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From the Woods to the Great Steppe: The Phylogenetic Affinities and New Distribution Records of the Smooth Snake *Coronella austriaca* in Kazakhstan

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Abstract: The smooth snake (*Coronella austriaca*) has a wide but fragmented distribution across the Western Palearctic, with limited records in Kazakhstan. This study aims to provide an updated distribution map and to explore the phylogenetic affinities of *C. austriaca* in Kazakhstan. The species had not been documented for over 60 years until its recent rediscovery in the region. Field surveys conducted between 2019 and 2024 in the West Kazakhstan and Aktobe regions have yielded novel records, including the southernmost observation in the Mugodzhar mountain range. Mitochondrial DNA analysis confirmed that the Kazakh populations belong to the Eastern lineage, sharing haplotypes with specimens from the northwestern Caucasus and Crimea. Habitat assessment revealed that the species' distribution is restricted to open habitats of petrophytic and calciphyte steppe communities on chalks and rocky steppes. Of particular interest is that 70% of the observed individuals exhibited patternless coloration, suggesting the potential for regional morphological variation. These findings offer the first evidence for the phylogenetic affiliation of the smooth snake in Kazakhstan and reflect its rarity in the country, highlighting the need for local conservation efforts, including habitat protection and population monitoring.

Keywords: Ophidia; Colubridae; Western Palearctic; DNA barcode; species range; habitats

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1. Introduction

The smooth snake, *Coronella austriaca* Laurenti, 1768, has a wide geographic distribution in the Western Palearctic, ranging from the Iberian Peninsula to the West Siberian Plain, and from the Åland Islands in the Baltic Sea to the northern part of Asia Minor, the southern Caspian region. The species is considered to be rare in most European countries (EU Habitats Directive–Annex IV: animal and plant species of community interest in need of strict protection; Bern Convention–Annex II: strictly protected fauna species) and is included in the Red Data Books of 35 regions of Russia [1]. The smooth snake has been known in Kazakhstan from the literature and museum collections based on several findings from 1871 to 1956, within the boundaries of the modern Aktobe region. Since then, the species was not recorded in the country for more than 60 years, until the new encounters

in 2019–2022 in the West Kazakhstan region, where the species had not been recorded before [2]. It has been suggested that the snake has been overlooked in the country for so long due to the lack of meticulous herpetofaunal surveys in the area coupled with its secretive lifestyle. The conservation status of the *C. austriaca* in Kazakhstan has not yet been assessed at the country level, and the species was recommended for inclusion in *The Red Data Book* of the Republic of Kazakhstan [2].

Multiple phylogenetic lineages of the smooth snake have been revealed in the whole area of its distribution [3,4]. Several molecular studies of geographically limited scope have also been performed for the Iberian Peninsula [5,6], Poland [7], the United Kingdom [8], and Finland [9], making it possible to refine colonization routes and clarify the phylogenetic affinities of peripheral populations. It was found that the Eastern European Plain and the Western Caucasus are occupied by a single phylogenetic lineage named "Eastern" [3,4]. However, the geographic extent of the localities studied in this part of the region was rather limited, and no samples from the northeastern periphery of the species' range (east of the Volga River) have been studied so far. It can be predicted from the phylogeographic patterns of other widespread western Palearctic reptiles [10–13] that this part of the range is also occupied by the Eastern lineage.

In the present study, we updated the distributional data for *C. austriaca* in the northeastern part of its range based on previous records and recent fieldwork results and explored the phylogenetic position of *C. austriaca* from Kazakhstan. This knowledge is essential for guiding future monitoring studies and research programs, facilitating the development of a comprehensive and sustainable strategy to conserve the species.

2. Material and Methods

2.1. Data Collection

From 2019 to 2024, we carried out field surveys of *C. austriaca* in the West Kazakhstan and Aktobe regions of Kazakhstan. We searched for actively moving snakes and looked under rocks and other flat objects. The exact geographical coordinates of presence sites were recorded with GPS (Garmin eTrex H, Garmin Ltd., New Taipei City, Taiwan).

