



MtDNA differentiation and taxonomy of Central Asian racerunners of *Eremias multiocellata*–*E. przewalskii* species complex (Squamata, Lacertidae)

VALENTINA F. ORLOVA^{1,6}, NIKOLAY A. POYARKOV, JR.^{2,6}, MARINA A. CHIRIKOVA³,
ROMAN A. NAZAROV¹, MUNKHBAYAR MUNKHBAATAR⁴, KHORLOOGHIYN MUNKHBAYAR⁴,
& KHAYANKHYARVAGIJN TERBISH⁴

¹Zoological Museum, Department of Herpetology, Moscow State University, B. Nikitskaya ul. 2, Moscow, 125009, Russia

²Department of Vertebrate Zoology, Biological faculty, Lomonosov Moscow State University, Leninskiye Gory, Moscow, GSP-1, 119991, Russia

³Institute of Zoology, Laboratory of Ornithology and Herpetology, Al-Farabi Prospect 93, Almaty, 480060, Kazakhstan

⁴Department of Biology, Mongolian National University of Education, Ulaanbaatar 210648, Mongolia

⁵Department of Ecology, Faculty of Biology, National University of Mongolia, Ulaanbaatar, 210153, Mongolia

⁶Corresponding authors. E-mail: val_orlova@mail.ru; n.poyarkov@gmail.com

Abstract

We provide an integrative analysis of the diversity of the *E. multiocellata*–*E. przewalskii* species complex in Central and Middle Asia using morphological and molecular (COI DNA-barcoding) data. We report preliminary data on mtDNA variation within this group and clarify the taxonomic status and distribution of the members of the species complex. We also provide a description of a new *Eremias* species from Eastern Kazakhstan and western Mongolia, where it occurs in sympatry with *E. multiocellata* sensu stricto, from which it can be clearly differentiated using both morphological and molecular characters. The new species, described as *Eremias dzungarica* **sp. nov.**, is assigned to the subgenus *Pareremias* on the basis of the following features: subocular not reaching mouth edge; one frontonasal; two supraoculars; the row of small granular scales between supraoculars and frontal with frontoparietals absent; distance between the femoral pore rows being wide; femoral pore rows not reaching knee-joint; coloration pattern with light colored ocelli with black edging. The new species can be distinguished from its congeners on the basis of the following morphological attributes: a medium-sized lacertid lizard, maximum snout-vent length (SVL) = 64.5 mm, tail being ca. 1.5 times longer than body length (SVL), hindlimbs relatively long (hindlimb length to SVL ratio 0.46); subocular scale not reaching mouth edge, in touch with 6–8 supralabials; males with bright coloration consisting of 2–3 dorsolateral rows of light-colored ocelli with thick black edging; the ventral row of ocelli in life is greenish to bluish; dorsal pattern consisting of black irregular blotches along the middorsal line. We also report on the high genetic and morphological diversity of *E. multiocellata* in Mongolia and China, synonymize *E. m. bannikowi* with the nominative form *E. m. multiocellata*, discuss variation within *E. przewalskii*, synonymize *E. p. tuvensis* with the nominative form *E. przewalskii*, provide new data on *E. cf. reticulata* and *E. m. tsaganbogdensis*, confirm validity and clarify distribution ranges of *E. stummeri*, *E. szczyrbaki* and *E. yarkandensis* and discuss further progress on taxonomic studies of the *E. multiocellata*–*E. przewalskii* species complex.

Key words: *Eremias dzungarica* **sp. nov.**, Biogeography, Sauria, Multi-ocellated Racerunner, Gobi Racerunner, Middle Asia, Central Asia, morphology, mitochondrial DNA, COI, phylogeography, distribution

Introduction

Racerunners of the genus *Eremias* represent one of the most taxonomically confusing and complicated group of the lizard family Lacertidae. The genus *Eremias* belongs to the lacertid subfamily Lacertinae, tribe Eremiadini of sub-Saharan origin with maximum diversity in Africa, and only four genera (*Acanthodactylus*, *Eremias*, *Mesalina* and *Ophisops*) penetrating to the Near East (Arnold 1989; Arnold *et al.* 2007; Harris *et al.* 1998; Fu 1998, 2000; Mayer & Pavlicev 2007; Tamar *et al.* 2016). Among them, only the genus *Eremias* is found exclusively in Asia and the taxonomy of this group remains insufficiently studied despite almost two centuries of extensive research, which

was especially intensive from the end of the XIX century following the exploration of Central Asian deserts (Strauch 1876; Bedriaga 1912; Nikolsky 1915; Boulenger 1918, 1921; Lantz 1928; Szczerbak 1971, 1974).

In his monographic review of *Eremias*, Szczerbak (1974) recognized 22 nominal species grouped in five subgenera: *Aspidorhinus* Eichwald, 1841 (previously treated as a nominative subgenus, see Eremchenko 1999; Leviton *et al.* 1992; Zhao & Adler 1993 and Barabanov 2009 for discussion), *Eremias* sensu stricto (= *Ommateremias* Lantz, 1928 sensu Szczerbak 1974), *Pareremias* Szczerbak, 1973, *Rhabderemias* Lantz, 1928 and *Scapteira* Wiegmann, 1834. This classification was later supported by data on hemipenial morphology (Arnold 1986), but has been questioned by recent molecular data (Guo *et al.* 2011).

Today, the genus *Eremias* consists of ca. 36–39 recognized species found in Middle and Central Asia, inhabiting steppes, sand dunes, stony and mountain deserts on various elevations on the vast arid territories from south-eastern Europe in the west to Mongolia, China and the Korean Peninsula in the east (Arnold *et al.* 2007; Mozaffari & Parham 2007; Uetz & Hošek 2017; see Appendix I).

Until recently, molecular genetic research on the lizards of the genus *Eremias* has been sparse and mostly focused on the Chinese species (Gong & Zhou 2000; Dai *et al.* 2004; Wan *et al.* 2007; Orlova 2008; Zhao *et al.* 2011). In their recent seminal paper, Guo *et al.* (2011) provided a preliminary account on the phylogeny and divergence times of some *Eremias* lizards inferred from 16S rRNA partial sequences. The resultant phylogeny, including representatives of 12 *Eremias* taxa, was however poorly resolved for the majority of the internal nodes. While this study confirmed the monophyly of *Eremias*, it questioned the taxonomic validity of the subgenera. However, taxonomic identification of certain specimens included in their analyses needs to be verified, and thus these data should be taken cautiously (Poyarkov *et al.* 2014).

The highest taxonomic diversity of the genus *Eremias* both in number of species and of subgeneric groups is found in the Iranian Plateau, with 8 species (*E. lalezharica* Moravec, *E. montana* Rastegar-Pouyani & Rastegar-Pouyani, *E. nigrolateralis* Rastegar-Pouyani & Nilson, *E. novo* Rastegar-Pouyani & Rastegar-Pouyani, *E. papenfussi* Mozaffari, Ahmadzadeh & Parham, *E. isfahanica* Rastegar-Pouyani, Hosseinian, Rafiee, Kami, Rajabizadeh & Wink, *E. andersoni* Darevsky & Szczerbak, and *E. kavirensis* Mozaffari & Parham) out of total 19 species recorded from this area being endemic (Anderson 1999; Rastegar-Pouyani & Rastegar-Pouyani 2001; Mozaffari & Parham 2007). Taxonomic diversity of the *Eremias* gradually decreases from west to east, with eight to nine species known from Kazakhstan (Brushko 1995; Dujsebayaeva *et al.* 2009), seven species for Kyrgyzstan, 10 species for China (Zhao & Adler 1993) and only five species reported for Mongolia (Orlova 1989; Orlova & Terbish 1997; Orlova 2008) and the single species recorded for Korean Peninsula. Among the species found in the Central Asia three species of the subgenus *Pareremias* show vast distribution ranges and significant level of morphological variability: *E. multiocellata* Günther, *E. przewalskii* (Strauch) and *E. argus* Peters (Szczerbak 1974). Despite the genetic variability of *E. argus* was recently assessed by Zhao *et al.* (2011), the genetic variability and phylogenetic relationships between *E. multiocellata*, *E. przewalskii* and allied taxa remain insufficiently studied. Further progress in this area is hampered by complicated taxonomy and lack of verified identifications and comparisons with type material. The available limited molecular phylogenetic data (Wan *et al.* 2007; Guo *et al.* 2011) in particular indicate that populations morphologically identified as *E. przewalskii* are nested deeply within the *E. multiocellata* clade; which allows recognizing this group as a species complex.

To date, eight nominal species are recognized within the *E. multiocellata*–*E. przewalskii* species complex. Morphological analysis of Multi-ocellated racerunners from Kyrgyzstan revealed four morphospecies, two of which were described as new to science, and the status of *E. stummeri* Wettstein was raised to full species (Eremchenko *et al.* 1992; Eremchenko & Panfilov 1999; Orlova *et al.* 2016).

In Mongolia, two subspecies of *E. multiocellata* are traditionally recognized (Szczerbak 1974): *E. m. bannikowi* Szczerbak is reported from western Mongolia and an adjacent part of Tuva Republic (Russia), whereas the nominative subspecies *E. m. multiocellata* inhabits the rest part of Mongolia and adjacent parts of central China. The latter form includes *E. m. planiceps* (Strauch, 1876) as a subjective junior synonym (Szczerbak 1974). The taxonomic status of populations from “Dzungaria” (now the northern parts of Chinese Xinjiang and westernmost parts of Mongolia) described as *E. m. reticulata* Bedriaga, 1907 remains unclear; morphologically this population was characterized by Szczerbak (1974) as an intermediate form between *E. m. yarkandensis* Blanford, 1875, *E. m. kozłowi* Bedriaga, 1907 and *E. m. multiocellata* (this conclusion was made based on examination of 12 specimens from “eastern Dzungaria”, see Szczerbak 1974). The populations of the *E. multiocellata*–*E. przewalskii* species complex from westernmost China and the territory of the former USSR, including Kyrgyzstan and eastern

Kazakhstan, were traditionally recognized as *E. m. yarkandensis* (Terentjev & Chernov 1949; Yakovleva 1964; Szczerbak 1974; Bannikov *et al.* 1977). However later morphological data supported the presence of four independent groups of specific status in this region: *E. stummeri* Wettstein, 1940 from Issyk-Kul Valley, *E. szczerbaki* Eremchenko & Panfilov, 1999 from central Kyrgyzstan, *E. yarkandensis* Blanford, 1875 from Chinese Kashgaria (now southern Xinjiang) penetrating to south-eastern Kyrgyzstan and *E. kokshaaliensis* Eremchenko & Panfilov, 1999 recorded only from a small area on the Chinese—Kyrgyz border in eastern Kyrgyzstan (Eremchenko & Panfilov, 1999). Three of the above mentioned forms were previously recognized as subspecies of *E. multiocellata* (Eremchenko *et al.* 1992), whereas *E. kokshaaliensis* was described as a new species.

In Kazakhstan, until recently only one form of the *E. multiocellata*—*E. przewalskii* species complex was reported, recognized as *E. m. yarkandensis* by Szczerbak (1974). Eremchenko *et al.* (1992) reported that at least two forms of the species complex can be found in Kazakhstan: *E. multiocellata* in the easternmost parts of the country; he also assumed that *E. stummeri* could inhabit the Kazakh part of Tian Shan Mountains, but did not provide any records for this species. This viewpoint was accepted by other authors (Dujsebajeva *et al.* 2009), however they surprisingly did not identify the newly discovered populations from Kegen and Tekes as *E. stummeri*, but assigned them to *E. multiocellata*. Our molecular and morphological data suggest that these Kazakh populations should be assigned to *E. stummeri* and this species should therefore be included in the herpetofaunal list of Kazakhstan (see Orlova *et al.* 2016 for details). According to our data, populations from Eastern Kazakhstan belong to a new species described below. It is remarkable, however, that old collections from the Saur and Saikan mountains in Eastern Kazakhstan (ZMMU R-8448, Coll. V.B. Sukhanov, 19-13.06.1958) are morphologically different from the Aigyrkum Sands population and their status requires further clarification (Orlova 1995).

From the adjacent parts of eastern and central China several forms were recognized by previous researchers, including *E. m. kozlowi* (from Nan Shan, central China), *E. m. reticulata* Bedriaga, 1907 (from Eastern Dzungaria, Xinjiang, China) and *E. buechneri* Bedriaga, 1907 (from southern Kashgaria, Xinjiang, China). The taxonomic status of these forms has to be evaluated using morphological and molecular data. Preliminary allozyme data indicated that specimens similar to the original description of *E. m. reticulata*, collected from the localities in vicinity of Altai Sum (Gobi-Altai Aimaq) were clearly differentiated from Mongolian populations of *E. przewalskii* and *E. multiocellata* in allozyme profiles and occupied an intermediate position between these forms in the resulting tree (Trueller *et al.* 1994).

Recently, an isolated mountain population of Multi-ocellated racerunner from Tsagaan Bogd Uul Mountain, Bayanhongor Aymak, southern Mongolia, close to the Chinese border, was described as a new subspecies, *E. multiocellata tsaganbogdensis* Munkhbayar & Borkin, 2010, based on the analysis of morphological characters of 10 adult specimens (Munkhbayar & Borkin 2010). Taxonomic status and relationships of this population requires further studies.

In south-west of Mongolia in Dzungarian Gobi and foothills of Mongolian Altai Mountains (around Uyench Sum) at least two forms of the *E. multiocellata*—*E. przewalskii* species complex were observed in sympatry; they are clearly different morphologically and likely represent independent taxa (Orlova & Terbish 1986, 1997). Since two morphotypes showed different ecological preferences we tentatively referred to them in previous works as the “rock form” and the “sand form”, respectively. Racerunners, morphologically similar to the “rock form” from western Mongolia were later found in Zaisan valley in Eastern Kazakhstan (Orlova 1995; Orlova & Terbish 1997). The preliminary data on allozyme electrophoresis assumed their distinctiveness from Kyrgyz *E. stummeri*, and Mongolian populations of *E. przewalskii* and *E. vermiculata* (Trueller *et al.* 1994), however did not shed light on their taxonomic status. In August 2008, within the frameworks of a joint Russian-Mongolian herpetological expedition, we examined the area of sympatry of the rock and sand forms around Uyench Sum 20 years after the discovery of these populations and recorded both forms in this area.

However, the taxonomy of the *E. multiocellata*—*E. przewalskii* species complex populations from the vast areas of Kazakhstan, China and Mongolia still remains unclear and requires further studies and clarification, also with application of molecular phylogenetic markers. In the present paper, based on the analyses of available museum collections and original materials, we provide preliminary molecular phylogenetic data (COI DNA-barcoding) and morphological data on the genetic and morphological variability and taxonomic diversity of the *E. multiocellata*—*E. przewalskii* species complex from Mongolia, China, southern part of Russia, East Kazakhstan and Kyrgyzstan.

Material and methods

Sample collection. Specimens were collected during the Joint Soviet-Mongolian Biological Expedition of 1977, 1982, 1983, 1984 and 1986, and later during the Joint Russian-Mongolian Biological Expedition of 2008. Additional samples for genetic and morphological analyses were collected during fieldwork in Mongolia, Kazakhstan and Kyrgyzstan between 2006 and 2014. The geographic position of the surveyed populations and samples included in the molecular analyses is given in Appendix II. Geographic coordinates and elevation were obtained using a Garmin GPSMAP 60CSx GPS receiver and recorded in datum WGS 84. The sampling strategy covers the entire range of the *Eremias multiocellata*—*E. przewalskii* species complex. Altogether, 126 samples from 56 populations were included in the phylogenetic analysis of the COI mtDNA gene (see Appendix II and Fig. 1). Specimens were photographed in life, euthanized, and tissue samples (muscles, heart or liver) were taken prior to preservation and stored in 96% ethanol for genetic analysis. Sex was determined by direct observation of sexually dimorphic characters or gonadal inspection by dissection.

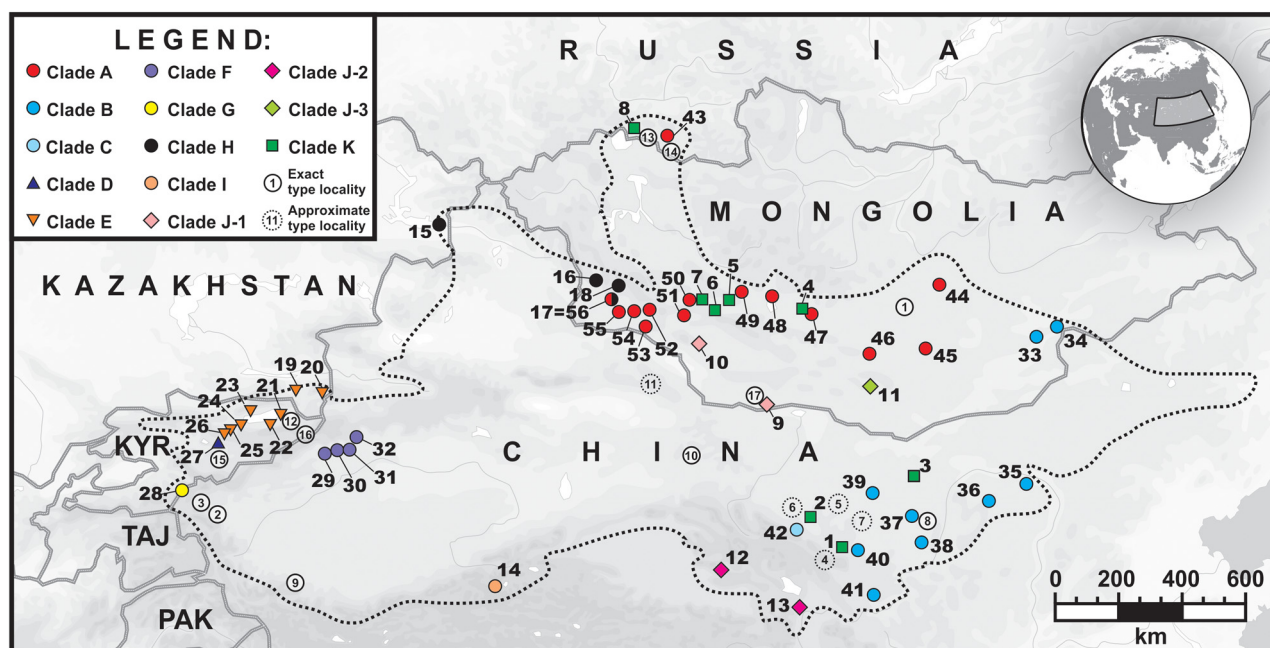


FIGURE 1. Distribution of *Eremias multiocellata*—*E. przewalskii* complex (following Szczerbak 1974, modified) and localities studied. Populations of *Eremias multiocellata*—*E. przewalskii* complex used in this study are shown, bold numbers correspond to those in Appendix II and Figure 2. The inset map shows the location of the sampling area on the globe. Icons represent the main lineages of *Eremias multiocellata*—*E. przewalskii* complex (see Figure 2). Numbers in circle correspond to exact (solid line) and approximate (dashed line) location of the type localities of taxa described within *Eremias multiocellata*—*E. przewalskii* complex: **1**—*multiocellata* Günther, 1872—Mongolia, Gobi, road from Sume to Tola [Tuul]; **2**—*yarkandensis* Blanford, 1875—China, southern Kashgaria, Yarkend; **3**—*saturata* Blanford, 1875—China, southern Kashgaria, Kashgar [Kashi]; **4**—*planiceps* (Strauch, 1876)—China, Gansu [no exact locality available]; **5**—*przewalskii* (Strauch, 1876)—China, Alashan Desert [no exact locality available]; **6**—*kessleri* (Strauch, 1876)—China, Gansu [no exact locality available]; **7**—*brachidactyla* (Strauch, 1876)—China, Alashan Desert [no exact locality available]; **8**—*quadrifrons* (Strauch, 1876)—China, Alashan Desert, vicinity of Narin-Ula Moutnain Ridge; **9**—*buechneri* Bedriaga, 1907—China, southern Kashgaria, between Yarkend and Chotan; lectotype ZISP 7087 from Dol, southern Kashgaria, Sampula oasis; **10**—*kozłowi* Bedriaga, 1907—China, Sachzheu envrions [Dunhuang]; **11**—*reticulata* Bedriaga, 1912—China, eastern Dzungaria [no exact locality available]; **12**—*stummeri* Wettstein, 1940—Kyrgyzstan, Issyk-Kul district, envrions of Przewalsk [Karakol]; **13**—*tuvensis* Szczerbak, 1970—Russia, Southern part of Tuva Republic, between Tere-Khol Lake and River Tes-Khem; **14**—*bannikowi* Szczerbak, 1973—Russia, Southern part of Tuva Republic, Sharasur; **15**—*szczerbaki* Eremchenko, Panfilov & Zarinenko, 1992—Kyrgyzstan, Naryn district, At-Bashi River and Arpa River valleys; **16**—*kokshaaliensis* Eremchenko & Panfilov, 1999—Kyrgyzstan, Issyk-Kul district, Sary-Jaz, ravine Terekty; **17**—*tsaganbogdensis* Munkhbayar & Borkin, 2010—Mongolia, Bayanhongor Aimaq, Tsagaan Bogd Uul Mountain.

In most of the cases, voucher specimens were collected, preserved, and deposited in the herpetological collection of the Zoological Museum of Moscow University (ZMMU), in Moscow, Russia. We examined type specimens of the *E. multiocellata*—*E. przewalskii* species complex deposited in the Zoological Institute RAS (ZISP) in St. Petersburg, Russia; we also examined photographs of the types of *Eremias velox stummeri* Wettstein deposited in the Naturhistorisches Museum Wien (NMW), Wien, Austria, and the type series of *Eremias multiocellata* var. *yarkandensis* Blanford from the British Museum of Natural History (BMNH = NHMUK), London, UK. Additional material deposited in the herpetological collection of the Mongolian National University of Education (MNUE); Ulaanbaatar, Mongolia; Almaty Institute of Zoology, Kazakhstan Academy of Sciences (AIZ); Zoological Museum of the Institute of Biology and Soil Science of Kyrgyzstan Academy of Sciences (ZMBPI) and Universität Humboldt, Zoologisches Museum, Berlin, Germany (ZMB) were examined.

Outgroup included two congeneric taxa of Central Asian racerunners: *Eremias vermiculata* (ZMMU R-12047-1), *E. nikolskii* (ZMMU R-11673-1); and two assumingly closer relatives: *E. argus barbouri* (ZMMU R-12605-1) and *E. brenchleyi* (EF490071; sequences from Rui *et al.* 2009) (members of the subgenus *Pareremias*).

Morphology. The type series of the new *Eremias* species examined includes 12 specimens (5 males, 2 females, 5 juveniles; see taxonomic account and Table 3 for morphometric data). For morphological comparisons with other populations of the *Eremias multiocellata*—*E. przewalskii* species complex in Mongolia we used morphometric data from Orlova & Terbish (1997), who examined large material on Mongolian *Eremias*, including the sympatric population of “rock” (n = 20) and “sand” (n = 30) forms of *E. multiocellata* sensu lato from Uyench (Orlova & Terbish 1997: 133–244) and from Orlova *et al.* (2016) who analyzed morphological variation of *E. stummeri* in Kazakhstan (n = 11) and Kyrgyzstan (n = 11). For additional comparisons with other *Eremias multiocellata*—*E. przewalskii* species complex members from China, Kazakhstan and Kyrgyzstan we examined specimens stored in ZMMU and ZISP; we also examined lectotype of *Eremias buechneri* Bedriaga, 1907 (ZISP 7081) and obtained photographic materials on syntypes of *Eremias yarkandensis* Blanford, 1875 (BMNH 1917.3.6.28–29) and *Eremias velox stummeri* Wettstein, 1940 (NMW 15664). The full list of accessed and examined specimens is given in Appendix III.

Morphological characters studied included body size and body shape, meristic characters of scalation and description of coloration pattern of adult and juvenile specimens. All measurements were taken using digital caliper under the light dissecting microscope to the nearest 0.1 mm. Morphometrics followed Orlova & Terbish (1997); morphological description followed Szczerbak (1974) and Rastegar-Pouyani & Rastegar-Pouyani (2001, 2006). For morphometric analysis the following standard characters were used: SVL—snout-vent length (from snout to vent); TL—tail length (from vent to the tip of the tail); Lpil.—pileus length (from rostrum to the posterior border of parietals); HL—head length (from rostrum to occipital sinus); HW—head width (maximum wide); HH—head height (maximum height); NL—head length from snout tip to the anterior edge of collar (measured from ventral side); Ga—gleno-acetabular distance (from axilla to groin measured from the posterior edge of forelimb to the anterior edge of hindlimb insertion); Pa—forelimb length (from forelimb insertion to the tip of the longest finger); Pp—hindlimb length (from hindlimb insertion to the tip of the longest toe); Dist.P.fm.—distance between the proximal femoral pores on right and left sides; measurements of frontal scale (FrL—frontal scale length; FrWmax—maximal width of frontal in its anterior part; FrWmin—minimal width of frontal at base). Morphometric indices included ratios SVL/TL, Pa/SVL, Pp/SVL, HL/SVL, HW/HL, HH/HL and the ratio of the femoral pore row length to the distance between femoral pore rows (Dist.P.fm.). The proportions of frontal were evaluated using ratios FrL/FrWmin and FrWmax/FrWmin.

The following scalation and meristic characters were examined: Sq.—number of scales around midbody; G.—number of gular scales along mid-line of throat; P.fm.r.—number of femoral pores on the right side of body; P.fm.l.—number of femoral pores on the left side of body; Ventr.—number of transverse rows of ventral scales; Ventr.long.—the maximal number of longitudinal rows of ventral scales (counted at midbody); Sq.c.cd.—number of scales around the 9–10th tail ring; Lam.subdig.—number of subdigital lamellae on the 4th toe of hindlimb; Sq.dors.—number of dorsal scales between parietals and the level of cloaca; Coll.—number of collar scales; Lab.min.—number of supralabial shields anterior to subocular (right/left); Lab.total—total number of supralabials (right/left); Infralab.—number of infralabial shields (right/left); subocular shield in contact with mouth margin or is separated from it by supralabials (yes or no); the 5th pair of the chin shields in contact with infralabial shield or is separated from it (yes or no); Submax.—number of submaxillary shields (= chin shields) (right/left); Submax.cont.—number of pairs of submaxillary shields (= chin shields) in contact with each other; supranumerary

(additional) shield between prefrontals present or absent; supraoculars separated from frontal and frontoparietals by a complete row of small granular scales (yes or no); number of enlarged scales in preloacal area.

All statistical analyses were performed with Statistica 6.0 (StatSoft, Inc. 2001). For univariate analyses, we used morphometric characters, corrected by body size. In addition to the characters mentioned above, for specimen description we recorded body coloration and pattern, including the presence or absence of blue, green or yellow light ocelli on dorsum and body sides in adult and juvenile specimens.

DNA isolation and sequencing. Total genomic DNA was extracted from a relatively small amount of tissue (tail muscles, voucher material remains) using the standard phenol-chloroform method (see Sambrook *et al.* 1989) and the Diatom DNA Prep 100 Tissue Kit (IsoGene) following the manufacturer instructions. The obtained DNA was purified, visualized in UV-light electrophoresis and the resultant concentration was measured. The final concentration of DNA was adjusted to approximately 100 ng/μL using NanoDrop 2000 (Thermo Scientific).

We amplified 651 bp of Cytochrome oxidase I (COI), a mitochondrial gene proved to be useful for species identification in reptiles and widely used as a barcoding marker for vertebrates (Hebert & Gregory 2005; Smith *et al.* 2008; Nagy *et al.* 2012; Murphy *et al.* 2013; Vasconcelos *et al.* 2016). Recently this gene was successfully applied for registration of cryptic diversity in Asian lizards (Solovyeva *et al.* 2011, 2012, 2014; Nazarov *et al.* 2012, 2014; Hartmann *et al.* 2013; Nazarov & Poyarkov 2013; Nguyen *et al.* 2014). PCRs and sequencing were performed after the protocol of Nazarov *et al.* (2012). PCR was conducted using the GenePack Core (IsoGene) in a total volume of 20 μl, which contained from 1.0 to 5.0 μl of DNA extraction, 1.0 μl of forward and reverse primers (10 μM), 0.2 μl of *Taq* polymerase (5 U/ml), 1 μl dNTP mix, and PCR buffer containing 15 mM MgCl₂. PCR conditions were as follows: initial denaturation for 5 min at 94° C, 31-35 cycles composed of the 30 seconds denaturation at 94° C, 45 seconds of annealing at 50-57° C, and 1 min extension at 72° C. PCR products were purified with the Wizard SV Gel and PCR Clean-up System (Promega). Cycle sequencing was done commercially through VGNKI RAMS, Moscow.

TABLE 1. Primers used for PCR amplification and sequencing.

Primer name	Primer sequence	Source
VF1-d	5'-TTCTCAACCAACCACAARGAYATYGG-3'	Ivanova <i>et al.</i> 2006
VR1-d	5'-TAGACTTCTGGGTGGCCRAARAAYCA-3'	Ivanova <i>et al.</i> 2006
RepCOI-F	5'-TNTTMTCAACNAACCACAAAGA-3'	Nagy <i>et al.</i> 2012
RepCOI-R	5'-ACTTCTGGRTGKCCAAARAATCA-3'	Nagy <i>et al.</i> 2012

Phylogenetic analysis. The sequence data were translated into amino acids to confirm the absence of premature stop codons. The forward and reverse sequences were checked visually in Chromas 2.0 and a consensus sequence was compiled with BioEdit 5.0.9 (Hall 1999). Sequences were also submitted to a BLAST search in GenBank to confirm that the required sequences had been amplified. Nucleotide sequences were initially aligned using ClustalX 1.81 (Thompson *et al.* 1997) with default parameters, and then checked for presence of deletions, stop-codons and optimized manually in BioEdit 7.0.5.2 (Hall 1999) and MEGA 5.0 (Tamura *et al.* 2011). Mean uncorrected genetic distances (*p*-distances) and nucleotide frequencies were determined with MEGA 5.0 (Tamura *et al.* 2011).

MODELTEST v.3.06 (Posada & Crandall 1998) was used to estimate the optimal evolutionary model to be used for the data set analysis. The preferred model of DNA evolution was (GTR + I + G), as suggested by the Akaike information criterion (AIC).

Phylogenetic trees were inferred using two different methods: Maximum Likelihood (ML) and Bayesian inference (BI). The ML analysis was conducted using Treefinder (Jobb *et al.* 2004). The BI analysis was carried out with MrBayes 3.1.2 (Huelsenbeck & Ronquist 2001; Ronquist & Huelsenbeck 2003) by implementing the model of sequence evolution. The analysis was run with four chains for twenty million generations sampling trees every 1000 generations. Analyses were repeated beginning with different starting trees to ensure that our analyses were not restricted from the global optimum. To confirm that the chains had achieved stationarity, we evaluated “burn-in” plots by plotting log-likelihood scores and tree lengths against generation number using the software Tracer v.1.5 (Drummond & Rambaut 2007). The first eight million generations, before this chain reached apparent

stationarity, were discarded. A majority rule consensus tree (BI tree) was calculated from the posterior distribution of trees.

Confidence in tree topology was tested by non-parametric bootstrap analysis (BS) (Felsenstein 1985) with 1000 replicates for the ML analysis, and by posterior probability (PP) for BI in MrBayes 3.1.2 (Huelsenbeck & Ronquist 2001). Branches with BS values 70% or greater and PP values over 0.95 were regarded as strongly supported (Huelsenbeck & Hillis 1993).

Results

Sequence data. Among the 126 sequences of the *Eremias multiocellata*—*E. przewalskii* species complex we obtained, 59 haplotypes of the COI fragment and all outgroup samples represented unique haplotypes (see Appendix II; GenBank Accession numbers: KY366548–KY366673). The final alignment used for the phylogenetic analyses comprised 651 bp for 126 *Eremias multiocellata*—*E. przewalskii* species complex and sequences of other Central Asian *Eremias* species, including *E. vermiculata* (KY366549), *E. nikolskii* (KY366550) and representatives of the subgenus *Pareremias*: *E. argus* (KY366548) and *E. brenchleyi* (EF490071), which were used as outgroups. No length variation, deletions or insertions were observed in the COI sequences of *Eremias*. Of the 651 aligned sites, 467 were found to be conserved, 184 variable and 159 parsimony-informative; the transition–transversion bias was estimated at 3.868 (all data given for ingroups only). The nucleotide frequencies were 25.16% (A), 27.85% (T), 29.79% (C), and 17.19% (G).

Matrilineal geneology and geographic distribution of mtDNA haplotypes within the *Eremias multiocellata*—*E. przewalskii* species complex. The results of the BI and ML phylogenetic analyses of the COI gene are shown in Figure 2. Phylogenetic relationships between the examined taxa of *Eremias multiocellata*—*E. przewalskii* species complex are poorly resolved with some nodes of the tree having low (BS<75%) or insignificant levels (PP<0.95; BS<50%) of support, whereas monophyly of species-level groups and species complexes, as well as some major basal nodes of the tree are significantly supported (PP≥0.95; BS>90%). ML and Bayesian inference analyses resulted in essentially similar topologies (see Fig. 2). The BI tree of Fig. 2 shows the following set of phylogenetic relationships among the studied *Eremias* species.

All studied samples of the *Eremias multiocellata*—*E. przewalskii* species complex form a monophyletic group (0.97/98; hereafter the node support values are given for BI/ML analyses respectively), with eastern species of the subgenus *Pareremias* (*E. argus*, *E. brenchleyi*) forming a well-supported sister clade to the *Eremias multiocellata*—*E. przewalskii* species complex.

The haplotypes of the *Eremias multiocellata*—*E. przewalskii* species complex mitochondrial DNA can be divided into three major groups (Groups I–III; see Fig. 2) comprising 11 clades (named from A to K), five of them well structured and subdivided into several subclades. In the case of clade J, the variation was pronounced and had some geographical pattern and therefore this clade was subdivided into J1, J2 etc. The distribution of the lineages obtained shows clear geographical structure (see Figs. 1 and 2).

Phylogenetic relationships between the groups I–III remain essentially unresolved (Fig. 2). Monophyly of the first group I is well supported (1.0/97), it joins populations from the eastern part of the species complex range (populations P.32–56) and comprises three clades: A–C that correspond to the *Eremias multiocellata* species group.

Clade A is distributed across a large area of southern, central and western Mongolia and Tuva Republic (Russia) (populations P.43–56; see Fig. 1). The range of this extends from the southern part of Tuva (population P.43) southwards along the Great Lakes valley to central Mongolia, where it is widespread from Dundgovi Aimaq in the East as far as Uyench Sum in Khovd Aimaq (population P.56, same locality as population P.17; see Fig. 1) in the west. This large area includes the type locality of *Eremias multiocellata* (Mongolia, Gobi, road from Sume to Tola [Tuul], see Fig. 1), which is close to populations P.44 and P.45 examined by us; thus this form corresponds to *E. multiocellata* sensu stricto. This form is relatively small-sized and was described as the “sand form” of *E. multiocellata* by Orlova & Terbish (1986; 1997) and Orlova (2008); in Uyench Sum these authors reported sympatric occurrence of this species with the “rock form” of *E. “multiocellata”* (see below). Populations of *Eremias multiocellata* from Tuva Republic were described as a subspecies *E. m. bannikowi* Szczerbak, 1973 (type locality: Russia, Southern part of Tuva Republic, Sharasur), however in our analysis we found no significant genetic differentiation between populations of *E. multiocellata* from central Mongolia and Tuva Republic (p -distance <0.70%, see Table 2).

TABLE 2. Mean uncorrected genetic *p*-distances (percentage) between (below diagonal) and within (diagonal, bold font) the different lineages revealed within *Eremias multiocellata* — *E. przewalskii* complex. The standard error (500 bootstrap replicates) is given above diagonal. Clade names correspond to those at Figure 2 and Appendix II.

Clade	1	2	3	4	A	B	C	D	E	F	G	H	I	J-1	J-2	J-3	K
1 — <i>E. nikolskii</i>	—	1.60	1.50	1.60	1.50	1.40	1.40	1.50	1.50	1.40	1.50	1.30	1.40	1.50	1.50	1.50	1.50
2 — <i>E. vermiculata</i>	19.30	—	1.50	1.60	1.40	1.40	1.50	1.50	1.50	1.40	1.40	1.40	1.40	1.50	1.50	1.50	1.40
3 — <i>E. argus</i>	17.80	20.90	—	1.30	1.50	1.50	1.40	1.40	1.40	1.30	1.30	1.30	1.30	1.40	1.40	1.40	1.40
4 — <i>E. brenchleyi</i>	18.50	21.10	17.30	—	1.50	1.40	1.40	1.60	1.50	1.50	1.60	1.50	1.60	1.50	1.50	1.50	1.40
A — <i>E. multiocellata</i> A	16.10	19.40	16.00	17.20	0.70	0.80	0.90	1.10	1.10	1.00	1.10	1.10	1.10	1.20	1.20	1.20	1.20
B — <i>E. multiocellata</i> B	16.10	20.50	16.90	16.40	6.70	3.30	0.80	1.10	1.10	0.90	1.10	1.00	1.10	1.10	1.10	1.10	1.00
C — <i>E. cf. multiocellata</i>	13.80	20.60	16.20	16.00	6.90	7.50	—	1.00	1.10	1.00	1.10	1.10	1.10	1.10	1.10	1.10	1.10
D — <i>E. szcherbaki</i>	15.70	20.40	18.60	16.20	10.70	9.90	10.70	0.30	1.00	0.90	1.00	1.00	1.00	1.10	1.00	1.10	1.00
E — <i>E. stummeri</i>	15.30	18.70	17.10	17.40	9.90	10.50	10.50	7.80	1.00	1.00	1.00	1.10	0.90	1.10	1.10	1.10	1.10
F — <i>Eremias</i> sp. 1	14.40	20.10	16.60	15.90	8.90	10.10	9.40	8.70	9.20	1.00	0.70	0.70	0.70	0.90	0.90	0.90	0.80
G — <i>E. yarkandensis</i>	14.70	19.10	15.70	15.60	8.40	9.60	9.70	8.10	7.80	3.90	0.00	0.70	0.50	0.80	0.70	0.80	0.70
H — <i>E. dzungarica</i> sp. nov.	14.20	18.70	16.10	15.60	10.00	10.70	11.10	9.20	9.30	5.70	3.50	0.50	0.60	0.80	0.80	0.90	0.80
I — <i>E. cf. buechneri</i>	13.90	18.80	15.90	15.10	8.40	9.20	9.60	8.40	7.80	4.60	1.50	3.20	0.00	0.80	0.70	0.80	0.70
J-1 — <i>E. cf. reticulata</i>	14.20	19.10	15.90	15.50	9.70	10.20	10.10	8.50	9.20	6.40	3.90	4.70	3.50	0.20	0.40	0.30	0.60
J-3 — <i>E. cf. przewalskii</i>	14.30	18.80	16.10	15.20	9.70	10.20	9.70	8.30	8.80	6.20	3.70	4.90	3.60	1.20	0.30	0.40	0.50
J-2 — <i>Eremias</i> sp. 2	14.40	19.00	16.40	15.60	9.60	10.30	9.90	8.60	9.00	6.30	4.10	5.10	3.90	0.90	1.30	0.30	0.50
K — <i>E. przewalskii</i>	15.40	19.10	16.50	15.30	9.40	10.00	10.50	8.40	9.50	6.50	4.40	5.50	4.20	2.30	1.90	2.30	0.80

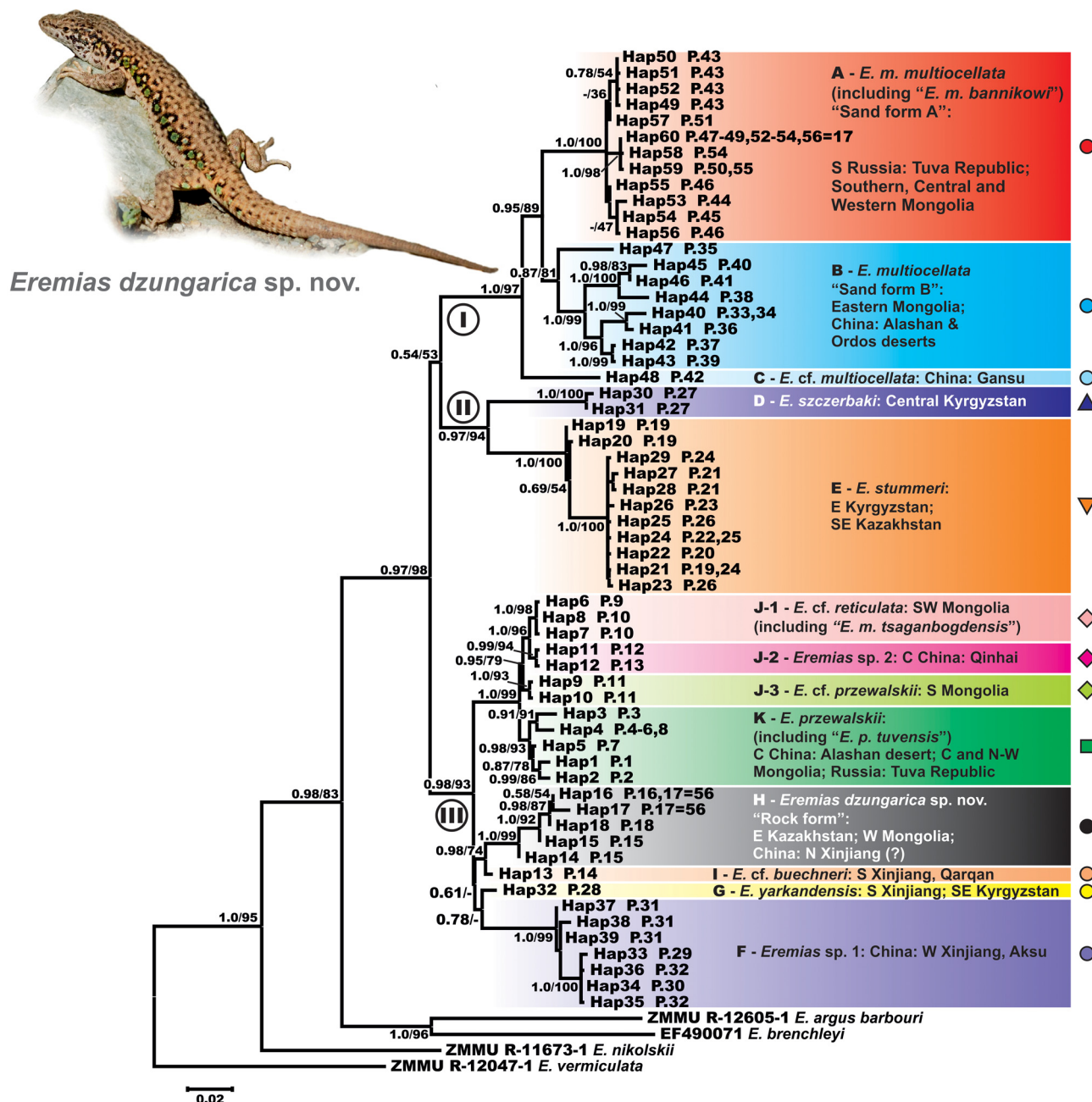


FIGURE 2. The tree resulting from the Bayesian Inference analysis of the studied samples of *Eremias multiocellata*–*E. przewalskii* complex. For the major cladogenetic events BI/ML posterior probabilities and bootstrap support values are given. Icons representing main lineages correspond to those in Fig. 1.

Clade B includes populations of the "sand" form of *E. multiocellata*, inhabiting central China from eastern Alashan Desert (populations P.40–41) to Ordos Desert and reaching easternmost Mongolia in Dornogovi Aimaq, Sainshand Sum (populations P.33–34) (see Fig. 1). This clade is characterized by comparatively large body-size and specific coloration pattern, as well as by comparatively large genetic distances between the revealed haplotypes (p -distance < 3.30%, Table 2), although they were identified in geographically close populations (see Fig. 1). Within the *Eremias multiocellata*–*E. przewalskii* species complex 2 taxa were described from southern Alashan: *Podarces (Eremias) planiceps* (Strauch, 1876) (type locality: China, Gansu [no exact locality available]) and *Podarces (Eremias) quadrifrons* (Strauch, 1876) (type locality: China, Alashan Desert, vicinity of Narin-Ula Mountain Ridge) (see Fig. 1). The latter taxon is known just from the single specimen (the holotype) and its taxonomic status and diagnostic features remain vague and enigmatic (Szczerbak 1974). Thus, it is unclear whether any names are applicable to clade B; it requires further morphological studies and examination of the type material.

Clades A and B are joined in a well-supported monophyletic group (0.95/89), and clade C is the sister-group to clades A+B. Clade C comprises a single population P.42 of *E. cf. multiocellata* from around Shandan (Gansu province, China, Fig. 1); lack of voucher specimens hindered morphological examination and taxonomic assignment of this population.

Group II includes populations from the westernmost part of the species complex range—western Tian Shan Mts. and Kyrgyzstan, which form a well-supported monophyletic group (0.95/91) and comprises two clades: D and E. Clade D (1.0/100) is restricted to the mountains of Naryn Province in central Kyrgyzstan (population P.27, Fig. 1) and corresponds to *Eremias szczerbaki* Eremchenko, Panfilov & Zarinenko, 1992.

Clade E (1.0/100) comprises populations of *E. stummeri* Wettstein, 1940, and include populations from the area around Issyk-Kul Lake in Kyrgyzstan (populations P.21–26, Fig. 1) and Tian Shan foothills in south-eastern Kazakhstan (populations P.19–20, Fig. 1). There is a certain divergence between haplotypes from Kazakhstan population P.19 (haplotypes 19–20; see Fig. 1, Appendix II) and Kyrgyz populations P.21–26 (haplotypes 21–29; see Fig. 1, Appendix II) (p -distance = 1.00%), however Kazakh populations P.19–20 also share some haplotypes (haplotypes 21–22) with Kyrgyz populations, thus the observed differences likely have no taxonomic value. *Eremias stummeri* was described from Kyrgyzstan, Issyk-Kul district, close to Przewalsk [now Karakol]. Our new data indicate that the distribution of *E. stummeri* includes the northern slopes of Tian Shan in south-easternmost Kazakhstan (populations P.19–20, Fig. 1), surroundings of the Issyk-Kul Lake in Issyk-Kul Province of Kyrgyzstan (populations P.21–24, Fig. 1) extending to the northern part of Naryn province; the range of *E. stummeri* is separated from the range of *E. szczerbaki* by Sonköl Too and Mondol Too Mountain Ridges.

The third Group III (monophyly support 0.96/90) includes six clades (clades F–K, see Fig. 2) spread across a vast area from eastern Kyrgyzstan and Kazakhstan in the west to the central Alashan desert in China, central Mongolia and southern Tuva Republic in Russia in the East. Phylogenetic relationships within group III remain essentially unresolved.

In the eastern part of the range, clade F (monophyly support 1.0/99) comprises four populations from vicinity of Aksu in the western part of Xinjiang Province of China (populations P.29–33, Fig. 1). These localities are in geographic proximity from Sary-Jaz in eastern Kyrgyzstan—the type locality of *E. kokshaaliensis* Eremchenko & Panfilov 1999; however for clarification of taxonomic status of the clade F populations, examination of material from *E. kokshaaliensis* type locality and additional research is needed.

Clade G in our analysis includes the single population from Nura, Osh Province of Kyrgyzstan (population P.28, Fig. 1), which was identified as *E. m. yarkandensis* by Eremchenko & Panfilov (1999). Indeed this population is geographically close to the type locality of *Eremias yarkandensis* Blanford, 1875 (China, southern Kashgaria, Yarkend) and its morphology corresponds well with the type material that we have examined (see Appendix III). The phylogenetic position of clade G supports the full species status of *E. yarkandensis*, as suggested by Eremchenko & Panfilov (1999).

Clades H and I form a monophyletic group (0.98/74) distributed in Dzungaria (clade H) and Kashgaria (clade I) regions of Xinjiang Province of China and surrounding areas. Clade I (1.0/99) in our analysis is represented by a single population in southern part of Xinjiang (Kashgaria, population P.14, see Fig. 1); morphologically this population agrees with diagnosis of *E. buechneri*; the locality also falls within the range of this species as given by Szczerbak (1974). Thus we tentatively indicate this population as *E. cf. buechneri*; specific status of this taxon is confirmed by mtDNA analysis.

Clade H (1.0/99) includes specimens previously identified as *E. multiocellata*, from easternmost Kazakhstan (East-Kazakhstan Province, population P.15, see Fig. 1) to Mongolian Dzungaria (Khovd Aimaq, populations P.16–18, Fig. 1); presumably, this lineage can be also found in Chinese Dzungaria in the northern part of Xinjiang Province. This form was described as the “rock form” of *E. multiocellata* for Mongolian Dzungaria by Orlova & Terbish (1986; 1997), Orlova (2008) and Orlova *et al.* (2014); these authors reported sympatric occurrence of this form with the “sand form” (= *E. multiocellata* *sensu stricto*) in Uyenich Sum of the Khovd Aimaq; in the area of sympatry, the “rock form” is found on rocky and stone substrates, whereas the “sand form” is observed on loose sands. Our study examined 14 specimens of *Eremias* from this locality (marked as population P.17 = 56 in Figs. 1 and 2); 9 of them were assigned to clade H (“rock form”; ZMMU R-12845; R-12846; see P.17 in Appendix II), and 5 of them proved to belong to clade A (“sand form”; ZMMU R-13132; see P.56 in Appendix II). All specimens are easily diagnosable by morphological characters (see below) and morphological differences are consistent with assignment by mtDNA data.

Clades J and K occupy central parts of the species complex range in central China, Mongolia and southern part of Tuva Republic (Russia) and are genetically very close to each other (p -distance = 1.90–2.30%), though they show great variation in adult body size, morphology and coloration.

Clade J includes three different subclades (J-1–J-3, see Fig. 2) genetically quite close to each other (p -distance = 0.90–1.30%). Subclade J-1 in our analysis corresponds to two populations from southern Mongolia (P.10–11). The first population from southern part of Gobi-Altai Aimaq (vicinity of Altai Sum, population P.10, see Fig. 1) morphologically fits in the diagnosis of the form *Eremias multiocellata* var. *reticulata* Bedriaga, 1912 described from eastern Dzungaria in China [no exact locality available]. The second population which is genetically very close to P.10 represents the isolated mountain-dwelling form found on Tsagan Bogdo Uul Mt. in Bayankhongor Aimaq (population P.9 see Fig. 1). Recently based on morphological evidence this population was described as a new subspecies *E. m. tsaganbogdensis* (Munkhbayar & Borkin 2010); genetically it is very close to the population P.10 from Gobi-Altai Aimaq (p -distance = 0.2%). However, our mtDNA data indicate that these two populations are not related to *E. multiocellata* sensu stricto and genetically closer to *E. przewalskii* (clade K, p -distance = 2.3%). Thus, taxonomic status of “*Eremias multiocellata* var. *reticulata*” as well as of *E. m. tsaganbogdensis* requires further investigation using morphological evidence and additional genetic markers. Therefore, we tentatively refer to this form as *E. cf. reticulata*.

Subclade J-2 joins two populations from Qinhai Province of central China at elevations above 2000–2600 m a.s.l. (populations P.12–13, see Fig. 1), which were preliminary identified as *Eremias multiocellata kozlowi* Bedriaga, 1907; however, the absence of voucher specimens does not allow us to confirm this identification; thus we preliminary refer to these populations as *Eremias* sp. 2. Subclade J-3 is represented by a single population from southern Mongolia (population P.11, see Fig. 1), which morphologically is similar to *E. cf. przewalskii*.

Clade K joins populations of large-sized sand-dwelling lizards, corresponding to the species *Eremias przewalskii* (Strauch, 1876); this lineage is distributed from central Alashan Desert northwards to central Mongolia and southern Tuva Republic, Russia (populations P.1–8, Fig. 1). Szczerbak (1970) described a new subspecies *E. przewalskii tuvensis* Szczerbak, 1970 from the southern part of the Tuva Republic (between Tere-Khol Lake and River Tes-Khem). Our analysis included a population from southern Tuva (population 8, Tuva republic, Ovyurskiy distr., Tere-Khol lake, Tsuger-Els sands), which shared the same haplotype with populations from central and southern Mongolia (populations P.4–6). Thus our mtDNA data show no support to the validity of the subspecies *E. przewalskii tuvensis*.

Intra- and interspecific differentiation of mtDNA haplotypes. Sequence divergence: The uncorrected p -distances among and within the COI gene fragment of the studied *Eremias multiocellata*–*E. przewalskii* species complex are shown in the Appendix II.

The observed interspecific p -distances within the *Eremias multiocellata*–*E. przewalskii* species complex members studied varied from 0.90% (between subclades J-1 and J-2) to 11.10% (between clade H, “rock form” and clade C of the “sand form”). The values of uncorrected genetic p -distances in ingroup and outgroup comparisons did not overlapped: distances between outgroup and ingroup species varied from 13.80% (between *E. nikolskii* and clade C of *E. multiocellata*) to 21.10%.

Intraspecific distances within *Eremias* species in our analysis normally were below 1.0% but varied from 0% (in *E. yarkandensis* and *E. cf. buechneri*) to 3.00% in clade B.

Taxonomic implications of the mtDNA and morphological data. Our data clearly indicate that *Eremias multiocellata* sensu lato (sensu Szczerbak 1974; Eremchenko *et al.* 1992; Sindaco & Jeremcenko 2008), which included clades A, B, C, F, H, J-1 and J-2 is paraphyletic with respect *E. szczerbaki*, *E. stummeri*, *E. yarkandensis*, *E. cf. buechneri* and *E. przewalskii*. Our mtDNA phylogenetic data provide support to the validity and species status of *E. stummeri*, *E. szczerbaki*, *E. yarkandensis* and *E. buecheri*; we clarify distribution ranges for some of these taxa. We also reveal lineage F of deep divergence and unclear taxonomic status, preliminary referred to as *Eremais* sp. 1. Our data also shed light on the complicated taxonomic status of *Eremias* populations from southern Mongolia and Central China; the populations from south-west Mongolia, corresponding to *Eremias multiocellata* var. *reticulata* Bedriaga, 1912 (subclade J-1), appear to be phylogenetically closely related to the *E. przewalskii* species complex sensu lato; here we preliminary list them as *E. cf. reticulata*. Populations which were preliminary identified as *Eremias multiocellata* var. *kozlowi* Bedriaga, 1907 (subclade J-2) also appear to be phylogenetically nested within the *E. przewalskii* species complex. However due to the lack of voucher specimens, we were not able to analyze morphological characters and avoid any precise identification, referring to these populations as *Eremias* sp. 2.

Based upon the phylogenetic analysis of COI mtDNA gene sequences and morphological analysis, the “rock form” of *Eremias* from western Mongolia and Eastern Kazakhstan represents an independent mtDNA lineage closely related to *E. buechneri* and *E. yarkandensis* and markedly distinct from all other species of the *Eremias multiocellata*—*E. przewalskii* species complex. The observed differences in mtDNA sequences are congruent with other lines of evidences, including diagnostic morphological characters (see below in “Comparisons”), comparison with type and topotype material, available for other members of the *Eremias multiocellata*—*E. przewalskii* species complex, and support the existence of a sympatric population of “sand” and “rock” forms of *Eremias multiocellata*—*E. przewalskii* complex in Mongolian Dzungaria with two forms being both morphologically and genetically distinct and ecologically segregated from each other. These results support our hypothesis that the genetically and morphologically distinct “rock form” of *Eremias* from Mongolian Dzungaria and Eastern Kazakhstan represents a previously undescribed species, which we describe below as:

***Eremias dzungarica* sp. nov.**

(Figs. 3–9; Table 3)

Chresonymy:

“*Eremias multiocellata*” (partim)—Ananjeva 1972; Bannikov *et al.* 1977; Prokopov 1978; Brushko & Kubykin 1988; Brushko 1995; Orlova 1995; Orlova & Terbish 1997; Sindaco & Jeremcenko 2008; Tuniyev & Ananjeva 2010.

“*Eremias multiocellata yarkandensis*”—Szczerbak 1974 (partim).

Holotype. ZMMU R-12845, adult male, individual label R-12845-4; collected on 12.08.2008 from Mongolia, Khovd Aimaq, Khoovor, 7 km west from Uyench Sum (= Uench-somon) (46° 05' N; 91° 56' E) by V.F. Orlova (Figs. 3–6).

Paratypes. ZMMU R-12846-2 and R-12846-5, two adult males, and R-12846-6 one adult female; collection data same as for the holotype: Mongolia, Khovd Aimaq, Khoovor, 7 km west Uench-somon 46° 05' N; 91° 56' E; collected on 12.08.2008 by V.F. Orlova (Fig. 7). ZMMU R-12846-7–R-12846-11, 5 juveniles; collection data same as for the holotype: Mongolia, Khovd Aimaq, Khoovor, 7 km west Uench-somon 46° 05' N; 91° 56' E; collected on 12.08.2008 by V.F. Orlova (Fig. 8). ZMMU R-12862-1 and R-12862-3, two adult males, and R-12862-2, one adult female; collected from: Mongolia, Khovd Aimaq, Bulgan-Somon, urochishe Bayan-Mod, 11 km west Ikher-Toli, on 13.08.2008 by G. Davaasuren (Fig. 7).

Referred Materials. Mongolia: ZMMU R-5415 (1 male, 6 females) from Mongolia, Khovd Aimaq, 6–7 km to the West of Uyench Sum [Uench-somon], coll. 05.07.1984; ZMMU R-5414 (1 male, 1 female) from the same locality as above, coll. 04.07.1984 (samples used in the allozyme study of Truweller *et al.* 1994); ZMMU R-5413 (1 male, 1 female), from the same locality as above, coll. 03.07.1984; ZMMU R-5417 (2 females, 1 male), from the same locality as above, coll. 05–06.07.1984; ZMMU R-5617 (2 adults), from the same locality as above, coll. 05–06.07.1984; ZMMU R-6415 (1 male, 3 females), from Mongolia, Khovd Aimaq, env. Uyench Sum [Uench-somon], 07.06.1984; ZMMU R-6417 (5 adults, 2 subad.), from Mongolia, Khovd Aimaq, 15 km E from Uyench Sum [Uench-somon] (Khuv-Us), coll. 07.06.1984; ZMMU R-6776 (2 females), from Mongolia, Khovd Aimaq, 15 km N from Uyench Sum [Uench-somon], coll. 10.08.1986; ZMMU R-5781 (2 males, 3 females), 6 km W of Uyench Sum [Uench-somon], coll. 23.07.1986; ZMMU R-5807 (1 male) from Mongolia, Khovd Aimaq, env. Uyench Sum [Uench-somon], coll. 23.07.1986; ZMMU R-8252 (4 males, 1 female) from Mongolia, Khovd Aimaq, 6–7 km to W from Uyench Sum [Uench-somon], coll. 04–05.07.1984; ZMMU R-7617 (2 males), from the same locality as above, coll. 04–05.07.1984; ZMMU R-8449 (2 juv.) and ZMMU R-12550 (1 subad.) from Mongolia, Khovd Aimaq, 24 km N of Uyench Sum [Uench-somon], coll. 18.06.2007. Kazakhstan: ZMMU R-8449 (2 juv.) from East Kazakhstan Province, Buran settlement, Chernyi Irtysh, coll. 23.08.1956; ZMMU R-10875 (1 adults), East Kazakhstan Province, Kurumcha district, env. of Kamyshinka, left bank of Irtysh River, coll. 05.1956; ZMMU R-11989 (2 adults, 1 subad.), East Kazakhstan Province, Aigyrkum sands, 5–7 km SW from Buran, coll. 27.05.2003; ZMMU R-14080 (1 adults), East Kazakhstan Province, NE from Ulken-Karatal, coll. 08.2013. Almaty Institute of Zoology, Kazakhstan №№ 3420 and 3421 (2 adults), East Kazakhstan Province, Zaisan valley, 10 km S from Ulken-Karatal, coll. 12.07.1985; ZIK 3753 (№№ 22692–22706) (15 adults), East Kazakhstan Province, Zaisan district, 5–6 km N from Karatal, coll. 14–20.04.1990.

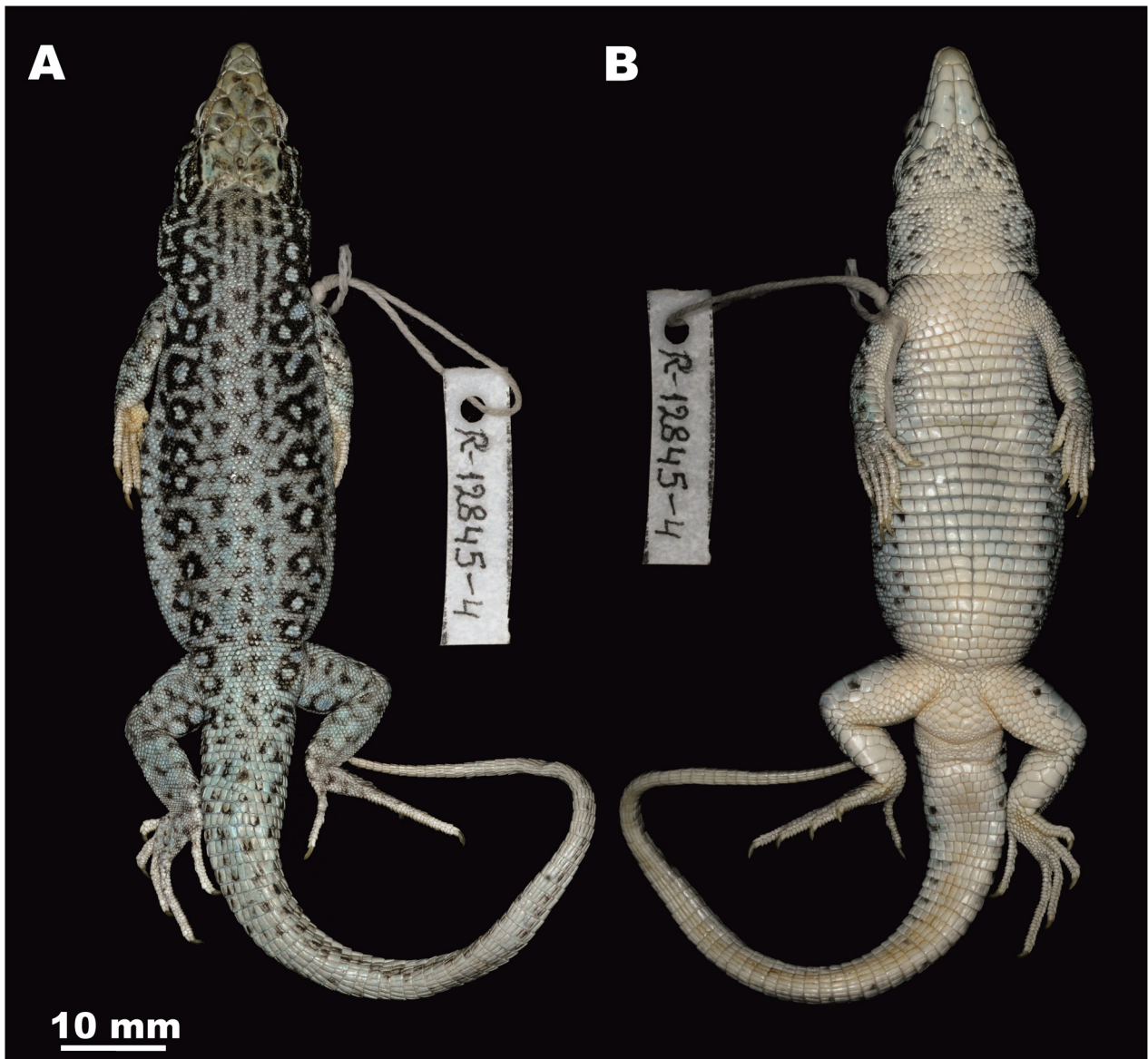


FIGURE 3. Holotype of *Eremias dzungarica* sp. nov. (ZMMU R-12845) in preservative in dorsal (A) and ventral (B) views. Scale bar equals 10 mm.

Diagnosis. A member of the genus *Eremias* on the basis of the following morphological attributes: ventrals arranged in oblique series, converging at the midline of belly; absence of occipital; subnasal in contact with 1–3 supralabials; large transparent scales on the lower eyelid absent; *canthus rostralis* not developed (following Szczerbak 1974). A species belonging to the subgenus *Pareremias* on the basis of the following features: subocular not reaching mouth edge; one frontonasal; two supraoculars; the row of small granular scales between supraoculars and frontal with frontoparietals absent; distance between the femoral pore rows being wide; femoral pore rows not reaching knee-joint; coloration pattern with light colored ocelli with black edging (see Szczerbak 1974). A medium-sized lacertid lizard, maximum snout-vent length (SVL) = 64.5 mm, tail being ca. 1.5 times longer than body length (SVL), hindlimbs relatively long (Pp/SVL ratio 0.46); subocular scale not reaching mouth edge, in touch with 6–8 supralabials; males with bright coloration consisting of 2–3 dorsolateral rows of light-colored ocelli with thick black edging; the ventral row of ocelli in life is greenish to bluish; dorsal pattern consisting of black irregular blotches along the the middorsal line.

Etymology. The specific name “*dzungarica*” is a Latin toponymic adjective in the nominative singular (feminine gender), referring to the distribution of the new species covering the area of Dzungaria, now in easternmost Kazakhstan, northern part of Chinese Xinjiang and the westernmost part of Mongolia (Dzungarian Gobi).

TABLE 3. Measurements and morphological characters of the type series of *Eremias dzungarica* sp. nov.; all measurements in mm; * — tail broken or regenerated; juv. — juvenile.

Characters	R-12846-2	R-12846-5	R-12846-6	R-12846-7	R-12846-8	R-12846-9	R-12846-10	R-12846-11	R-12862-1	R-12862-2	R-12862-3
	m	m	f	juv.	juv.	juv.	juv.	juv.	m	f	m
SVL	62.5	53.8	64.5	37.0	38.0	34.0	32.0	26.5	60.3	61.4	52.0
TL	37.0*	67.3	57.0*	55.1	55.7	53.0	52.0	39.0	35.0*	53.0*	45.0*
Ga	31.0	24.0	35.0	18.5	18.8	15.0	14.2	14.0	29.0	33.8	25.2
HL	16.0	14.8	15.0	9.0	9.0	9.0	9.2	7.8	17.0	14.0	13.6
HW	9.8	7.6	8.2	5.0	6.5	4.8	4.8	3.8	10.0	7.0	7.3
HH	8.0	6.0	7.2	3.0	3.5	3.2	3.5	2.7	7.0	6.0	5.0
NL	21.3	18.7	19.0	12.5	12.5	12.5	11.0	9.0	21.4	20.5	12.5
Pa	20.0	19.0	18.0	12.3	12.5	11.0	9.5	10.0	19.5	19.0	17.5
Pp	29.0	27.7	26.2	17.2	18.2	16.0	17.0	14.0	30.0	25.4	25.7
G.	22	25	23	22	22	23	22	21	26	22	25
Coll.	13	13	13	9	11	12	12	—	8	7	12
P.fm.	11/11	12/12	12/12	12/11	12/12	12/13	12/12	9/9	15/14	13/13	13/13
Dist.P.fm.	2.1	2.5	1.6	1.7	1.8	2.0	1.9	1.1	2.0	1.7	1.7
Ventr.	31	31	30	31	31	31	31	30	32	30	32
Sq.c.cd.	24	26	23	24	22	23	25	23	27	23	25
Lam.subdig.	21	23	20	22	22	22	24	21	21	19	22
Sq.	50	48	46	50	46	46	52	49	51	46	49
Sq.dors.	119	105	112	108	110	107	128	104	115	108	112
Lab.min.	6/6	6/6	6/5	6/6	6/6	6/6	6/6	5/5	6/6	6/6	6/6
Lab.total	11/11	11/11	11/9	10/10	10/10	11/10	10/9	9/9	11/11	10/10	10/10
Infralab.	7/7	6/9	7/6	8/7	7/6	6/6	7/8	6/6	7/7	7/7	7/7
Submax.	6/6	6/6	6/5	5/5	5/6	5/5	5/5	5/6	6/6	5/6	6/6
Submax.Cont.	3/3	3/3	3/3	3/3	3/4	3/3	3/3	3/3	3/3	3/3	3/3

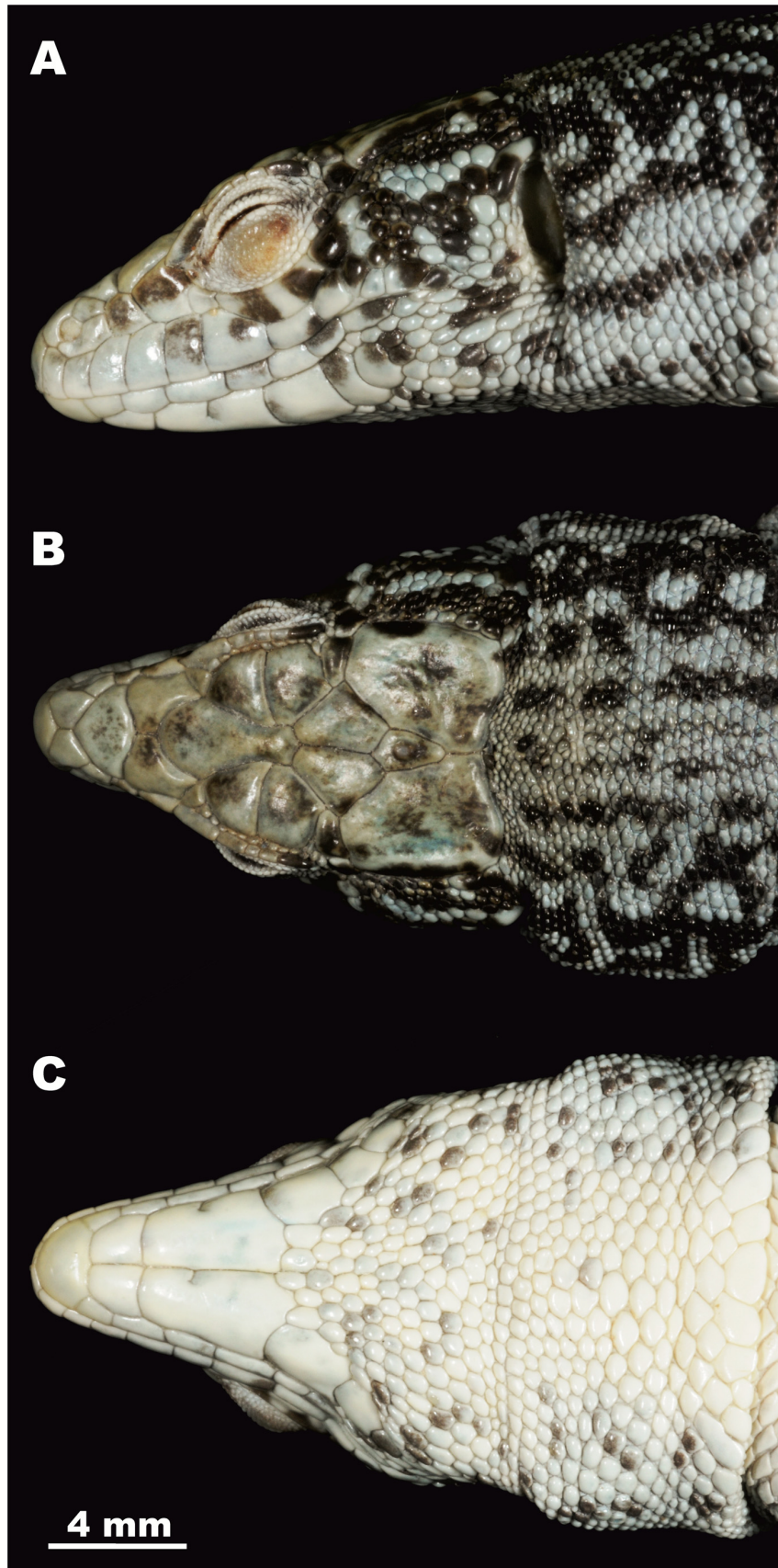


FIGURE 4. Head scalation of *Eremias dzungarica* **sp. nov.** holotype (ZMMU R-12845) in lateral (A), dorsal (B) and ventral (C) aspects. Scale bar equals 4 mm.

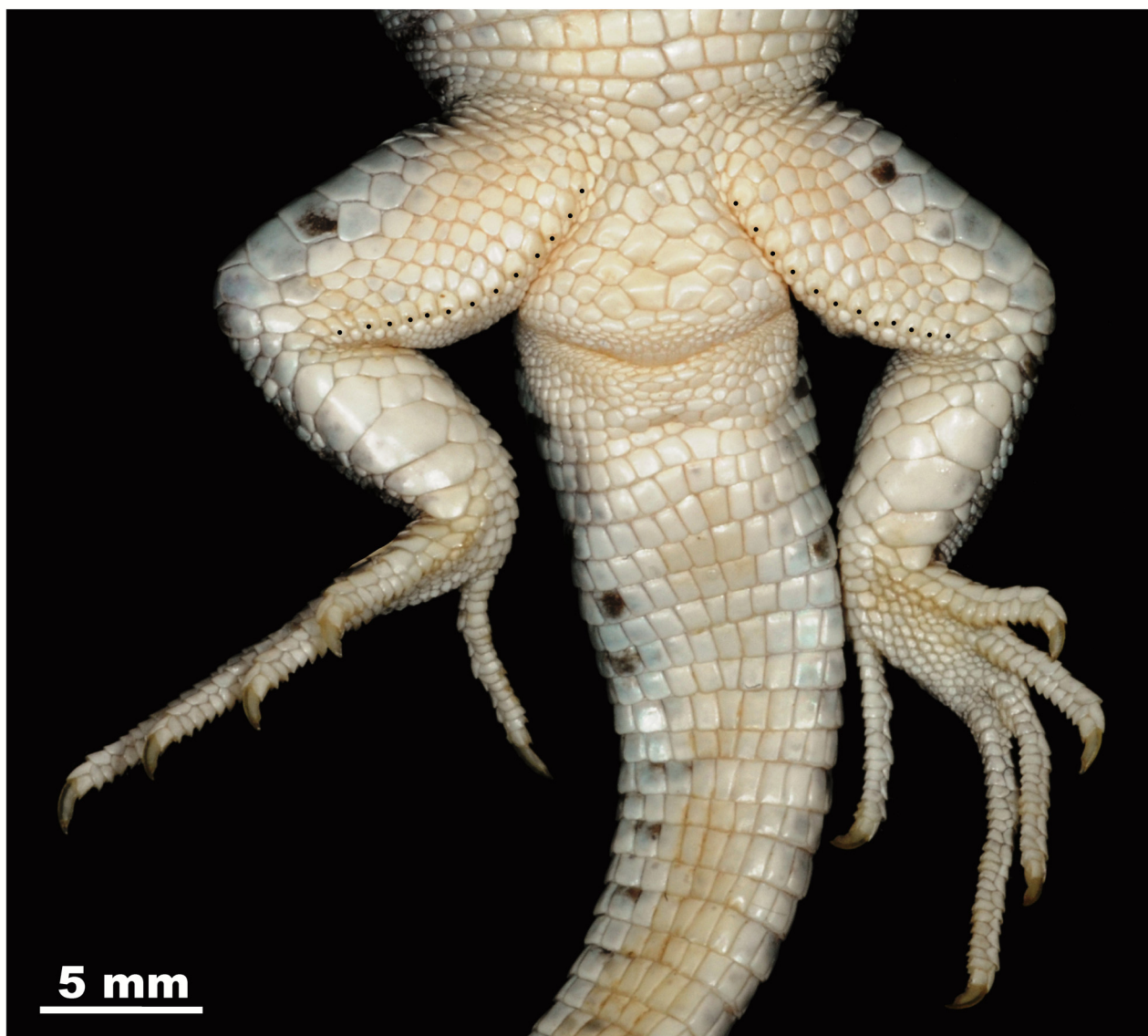


FIGURE 5. