serpentium Indicorum [parts 1–2]. Proceedings of the Zoological
1178   Society of London part 7: 31–34 + 49–55.

1179

1180   Chen M, Liu J, Cai B, Li J, Wu N, Guo X (2021) A new species of *Psammophis* (Serpentes:
1181   Psammophiidae) from the Turpan Basin in northwest China. *Zootaxa* 4974(1): 116–134.
1182   https://doi.org/10.11646/zootaxa.4974.1.4

1183

1184 Chernov SA (1935) Two specimens of the genus *Oligodon* (Ophidia, Colubridae) in the USSR.
1185 Doklady Akademii Nauk S.S.S.R. / Comptes rendus (Doklady) de l'Académie des Sciences
1186 de l'URSS 1: 348–352. (in Russian)

1187

1188 Chernov SA (1949) Reptiles of Tajikistan and the genesis of modern herpetofauna of Middle
1189 Asia. Doctoral thesis abstract, Leningrad, 9 pp. (in Russian)

1190

1191 Constable JD (1949) Reptiles from the Indian Peninsula in the Museum of Comparative Zoology.
1192 Bulletin of the Museum of Comparative Zoology at Harvard College 103(2): 59–160.

1193

1194 Das A, Gower DJ, Narayanan S, Pal S, Boruah B, Magar S, Das S, Moulick S, Deepak V (2022)
1195 Rediscovery and systematics of the rarely encountered Blue-bellied kukri snake (*Oligodon*
1196 *melaneus* Wall, 1909) from Assam, India. Zootaxa 5138(4): 417–430.
1197 https://doi.org/10.11646/zootaxa.5138.4.4

1198

1199 Daudin FM (1803) Histoire naturelle, générale et particulière, des reptiles : ouvrage faisant suite
1200 à l'Histoire naturelle générale et particulière, composée par Leclerc de Buffon, et rédigée
1201 par C.S. Sonnini, Member de Plusieurs Sociétés Savantes. Tome sixième. Imprimerie F.
1202 Dufart, Paris, 447 pp. + pls. 71–80.

1203

1204 De Queiroz K (2007) Species Concepts and Species Delimitation. Systematic Biology 56(6):
1205 879–886.
1206 https://doi.org/10.1080/10635150701701083

1207

1208 Deraniyagala PEP (1936) The snake *Oligodon albiventer* (Günther). Spolia Zeylanica 20: 89–91.

1209

1210 Deraniyagala PEP (1955) A Colored Atlas of some Vertebrates from Ceylon, vol. 3. Serpentoid
1211 Reptilia. Ceylon National Museums Publication, Colombo, xix + 112 pp. + 48 pls.

1212

1213 Dotsenko LB (1984) Morphological characters and ecological features of *Oligodon taeniolatus*
1214 (Serpentes, Colubridae). Vestnik Zoologii 1984(4): 23–26. (in Russian)

1215

1216 Dowling HG (1951) A proposed standard system of counting ventrals in snakes. British Journal
1217 of Herpetology 1: 97–99.

1218

1219 Dufresnes C, Mahony S, Prasad VK, Kamei RG, Masroor R, Khan MA, Al-Johany AM, Gautam
1220 KB, Gupta SK, Borkin LJ, Melnikov DA, Rosanov JM, Skorinov DV, Borzée A, Jablonski
1221 D, Litvinchuk SN (2022) Shedding light on taxonomic chaos: Diversity and distribution of

1222   South Asian skipper frogs (Anura, Dicroglossidae, *Euphlyctis*). Systematics and
1223   Biodiversity 20(1): 2102686.
1224   https://doi.org/10.1080/14772000.2022.2102686
1225

1226 Duméril C, Bibron G, Duméril AHA (1854) Erpétologie Générale ou Histoire Naturelle
1227   Complète des Reptiles. Tome septième. Première Partie, Comprenant l'Histoire des
1228   Serpents Non Venimeux. Librairie Encyclopédique de Roret, Paris, vii + xvi + 780 pp + 1
1229   folding table + pls. 59, 62–69, 76, 79–83
1230

1231 Eichwald KE (1831) Zoologia Specialis quam expositis Animalibus tum Vivis tum Fossilibus
1232   Potissimuni rossiae in Universum, et Poloniae in Specie, in usum Lectionum Publicarum in
1233   Universitate Caesarea Vilnensi Habendarum. Pars Posterior; Specialem expositionem
1234   Spondylzoorum Continents, Pars Posterior. Jospehi Zawadski, Vilnius. 3 blank pgs. + 404
1235   pp. + 2 folding pls.
1236

1237 Eskandarzadeh N, Rastegar-Pouyani N, Rastegar-Pouyani E, Zargan J, Hajinourmohamadi A,
1238   Nazarov RA, Sami S, Rajabizadeh M, Nabizadeh H, Navaian M (2020) A new species of
1239   *Eryx* (Serpentes: Erycidae) from Iran. Zootaxa 4767(1): 182–192.
1240   https://doi.org/10.11646/zootaxa.4767.1.8
1241

1242 Fordham DA, Saltré F, Haythorne S, Wigley TML, Otto-Bliesner BL, Chan KC, Brook BW
1243   (2017) PaleoView: a tool for generating continuous climate projections spanning the last
1244   21,000 years at regional and global scales. Ecography 40(11): 1348–1358.
1245   https://doi.org/10.1111/ecog.03031
1246

1247 Geptner VG (1938) Zoogeographical features of the desert fauna of Turkestan and its origin.
1248   Bulleten' Moskovskogo Obschestva Ispytateley Prirody / Bulletin of Moscow Society of
1249   Nature Researchers, Biological series 47(5–6): 329–338. (in Russian)
1250

1251 Gowande G, Pal S, Jablonski D, Masroor R, Phansalkar PU, Dsouza P, Jayarajan A, Shanker K
1252   (2021) Molecular phylogenetics and taxonomic reassessment of the widespread agamid
1253   lizard *Calotes versicolor* (Daudin, 1802) (Squamata, Agamidae) across South Asia.
1254   Vertebrate Zoology 71: 669–696. https://doi.org/10.3897/vz.71.e62787
1255

1256 Green MD (2010) Molecular Phylogeny of the Snake Genus *Oligodon* (Serpentes: Colubridae),
1257   with an Annotated Checklist and Key. M.S. Thesis, University of Toronto, Toronto, 169 pp.
1258

1259 Green MD, Orlov NL,Murphy RW (2010) Toward a phylogeny of the Kukri snakes, genus
1260   *Oligodon*. Asian Herpetological Research, 1: 1–21.
1261

Günther ACLG (1862) On new species of snakes in the collection of the British Museum. The
    Annals and Magazine of Natural History, Zoology, Botany, and Geology 9: 52–67.

Hall T (1999) BioEdit: a user-friendly biological sequence alignment editor and analysis program
    for Windows 95/98/NT. Nucleic Acids Symposium Series 41: 95–98.

Hoang DT, Chernomor, O, von Haeseler A, Minh BQ, Vinh LS (2018) UFBoot2: improving the
    ultrafast bootstrap approximation. Molecular Biology and Evolution 35(2): 518–522.
    https://doi.org/10.1093/molbev/msx281

Hoorn C, Ohja T, Quade J (2000) Palynological evidence for vegetation development and
    climatic change in the Sub-Himalayan Zone (Neogene, Central Nepal). Palaeogeography,
    Palaeoclimatology, Palaeoecology 163: 133–161.
    https://doi.org/10.1016/S0031-0182(00)00149-8

Huelsenbeck JP, Hillis DM (1993) Success of Phylogenetic Methods in the Four-Taxon Case.
    Systematic Biology 42(3): 247–264.
    https://doi.org/10.1093/sysbio/42.3.247

iNaturalist (2022) iNaturalist.org. *iNaturalist*. Available from: iNaturalist.org/home (accessed 31
    October 2022)

Jablonski D, Koleska D (2017) Molecular identification of *Eremias stummeri* (Squamata:
    Lacertidae) as a prey for *Gloydius halys* complex (Serpentes: Viperidae) from Kyrgyzstan.
    Phyllomedusa: Journal of Herpetology 16(1): 121–124.
    https://doi.org/10.11606/issn.2316-9079.v16i1p121-124

Jablonski D, Basit A, Farooqi J, Masroor R, Böhme W (2021) Biodiversity research in a
    changing Afghanistan. Science 372(6549): 1402.
    https://doi.org/10.1126/science.abj8118

Jerdon TC (1853) Catalogue of reptiles inhabiting the peninsula of India. Journal of the Asiatic
    Society of Bengal 22: 461–479 + 522–534.

Kaiser CM, O'Shea M, Kaiser H (2019) A new species of Indo-Papuan groundsnake, genus
    Stegonotus Duméril et al., 1854 (Serpentes, Colubridae), from the Bird's Head Peninsula of
    West Papua, Indonesia, with comments on differentiating morphological characters.
    Zootaxa 4590(2): 201–230.
    https://doi.org/10.11646/zootaxa.4590.2.1

1302 Karger DN, Conrad O, Böhner J, Kawohl T, Kreft H, Soria-Auza RW, Zimmermann NE, Linder
1303   HP, Kessler M (2017) Climatologies at high resolution for the earth's land surface areas.
1304   Scientific Data 4: 170122.
1305   https://doi.org/10.1038/sdata.2017.122
1306
1307 Katoh K, Standley DM (2013) MAFFT Multiple Sequence Alignment Software Version 7:
1308   Improvements in Performance and Usability. Molecular Biology and Evolution 30(4): 772–
1309   780.
1310   https://doi.org/10.1093/molbev/mst010
1311
1312 Khan MS (2002) Guide to the Snakes of Pakistan. Edition Chimaira, Frankfurt au Main, 265 pp.
1313
1314 Král B (1969) Notes on the Herpetofauna of Certain Provinces of Afghanistan. Zoologické Listy
1315   18(1): 55–66.
1316
1317 Kumar S, Stecher G, Tamura, K (2016) MEGA7: Molecular Evolutionary Genetics Analysis
1318   Version 7.0 for Bigger Datasets. Molecular Biology and Evolution 33(7): 1870–1874.
1319   https://doi.org/10.1093/molbev/msw054
1320
1321 Latifi M (1991) The snakes of Iran (English edition). In: Leviton AE, Zug GR (Eds)
1322   Contributions to Herpetology, Number 7. Society for the Study of Amphibians and Reptiles,
1323   Oxford, viii + 159 pp. + 25 pls.
1324
1325   Latifi M (2000) Snakes of Iran, 3rd edition. Tehran: Department of the Environment. 237 pp. (in
1326   Farsi)
1327
1328 Linnaeus CV (1758) Systema naturae per regna tria naturae: secundum classes, ordines, genera,
1329   species, cum characteribus, differentiis, synonymis, locis. Tomus I. Edito Decima,
1330   Reformata. Laurentii Salvii, Holmiae [Stockholm], iii + 824 pp.
1331
1332 Mahony S, Kamei RG (2021) A new species of *Cyrtodactylus* Gray (Squamata: Gekkonidae)
1333   from Manipur State, northeast India, with a critical review highlighting extensive errors in
1334   literature covering bent-toed geckos of the Indo-Burma region. Journal of Natural History
1335   55(39–40): 2445–2480.
1336   https://doi.org/10.1080/00222933.2021.1994667
1337
1338 Merceron G, Blondel C, Brunet M, Sen S, Solounias N, Viriot L, Heintz E (2004) The Late
1339   Miocene paleoenvironment of Afghanistan as inferred from dental microwear in
1340   artiodactyls. Palaeogeography, Palaeoclimatology, Palaeoecology 207: 143–163.
1341   https://doi.org/10.1016/j.palaeo.2004.02.008

1342

1343 Mertens R (1969) Die Amphibien und Reptilien West-Pakistans. Stuttgarter Beiträge zur
1344   Naturkunde 197: 1–96.

1345

1346 Minton SA (1962) An annotated key to the amphibians and reptiles of Sind and Las Bela, West
1347   Pakistan. American Museum Novitates 2081: 1–60.

1348

1349 Minton SA (1966) A contribution to the herpetology of West Pakistan. Bulletin of the American
1350   Museum of Natural History 134(2): 29–184 + pls. 9–36.

1351

1352 Mirza ZA, Bhardwaj VK, Patel H (2021) A new species of snake of the genus *Oligodon* Boie in
1353   Fitzinger, 1826 (Reptilia, Serpentes) from the Western Himalayas. Evolutionary Systematics
1354   5: 335–345.
1355   https://doi.org/10.3897/evolsyst.5.72564

1356

1357 Modarres MH, Lahijani HAK, Keshavarz N, Lahaye Y, Rehfeld K, Manttari I, Naderi-Beni A,
1358   Ojala A, Moradpour M (2019) Late Tortonian – Piacenzian multi-proxy record of Asian
1359   southwest monsoon intensification: evidence from Coastal Makran, southeast Iran.
1360   Canadian Journal of Earth Sciences 56: 347–362.
1361   https://doi.org/10.1139/cjes-2018-0071

1362

1363 Nguyen HN, Tran BV, Nguyen LH, Neang T, Yushchenko PV, Poyarkov NA (2020) A new
1364   species of *Oligodon* Fitzinger, 1826 from the Langbian Plateau, southern Vietnam, with
1365   additional information on *Oligodon annamensis* Leviton, 1953 (Squamata: Colubridae).
1366   *PeerJ* 8: e8332.
1367   https://doi.org/10.7717/peerj.8332

1368

1369 Nguyen L-T, Schmidt HA, von Haeseler A, Minh BQ (2015) IQ-TREE: A Fast and Effective
1370   Stochastic Algorithm for Estimating Maximum-Likelihood Phylogenies. Molecular Biology
1371   and Evolution 32(1): 268–274.
1372   https://doi.org/10.1093/molbev/msu300

1373

1374 Nikolsky AM (1902) Gady i ryby (Herpetiles and Fishes). Brockhaus-Efron publishing, St.
1375   Petersburg, 872 pp. (in Russian and Latin)

1376

1377 Nikolsky AM (1903a) *Contia transcaspica* n. sp. (Ophidia, Colubridae). Annuaire du Musée
1378   Zoologique de l'Académie des Sciences de St. Pétersbourg 8(1): 11−13. (in Russian and
1379   Latin, with French titles)

1380

1381 Nikolsky AM (1903b) Sur trois nouvelles espèces de reptiles, recueillis par Mr. N. Zarudny dans
1382   la Perse orientale en 1901 [*Alsophylax persicus* sp.n., *Contia bicolor* sp.n., et *Bufo persicus*
1383   sp.n.]. Annuaire du Musée Zoologique de l'Académie des Sciences de St. Pétersbourg 8(1):
1384   95–98. (in Russian and Latin, with French titles)

1385

1386 Nurgeldyev ON, Shammakov S, Atayev Ch (1970) On distribution of some snake species in
1387   Turkmenia. In: Gladkov NA (Eds), Zhivotnyi mir Turkmenii (Animal Life of Turkmenia).
1388   Ylym Press, Ashkhabad, 187–190. (in Russian)

1389

1390 Orlov NL, Atayev ChA, Ananjeva NB, Shammakov SM, Shestopal AA (2018) Pieces of tropical
1391   mesophilic herpetofauna in the deserts of Turkmenistan. In: Herpetological and
1392   ornithological research: current aspects. Dedicated to the 100th Anniversary of A.K.
1393   Rustamov (1917–2005). KMK Scientific Press, St. Petersburg–Moscow, 58–67. (in Russian
1394   with English abstract)

1395

1396 Padial JM, Miralles A, De la Riva I, Vences M (2010) The integrative future of taxonomy.
1397   Frontiers in Zoology 7: 1–14.
1398   https://doi.org/10.1186/1742-9994-7-16

1399

1400 Posada D, Crandall KA (1998) MODELTEST: testing the model of DNA substitution.
1401   Bioinformatics 14(9): 817–818.
1402   https://doi.org/10.1093/bioinformatics/14.9.817

1403

1404 Phillips SJ, Anderson RP, Schapire RE (2006) Maximum entropy modeling of species
1405   geographic distributions. Ecological Modelling 190: 231–259.
1406   https://doi.org/10.1016/j.ecolmodel.2005.03.026

1407

1408 QGIS Development Team (2021) QGIS Geographic Information System. Open Source
1409   Geospatial Foundation Project. Available from: http://qgis.osgeo.org (accessed 11
1410   December 2022)

1411

1412 Rai TP, Adhikari S, Antón PG (2022) An Updated Checklist of Amphibians and Reptiles of
1413   Nepal. ARCO-Nepal Newsletter 23: 1–23.

1414

1415 Rajabizadeh M (2018) Snakes of Iran. Iranshensai Publishing, Tehran, 496 pp. (in Farsi)

1416

1417 Rajabizadeh M, Pyron RA, Nazarov RA, Poyarkov NA, Adriaens D, Herrel A (2020) Additions
1418   to the phylogeny of colubrine snakes in Southwestern Asia, with description of a new genus
1419   and species (Serpentes: Colubridae: Colubrinae). PeerJ 8: e9016.
1420   https://doi.org/10.7717/peerj.9016

1421

1422 Rambaut A, Suchard MA, Xie D, Drummond AJ (2020) Tracer v1.6. Available from:
1423   http://beast.bio.ed.ac.uk/Tracer (accessed 29 May 2018)

1424

1425 Ronquist F, Teslenko M, van der Mark P, Ayres DL, Darling A, Höhna S, Larget B, Liu L,
1426   Suchard MA, Huelsenbeck JP (2012) MrBayes 3.2: Efficient Bayesian Phylogenetic
1427   Inference and Model Choice Across a Large Model Space. Systematic Biology 61(3): 539–
1428   542.
1429   https://doi.org/10.1093/sysbio/sys029

1430

1431 Rustamov EA, Atayev Ch (1976) New data on the herpetofauna of Turkmenistan. Proceedings of
1432   the Academy of Sciences of the Turkmen SSR. Series of Biological Sciences 5: 47–53. (in
1433   Russian)

1434

1435 Rustamov AK, Sopyev O (1994) Vertebrates in the Red Data Book of Turkmenistan. In: Fet V,
1436   Atamuradov KI (Eds), Biogeography and Ecology of Turkmenistan. Monographiae
1437   Biologicae. Springer, Dordrecht, 205–230.

1438

1439 Rustamov [Rustamow] AK (2011) Wildlife of Turkmenistan and its protection. Ylym Press,
1440   Ashgabat, 502 pp. (in Turkmen)

1441

1442 Shaw G (1802) General zoology, or Systematic natural history, Volume III, Part 2. G. Kearsley,
1443   Thomas Davison, London, vi + 313–615 pp. + pls. 87–140

1444

1445 Szczerbak NN (1979) New records of lizards and snakes in Middle Asia. Vestnik Zoologii 1:,
1446   68–70. (in Russian)

1447

1448 Szczerbak NN (1994) Zoogeographic Analysis of the Reptiles of Turkmenistan. In: Fet V,
1449   Atamuradov KI (Eds), Biogeography and Ecology of Turkmenistan. Monographiae
1450   Biologicae. Springer, Dordrecht, 307–328.

1451

1452 Szczerbak NN, Khomustenko YD, Golubev MV (1986) Amphibians and reptiles of the
1453   Kopetdagh State Reserve and adjacent territories. In: Szczerbak NN (Ed), Nature in Central
1454   Kopetdagh. Ylym Press, Ashkhabad, 76–110 pp. (in Russian)

1455

1456 Shestopal AA, Rustamov EA (2018a) An annotated Checklist of the fauna of amphibians and
1457   reptiles of Turkmenistan, ver. 2018. In: Herpetological and ornithological research: current
1458   aspects. Dedicated to the 100th Anniversary of A.K. Rustamov (1917–2005). KMK
1459   Scientific Press, St. Petersburg–Moscow, 31–42. (in Russian with English abstract)

1460

1461   Shestopal AA, Rustamov EA (2018b) New data on the distribution and numbers of reptiles in
1462   some landscapes of Turkmenistan. In: Herpetological and ornithological research: current
1463   aspects. Dedicated to the 100th Anniversary of A.K. Rustamov (1917–2005). KMK
1464   Scientific Press, St. Petersburg–Moscow, 43–57. (in Russian with English abstract)
1465
1466   Sindaco RA, Venchi A, Grieco C (2013) The Reptiles of the Western Palearctic, Volume 2:
1467   Annotated Checklist and Distributional Atlas of the Snakes of Europe, North Africa, Middle
1468   East and Central Asia, with an Update to Volume 1. Edizioni Belvedere, Latina, 543 pp. +
1469   342 col. photos + 184 col. maps.
1470
1471   Smith MA (1943) The Fauna of British India, Ceylon and Burma, including the whole of the
1472   Indo-chinese subregion. Reptilia and Amphibia. Vol. III, Serpentes. Taylor & Francis,
1473   London, xii + 583 pp.
1474
1475   Tamura K, Stecher G, Peterson D, Filipski A, Kumar S (2013) MEGA6: Molecular Evolutionary
1476   Genetics Analysis Version 6.0. Molecular Biology and Evolution 30(12): 2725–2729.
1477   https://doi.org/10.1093/molbev/mst197
1478
1479   Taylor EH (1950) The Snakes of Ceylon. The University of Kansas Science Bulletin 33(2): 519–
1480   603 + pls. 12–25.
1481
1482   Terentjev PV, Chernov SA (1949) Opredelitel' presmykayuschikhsiya I zemnovodnykh (The
1483   Guide to Reptiles and Amphibians). Sovetskaya Nauka, Moscow, 320 pp. (in Russian)
1484
1485   Trifinopoulos J, Nguyen L-T, von Haeseler A, Minh BQ (2016) W-IQ-TREE: a fast online
1486   phylogenetic tool for maximum likelihood analysis. Nucleic Acids Research 44(1): 232–
1487   235.
1488   https://doi.org/10.1093/nar/gkw256
1489
1490   Uetz P, Freed P, Aguilar R, Reyes F, Hošek J (2023) The Reptile Database. Available from:
1491   http://www.reptile-database.org/ (accessed 1 January 2023).
1492
1493   Wagner P, Bauer AM, Leviton AE, Wilms TM, Böhme W (2016a) A Checklist of the
1494   Amphibians and Reptiles of Afghanistan - Exploring Herpetodiversity using Biodiversity
1495   Archives. Proceedings of the California Academy of Sciences, Series 4 63(13): 457–565.
1496
1497   Wagner P, Tiutenko A, Mazepa G, Borkin LJ, Simonov E (2016b) Alai! Alai! – a new species of
1498   the *Gloydius halys* (Pallas, 1776) complex (Viperidae, Crotalinae), including a brief review
1499   of the complex. Amphibia-Reptilia 37(1): 15–31.
1500   https://doi.org/10.1163/15685381-00003026

1501

1502   Wall F (1909) Notes on snakes from the neighbourhood of Darjeeling. Journal of the Bombay
1503   Natural History Society 19: 337–357 + 1 pl.

1504

1505   Wall F (1910) A new snake from Assam (*Oligodon erythrorachis*). The Journal of the Bombay
1506   Natural History Society 19: 923-924 + 1 pl.

1507

1508   Wall F (1921) Ophidia taprobanica; or, The snakes of Ceylon. H.R. Cottle, govt. printer,
1509   Colombo, xxii + errata + 581 pp. + 1 foldout map.

1510

1511   Wall F (1923) A Review of the Indian Species of the Genus *Oligodon* Suppressing the Genus
1512   *Simotes* (Ophidia). Records of the Zoological Survey of India 25(3): 305–334.
1513   https://doi.org/10.26515/rzsi/v25/i3/1923/162698

1514

1515   Warren DL, Glor RE, Turelli M (2010) ENMTools: a toolbox for comparative studies of
1516   environmental niche models. Ecography 33: 607–611.
1517   https://doi.org/10.1111/j.1600-0587.2009.06142.x

1518

1519   Welch KRG (1983) Herpetology of Europe and Southwest Asia: a checklist and bibliography of
1520   the orders Amphisbaenia, Sauria and Serpentes. Robert E. Krieger Publishing Company,
1521   Malabar, Florida, 135 pp.

1522

1523   Yushchenko PV, Lee JL, Neang T, Seiha H, Tan NV, Vogel G, Poyarkov Jr NA (2023a). A
1524   taxonomic re-assessment of *Oligodon cinereus* (Günther, 1864) (Squamata, Serpentes,
1525   Colubridae) populations from southern Indochina. Vertebrate Zoology 73: 75–96.
1526   https://doi.org/10.3897/vz.73.e91230

1527

1528   Yushchenko PV, Lee JL, Pham HM, Geissler P, Syromyatnikova EV, Poyarkov Jr NA (2023b).
1529   The taxonomic status of the kukri snake *Oligodon arenarius* Vassilieva, 2015 with a
1530   redescription of *Oligodon macrurus* (Angel, 1927) (Squamata, Serpentes,
1531   Colubridae). Vertebrate Zoology 73: 97–125.
1532   https://doi.org/10.3897/vz.73.e96958

1533

1534 Supplementary Material and Table Legends:

1535

1536 **Supplementary Material 1.** Other Specimens of *Oligodon* examined, organized based on their

1537 morphological identification based on Bandara et al. (2022).

1538

1539 **Supplementary Table 1.** Tabled list of localities of *Oligodon transcaspicus* **comb. et stat. nov.**

1540 with latitude and longitude coordinates used for species distribution modelling.

1541

1542 **Supplementary Table 2.** Primers used in this study

1543

1544   Table Legends:

1545

1546   **Table 1. Sequences and voucher specimens of *Oligodon* and outgroup taxa used in**
1547   **molecular analyses of this study.**
1548   Note that the numbers (column one) included in this table are not the same as those found in
1549   other tables or figures. Acronyms present here that are not noted in the materials and methods
1550   include the following: CHS, unknown field tag series (from Li et al., 2020); KIZ, Kunming
1551   Institute of Zoology, Chinese Academy of Sciences, Kunming, China; NCBS, National Center
1552   for Biological Sciences, Bangalore, India; RAP, field tags of R. Alexander Pyron; ROM, Royal
1553   Ontario Museum, Toronto, Canada; RS, field tags of Ruchira Somaweera; SIEZC, Department of
1554   Zoology, Southern Institute of Ecology, Ho Chi Minh City, Vietnam; SYNU, Shenyang Normal
1555   University, Shenyang, China; TNHC, Texas Natural History Collections, Austin, USA; UMMZ,
1556   University of Michigan Museum of Zoology, Ann Arbor, USA; ZMUVAS, Zoological Museum
1557   of the University of Veterinary and Animal Sciences, Punjab, Pakistan. Additional abbreviations
1558   include NP: National Park, NR: Nature Reserve, and WS: Wildlife Sanctuary.

1559

1560   **Table 2. Selected morphological characters of *Oligodon transcaspicus* comb. et stat. nov.**
1561   **based on examined specimens.**
1562   Abbreviations for males and females are denoted by (m) or (f) respectively. For abbreviations of
1563   characters, see materials and methods section for details.

1564

1565   **Table 3. Morphological comparisons of *Oligodon russelius* specimens from Afghanistan,**
1566   **northern India, and Pakistan hitherto recognized as *Oligodon* "*arnensis*" or *Oligodon***
1567   ***churahensis*.**
1568   Data from the literature are combined from multiple authors unless denoted with an asterisk (*),
1569   which indicates that only a single source was used. Abbreviations for males and females are
1570   denoted by (m) or (f) respectively and (total) is used to indicate that the data combines both
1571   sexes or combines the total number of body and tail blotches.

1572

1573   **Table 4. Pairwise matrix of genetic distances between and within *Oligodon* species sampled**
1574   **in this study.**
1575   Uncorrected p-distances (given as percentages) are based on sequences of the cytochrome *b*
1576   mtDNA gene are shown below the diagonal. Intraspecific genetic p-distances are shown along
1577   the diagonal and are highlighted in bold. See Table 1 for the list of samples used to create this
1578   matrix.

1579

1580   Figure Legends:

1581

1582   **Figure 1. Approximate distribution and location of samples utilized in this study for**

1583   **molecular and morphological analyses (A); and approximate distribution of *Oligodon***

1584   ***transcaspicus* comb. et stat. nov in the Köpet–Dag Mountain range of Iran and**

1585   **Turkmenistan (B).**

1586   Triangle icons denote specimens with only molecular data; square icons denote specimens with

1587   only morphological data; rhombic icons denote specimens without molecular and morphological

1588   data (only locality is known); round icons denote specimens with both molecular and

1589   morphological data. Stars/asterisks next to numbers indicate type localities. Localities: (1)

1590   Ashgabat, Ahal Prov., Turkmenistan (type locality of *Oligodon transcaspicus* **comb. et stat.**

1591   **nov**); (2) Chuli, Ahal Prov., Turkmenistan; (3) Geok-Tepe, Ahal Prov., Turkmenistan; (4)

1592   Karanki, Ahal Prov., Turkmenistan; (5) "Goalon" (Goudan), Ahal Prov., Turkmenistan; (6)

1593   Aidere, Ahal Prov., Turkmenistan; (7) Bazangan Lake, Razavi Khorasan Prov., Iran; (8) Punjab

1594   Prov., Pakistan; (9) Kallar Kahar, Punjab Prov., Pakistan; (10) Chamba Distr., Himachal

1595   Pradesh, India (type locality of *Oligodon churahensis*); (11) Jalalabad, Nangarhar Prov.,

1596   Afghanistan; (12) Dara-i-Pech district, Kunar Prov., Afghanistan; (13) Maharashtra, India; (14)

1597   Chitwan NP, Bagmati Prov., Nepal; (15) Ganjam, Odisha, India; (16) 24.1 km SW of

1598   Rajamahendravaram, Andhra Pradesh, India; (17) Bangalore, Karnataka, India; (18) Tamil Nadu,

1599   India; (19) Puttalam Distr., North Western Prov., Sri Lanka; (20) Udawalawe National Park, Uva

1600   Prov.; (21) Monargala Distr., Southern Prov., Sri Lanka; (22) Hambantota Distr., Southern Prov.,

1601   Sri Lanka; (23) Gampaha Distr., Western Prov., Sri Lanka; (24) Polonnaruwa Distr., North

1602   Central Prov., Sri Lanka; (25) Paramikulam, Kerala, India; (26) Barengabari, Assam, India.

1603

1604   **Figure 2. Phylogenetic tree of *Oligodon* derived from the analysis of 3,019 bp of 12S rRNA,**

1605   **16S rRNA and cyt *b* mitochondrial DNA gene sequences.**

1606   For voucher specimen information and GenBank accession numbers see Table 1. Numbers at

1607   tree nodes correspond to BI PP/ML BS support values, respectively; n-dash denotes no support.

1608   Outgroup taxa are not shown. Colors of clades and locality numbers correspond to Figure 1.

1609

1610   **Figure 3. Species distribution model (SDM) map based on geolocation points of *Oligodon***

1611   ***transcaspicus* comb. et stat. nov. from Iran and Turkmenistan.**

1612   Darker red coloration indicates more suitable habitat, whereas lighter colors indicate less suitable

1613   habitat.

1614

1615   **Figure 4. Photographs of the preserved holotype specimen of *Contia transcaspica* (ZISP**

1616   **9868) now *Oligodon transcaspicus* comb. et stat. nov. from "Köpet–Dag, Transcaspica".**

1617   Scale bars equal 10 millimeters. Photos by Konstantin D. Milto.

1618

1619 **Figure 5. Live photographs of *Oligodon transcaspicus* comb. et stat. nov. (ZMMU Re-**
1620 **16687; field number RAN-3264) from Khorasan Province, Iran.**
1621 (a) Right lateral, (b) left lateral, (c) ventral, (d) ventral views of the head, and (e) general habitus.
1622 Photographs by Roman A. Nazarov.
1623
1624 **Figure 6. Two unvouchered specimens of *Oligodon transcaspicus* comb. et stat. nov.**
1625 Specimens photographed from (a) Podere, Sumbar Valley, Turkmenistan and (b) Seqiz-Khan
1626 Gorge, Turkmenistan. Photographs taken by Alexander V. Pavlenko.
1627
1628 **Figure 7. Photographs of *Oligodon russelius* from Pakistan (a–e) and Afghanistan (f).**
1629 Shown in a–e is specimen CUHC 7904 from Kallar Kahar, Punjab Province, Pakistan, showing
1630 (a) general habitus in life, (b) right lateral, (c) left lateral, (d) dorsal, and (e) ventral views of the
1631 head in preservative. Shown in (f) is a cropped image of *O. russelius* from Kunar Province,
1632 Afghanistan observed on iNaturalist (obs. 110932106). Photographs a–e by Daniel Jablonski,
1633 photograph f taken by iNaturalist user Mohammad Farooq, image used under Creative Commons
1634 License CC BY-NC.
1635
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1637

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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4 Zoology, Chinese Academy of Sciences, Kunming, China; NCBS, National Center for Biological Sciences, Bangalore, India; RAP,
5 field tags of R. Alexander Pyron; ROM, Royal Ontario Museum, Toronto, Canada; RS, field tags of Ruchira Somaweera; SIEZC,
6 Department of Zoology, Southern Institute of Ecology, Ho Chi Minh City, Vietnam; SYNU, Shenyang Normal University, Shenyang,
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.

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

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

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.

1 **Table 3. Morphological comparisons of *Oligodon russelius* specimens from Afghanistan,**
2 **northern India, and Pakistan hitherto recognized as *Oligodon* "*arnensis*" or *Oligodon***
3 ***churahensis*.**
4 Data from the literature are combined from multiple authors unless denoted with an asterisk (*),
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*)

10

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.**
2 Uncorrected p-distances (given as percentages) are based on sequences of the cytochrome *b* mtDNA gene are shown below the
3 diagonal. Intraspecific genetic p-distances are shown along the diagonal and are highlighted in bold. See Table 1 for the list of samples
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.
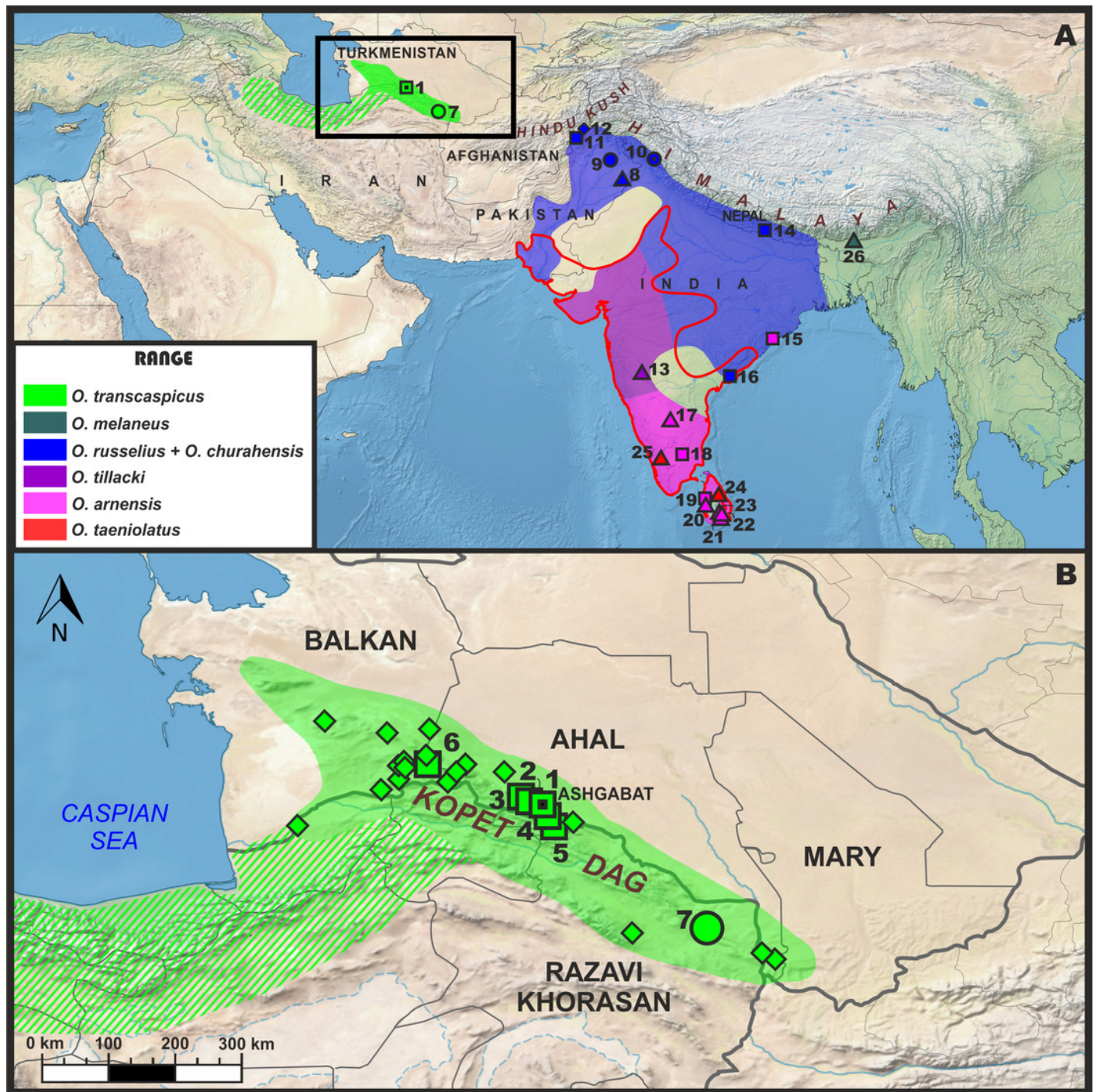
Figure 2

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.
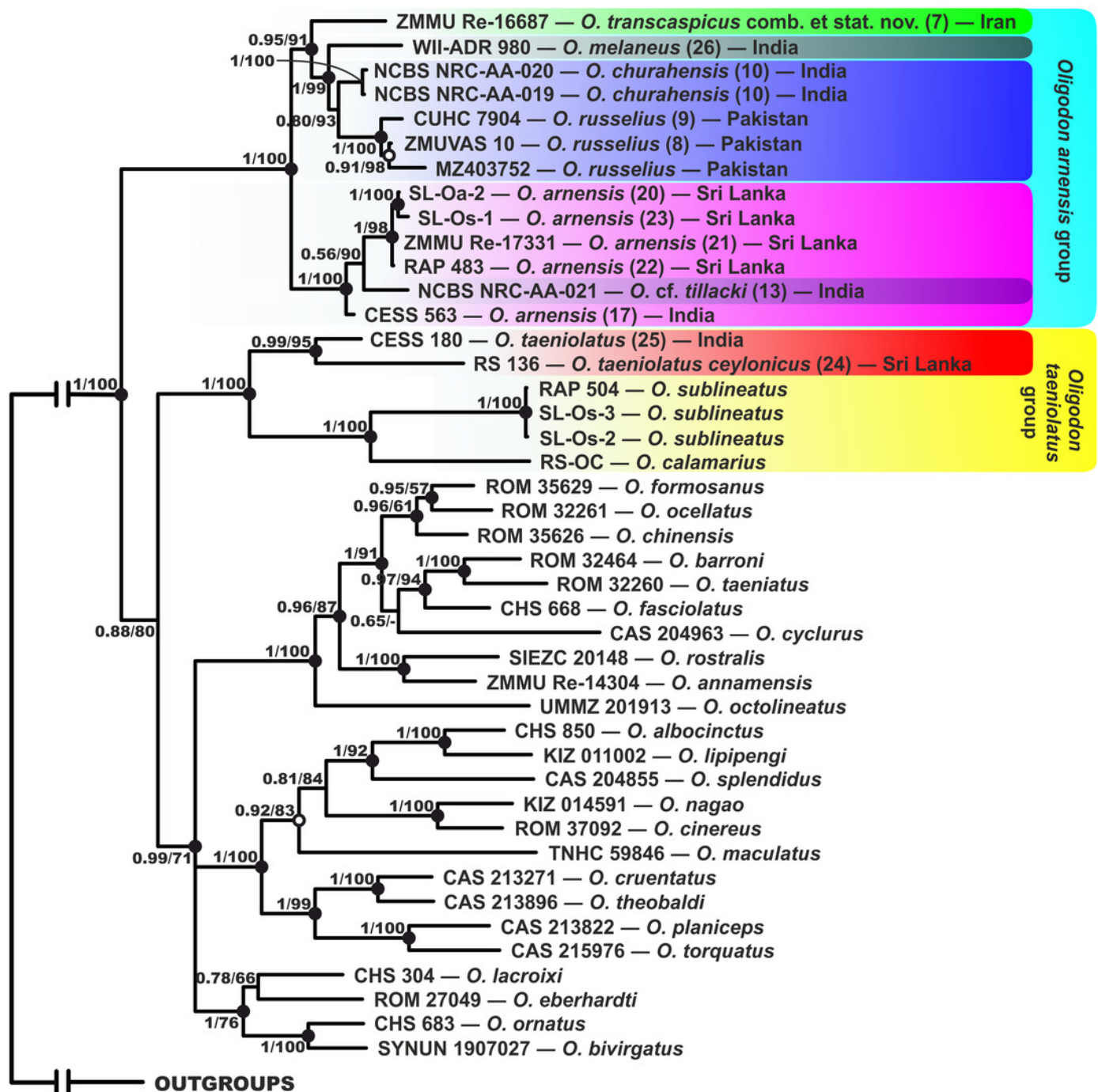
Figure 3

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.
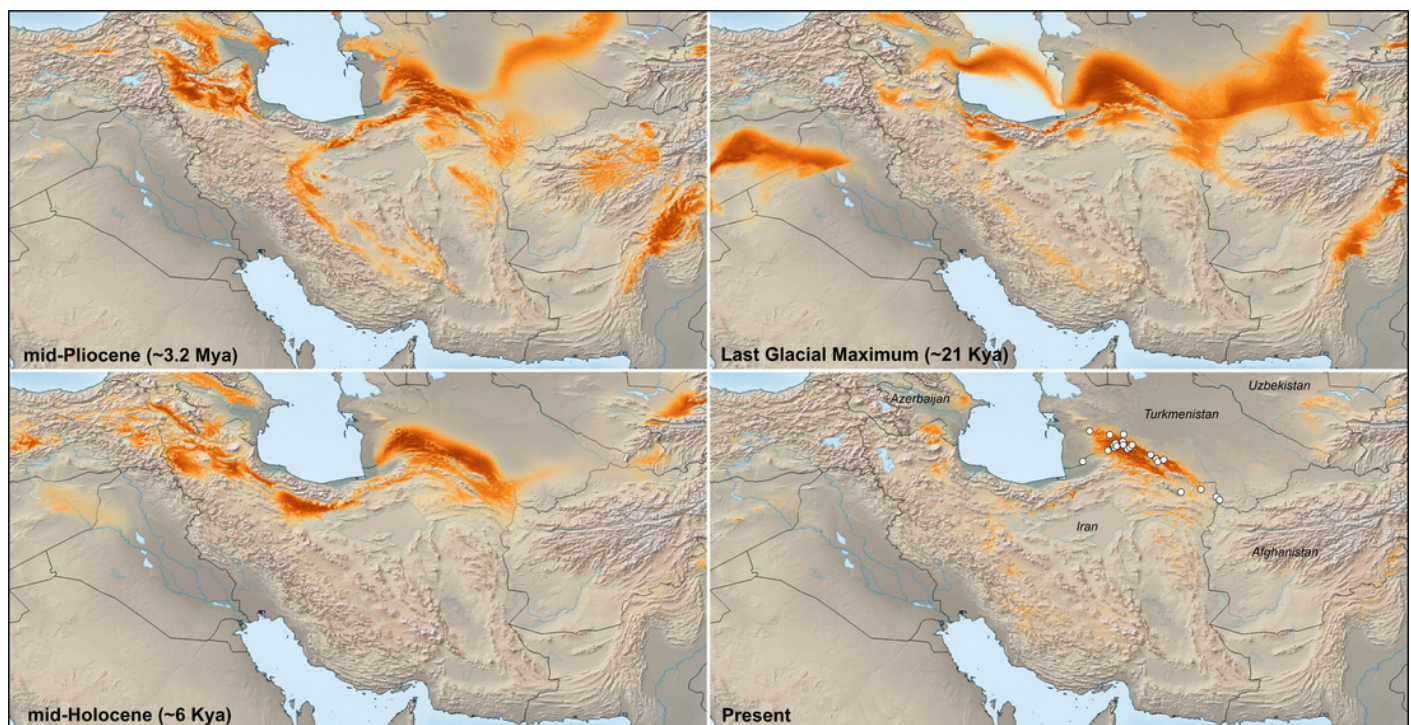
Figure 4

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.
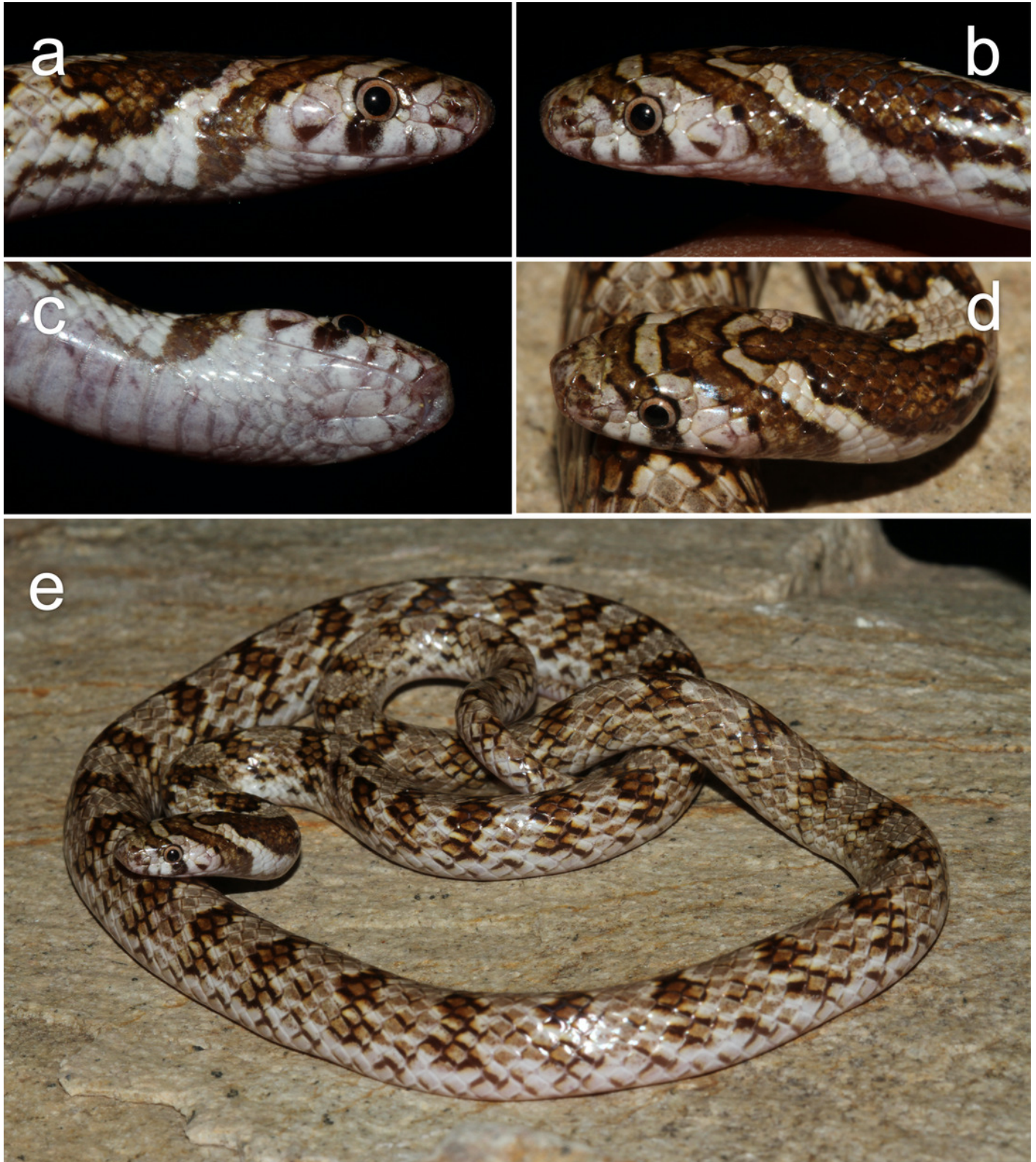
Figure 6

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.