We collated the dataset of reliable distribution records for the northeastern portion of the *C. austriaca* range in Russia and Kazakhstan to comprehensively outline its northern, eastern, and southern distribution limits in the area. Original field survey data, bibliographic records, museum collections, personal reports, GBIF, and iNaturalist (https://www.inaturalist.org (accessed on 3 April 2025)) observations were used to arrange the dataset following the Darwin Core format for biodiversity data (Supplementary Table S1). QGIS Desktop 3.30.0 [14] was utilized to create a map and visualize the records.

2.2. Analysis of Mitochondrial DNA

Total DNA was isolated from four samples consisting of three ethanol-preserved ventral scale samples collected in the field from alive and road-killed specimens and a shed skin sample (Supplementary Table S2). DNA was extracted by a standard procedure including treatment with sodium dodecyl sulfate and proteinase K and subsequent phenol–chloroform extraction [15]. We amplified fragments of the mitochondrial gene of subunit I of cytochrome c oxidase (*COI*) using the vertebrate universal primer pair VUTF (5′-TGTAAAACGACGGCCAGTTCTCAACCAAYCAYAARGAYATYGG-3′) and VUTR (5′-CAGGAAACAGCTATGACTARACTTCTGGRTGKCCRAARAAYCA-3′) [16]. The shed skin sample failed to produce PCR products with these primers and was amplified with a pair of primers L14724NAT (5′-GACCTGCGGTCCGAAAAACCA-3′, [17]) and Natrix_Cytb_Rev2 (5′-AGGGCAAAGAATCGGGTT-3′, [18]) for a fragment of the cytochrome *b* gene (*Cytb*) of shorter length, as the primary goal of the analysis of this

sample was to confirm identification of the shedding. For *COI*, the PCR protocol consisted of a 3 min denaturation step at 95 °C, followed by 35 cycles of denaturation for 30 s at 95 °C, primer annealing for 30 s at 54 °C, and extension for 1 min at 72 °C, with a final extension step at 72 °C for 5 min. *Cytb* amplification conditions followed those in [18]. PCR products were purified by extraction from polyacrylamide gel. Sequencing was performed by the Evrogen company (Moscow, Russia) on an ABI 3500 automated capillary sequencer (Applied Biosystems, Austin, TX, USA) with the BigDye™ Terminator v.3.1 Cycle Sequencing Kit (Thermo Fisher Scientific, Vilnius, Lithuania) using the same primers. New sequences have been deposited in GenBank (NCBI) under accession numbers PV491238-PV491240 and PV504883 (Supplementary Table S2).

The newly obtained sequences were manually curated using Chromas 2.6.2 (Technelysium Pty Ltd., Tewantin, Australia), checked for unexpected stop codons with SeaView 4.4.2 [19], and then searched against the NCBI nucleotide sequence database using the BLASTN algorithm to identify matching haplotypes. To place our data in a phylogeographic context, the obtained *COI* sequences were combined with those available in GenBank (see Supplementary Table S1) and manually aligned, resulting in a dataset with a length of 644 bp and 50 sequences. The gene tree was estimated using a maximum likelihood (ML) approach in IQ-TREE 2.4.0 [20]. The best-fitting partitioning scheme and substitution models by codon position were selected using ModelFinder [21], as implemented in IQ-TREE2. The K3Pu+F+I model was selected for a first partition containing codon positions 1 and 2, and the HKY+F+G4 model was selected for a second partition containing codon position 3. Branch support was assessed by 1000 nonparametric bootstraps. The resulting phylogenetic tree was visualized and edited using FigTree 1.4.4 [22].

3. Results and Discussion

3.1. Distribution Records

On 14 May 2024, we found a female of *C. austriaca* in the border area of West Kazakhstan and Aktobe regions of Kazakhstan (locality 11, Figure 1). The specimen was found in the late afternoon (5 p.m.) under a stone together with a grass snake *Natrix natrix*. This site is located 70 km southeast of our previous encounters in the West Kazakhstan region (localities 9–10, Figure 1, [2]). On 17 May 2024, a piece of shed skin identified as *C. austriaca* (smooth dorsal scales in 19 rows) was found in the Mugodzhar range of the Aktobe region of Kazakhstan (locality 12, Figure 1). The accuracy of the morphological identification was further validated through the sequencing of a *Cytb* fragment (see below). This finding signifies a rediscovery of the species in the Aktobe region since 1956 [23] and the southernmost distribution record in Kazakhstan.

A total of 365 distribution records for *C. austriaca* in the northeastern part of its geographic range in Russia and Kazakhstan were collected and mapped (Figure 1; Supplementary Table S1). Most of the observations (89.6%) were modern (after 2000). Only three observations dated back to the 19th century, and one of them was for the territory of Kazakhstan. The northernmost documented occurrences in the considered area roughly coincided with a latitude of 57° N. The easternmost record for the entire species range (69.5° E longitude) was located at a considerable distance (260–280 km) from the other documented localities. This observation was made from the steep slopes of the right bank of the Ishim River [24], which is surrounded by unfavorable habitats of the southern part of the West Siberian plain. It appears to be disjunct from the primary range. However, the upper reaches of the Ishim River are located in the North Kazakhstan region and possess analogous habitats, suggesting the potential for the occurrence of the smooth snake in this area as well. In the south, the observations were concentrated along the southern Ural Mountains, its foothills, and the Mugodzhar range, with no records of the species

in the surrounding plains. In the West Kazakhstan region (Figure 1, localities 1–11), the species is found exclusively on the steep southern slopes of the Obshchy Syrt upland. This upland extends 500 km southwest from the Ural Mountains to the Bolshoy Uzen River and presumably constitutes the southern distribution limit of the smooth snake in this area. There were no records of the species from the plain steppe area along the eastern bank of the Volga River, and the distribution limit in this area followed the Volga River in a southward direction.

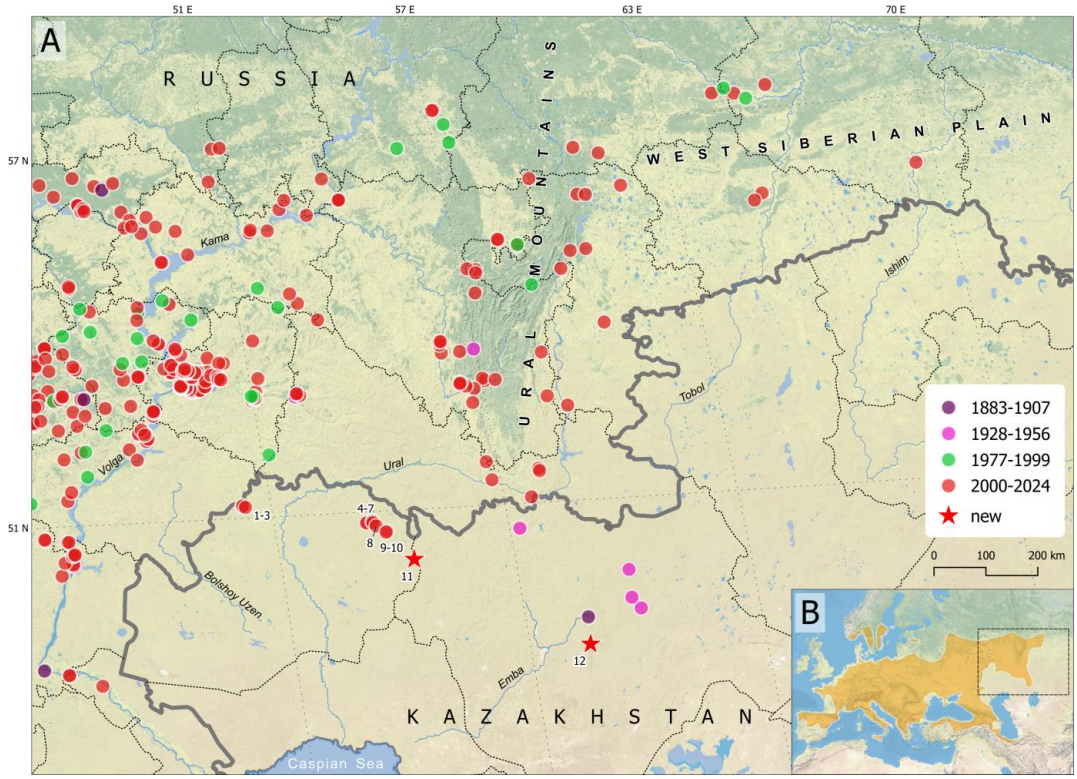


Figure 1. Distribution records for *Coronella austriaca* in the northeastern part of its geographic range. (**A**) Historical and new records are indicated by different colors as explained in the inset legend. Recent records in Kazakhstan are numbered (see Table 1). The administrative boundary between Russia and Kazakhstan (solid gray line) and the boundaries of administrative regions within countries (dashed black lines) are shown. (**B**) A map of the entire geographical range of *C. austriaca* (orange fill) and the area covered by the main map (the rectangle with a dashed border).

Table 1. Modern occurrence records for *Coronella austriaca* in Kazakhstan.

Locality ID	Latitude, N	Longitude, E	Date	GenBank Accession Number/Sample ID
1 *	51.2070	50.2474	20 May 2019	-/-
2 *	51.2157	50.2668	25 April 2022	PV491239/KZ1
3 *	51.1873	50.3282	22 August 2020	-/-
4 *	50.8183	53.3659	3 May 2019	-/-
5 *	50.818	53.3627	3 May 2019	-/-
6 *	50.8385	53.5168	8 August 2019	-/-
7 *	50.8183	53.5242	8 August 2019	-/-
8 *	50.7596	53.5934	18 September 2021	PV491240/GK6
9 *	50.6606	53.8487	9 August 2019	-/-
10 *	50.6446	53.8204	14 May 2020	-/-
11 **	50.1586	54.4172	14 May 2024	PV491238/KZ270
12 **	48.5441	58.5092	17 May 2024	PV504883/KZ348

* Occurrence records from [2]; ** this study.

3.2. Phylogenetic Affinities

Three sequences of a single haplotype of the *COI* (644 bp) were obtained from localities 2, 8, and 11 (Table 1, Figure 1) from Kazakhstan, which completely matched the *C. austriaca* haplotype "RusWestHap3" (KC997593; [9]) from the Rostov region of Russia (approximately 800 km southwest). The gene tree (Figure 2) showed the position of the examined samples in the Eastern clade of *C. austriaca* (sensu [3]). The single sequence of *Cytb* (388 bp) obtained from a shed skin sample from the Mugodzhar Range (locality 12, Figure 1) had a 100% identity with *C. austriaca* isolates "Russia_177", "Russia_180", and "Russia_181" (ON236694–ON236696; [4]) originating from the Crimean Peninsula and northwestern Caucasus (about 1600 km west), which also belong to the Eastern clade.

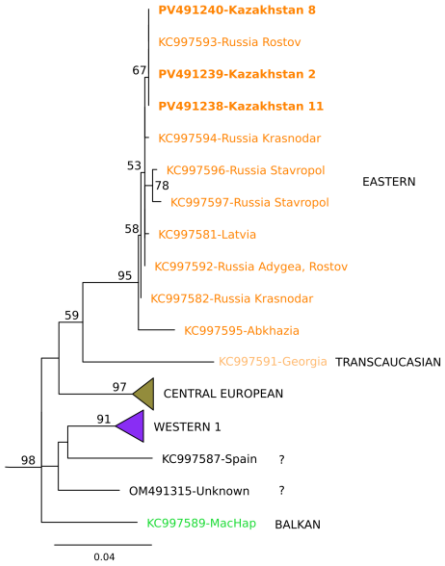


Figure 2. Maximum likelihood *COI* gene tree of *C. austriaca* showing the phylogenetic placement of the examined specimens from Kazakhstan. Phylogenetic clades are colored and named (in capitals) according to [3]. New sequences are indicated by bold font, along with the respective locality numbers (see Table 1). Numbers near the nodes depict the non-parametric bootstrap support values. GenBank accession number and name of the country or region of origin are given for the expanded branches (see Supplementary Table S2). Outgroups are not shown.

Our findings confirm, for the first time, the phylogenetic affinities of *C. austriaca* from some of the easternmost parts of its range with the Eastern lineage of the species. It was previously shown that the Eastern clade is distributed in a large part of the species range in the east, including the Baltic region, the European part of Russia, the western Caucasus, Abkhazia, and Crimea [3]. The mtDNA variation data suggested that most of the range of this clade was colonized relatively quickly, presumably from the Caucasian region [3]. Our results support these conclusions by demonstrating the distribution of a single haplotype of the Eastern lineage in Kazakhstan. This pattern of spatial mtDNA variation is congruent with those documented for a number of other widespread West Palearctic reptile species that have colonized northern areas from glacial refugia in the Caucasus (e.g., Lacerta *agilis* [10], *Natrix tessellata* [13], and *N. natrix* [25]).

3.3. Notes on Natural History

The distribution of the smooth snake in the West Kazakhstan region is confined to chalks with vegetation of petrophytic and calciphyte steppe communities of forbs, feather grass, fescue, and other grasses (Figure 3A). In the Mugodzhar range of Aktobe region, the snake was found in rocky steppe, dominated by *Artemisia* and Poaceae grasses with *Spirea* and *Caragana* shrubs (Figure 3B). Throughout the range, *C. austriaca* inhabits various

semi-open habitats, often with rocky or sandy soils. These include forest edges [26–28], clearings [26], heathlands [28–30], grasslands [28,31], montane shrublands [32], subalpine and alpine meadows [33], or even drained peat bogs [34,35]. The smooth snake was also observed on chalk deposits in other parts of its range; for example, in the Volgograd region of Russia [36] and the Kharkov region of Ukraine [37]. Thus, the habitat types occupied by the species in Kazakhstan align to its known preferences, but also represent a rare case of it being found in an open steppe landscape.

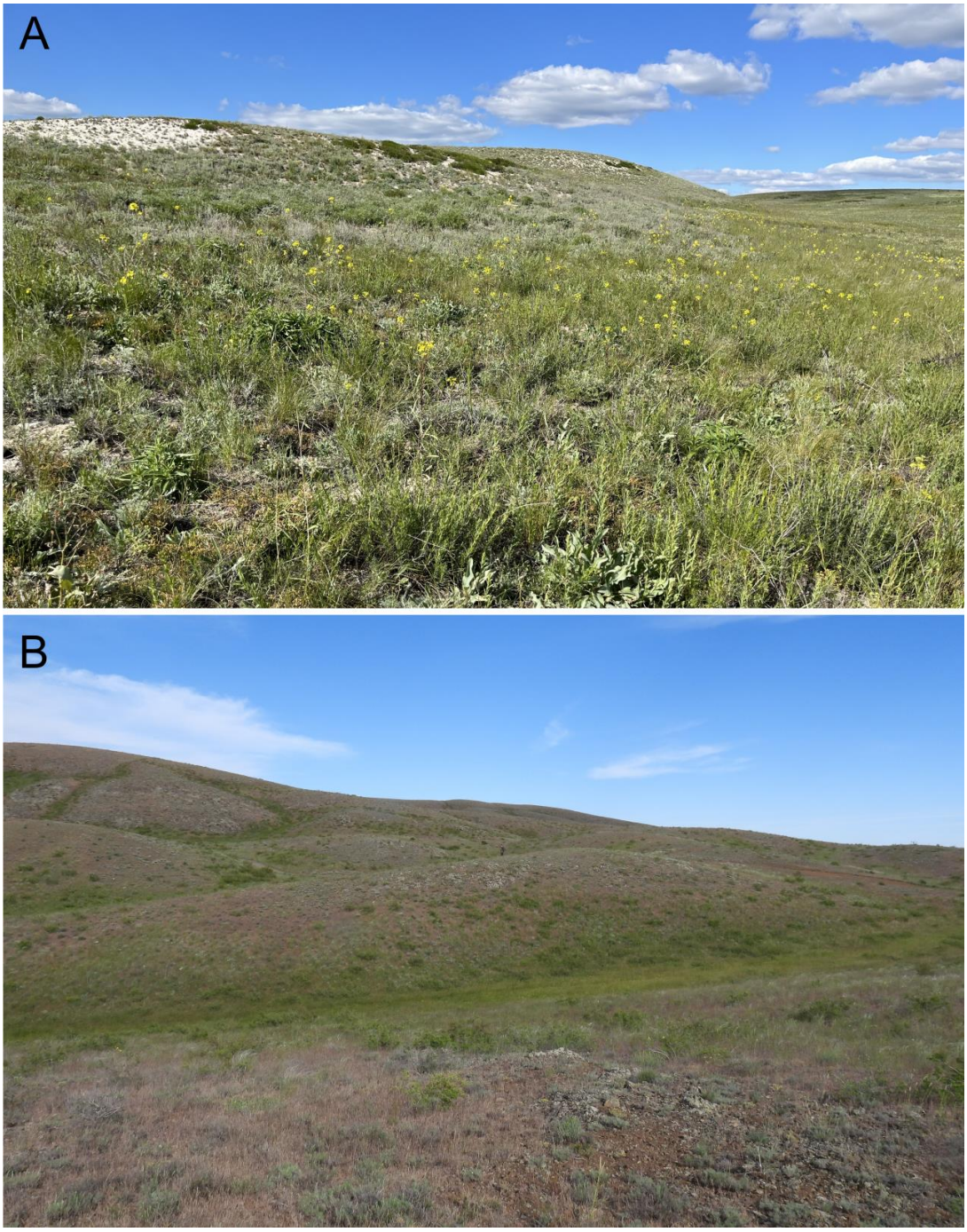


Figure 3. Habitats of *Coronella austriaca* in Kazakhstan: (**A**) locality 11, West Kazakhstan region, south-west of the Obshchy Syrt upland; (**B**) locality 12, Aktobe region, the Mugodzhar range. For further details on the locality numbers, refer to both Table 1 and Figure 1. Photos: Evgeniy Simonov and Kazhmurat Akhmedenov.

Reptiles, especially lizards, are considered to be the most frequent prey for the smooth snake [26,27,31,35,38–41] and the occupancy of the snake is known to depend upon prey availability [31,35]. Additionally, the consumption of lizard eggs [41] and instances of cannibalism [27] have been observed. There is also evidence that cannibalism may have an effect on the spatial distribution of juvenile smooth snakes [42]. In West Kazakhstan, the sand lizard *Lacerta agilis* (Linnaeus, 1758), the steppe-runner *Eremias arguta* (Pallas, 1773), the grass snake *Natrix natrix* (Linnaeus, 1758), the dice snake *N. tessellata* (Laurenti, 1768), the steppe rat snake *Elaphe dione* (Pallas, 1773), and the steppe viper *Vipera renardi* (Christoph, 1861) were found in syntopy with *C. austriaca*. In the Mugodzhar area, we revealed only the presence of *L. agilis* and *E. dione*. The sand lizard was identified as the most abundant reptile species in all localities where *C. austriaca* was present, hypothesizing that it could serve as a potential primary prey item. Additionally, we observed the co-presence of *N. natrix* and *C. austriaca* individuals of nearly equal length within the same shelter. In a study of habitat use by *C. austriaca* and its potential reptile prey species in Latvian bogs, using the artificial refuge method, co-presence with *N. natrix* was also detected [35]. It is also worth noting that, in certain populations, adult smooth snakes have been observed to consume more mammals than lizards [43]. This highlights the necessity for further ecological investigation of this species in Kazakhstan to better understand its habitat and prey availability requirements.

The majority (7 out of 10) of smooth snakes encountered in Kazakhstan from 2019 to 2024 had a patternless coloration (Figure 4). The typical coloration of the dorsal side of the species is a light brownish-gray background with dark brown/gray spots. The patternless individuals from Kazakhstan have an almost uniform dorsal coloration (gray or light brown) with spots completely absent or with tiny black markings on the edges of the scales, while the dark spots and stripes on the head and neck are retained. The coloration of the ventral side of these individuals is also typical of the species (brown, orange, or gray with numerous small dark spots). The only similarly colored patternless smooth snake we found in the literature was from the South Urals (Orenburg Oblast, Russia), bordering Kazakhstan [44]. Patternless individuals were also observed in Samara Oblast of Russia (our data). Various color aberrations are known in *C. austriaca* (reviewed in [45]) that are associated with disturbed development or abnormal distribution of chromatophores in the skin, such as melanism, anerythrism, albinism, leucism, and others. Some of these types of aberrations may result in uniform, patternless coloration of the dorsal side, such as the case of erythrism described in [45]. The uniform coloration observed in the region of Kazakhstan is likely attributable to geographical variation influenced by genetic and environmental factors. It is improbable that such patterns are the result of aberrations. To further confirm this, we reviewed observations of the smooth snake from the iNaturalist portal for the northeastern part of its range. We found good quality photos of unpatterned *C. austriaca* taken throughout the Ural Mountains and along both banks of the Volga River. We also noticed that patterned individuals usually have much smaller dorsal spots than individuals from the western part of the range. However, this has not been systematically evaluated and still remains to be further studied.

In conclusion, the results of this study provide the first data on the phylogenetic affinities of the *C. austriaca* from the easternmost portion of its range and the southernmost distribution limit in Kazakhstan. We also confirmed the current distribution of the species in the Aktobe region of Kazakhstan in the Mugodzhar range. A future monitoring program for the smooth snake in Kazakhstan is needed to establish its population densities and demographic trends, as it is virtually one of the rarest snake species in the country. The data obtained in this study can also be used for the conservation and sustainable management

of its habitats and the development of the specific conservation objectives for the already protected sites where the smooth snake has been documented.



Figure 4. The patternless individuals of *Coronella austriaca* from different localities in Kazakhstan: (**A**) male, 3 May 2019, locality 4; (**B**) male, 25 April 2022, locality 2; (**C**) female, 14 May 2024, locality 11. For further details on the locality numbers, refer to both Table 1 and Figure 1. Photos: Andrey Bakiev and Kazhmurat Akhmedenov.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/d17050348/s1. Table S1: Locality data for the northeastern portion of the *C. austriaca* range in Russia and Kazakhstan (Darwin Core standard). Table S2: GenBank accession numbers and metainformation for the DNA sequences generated and used in this study. References [46–49] are cited in the Supplementary Materials.

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Institutional Review Board Statement: The animal study protocol was approved by the Ethics Council of M. Utemisov West Kazakhstan University (No 2480; date of approval 4 September 2023).

Data Availability Statement: All sequences generated in this study were deposited to the GenBank under the accession numbers PV491238-PV491240, PV504883. All locality data provided in the Supplementary Table S1.

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Conflicts of Interest: The authors declare no conflicts of interest.

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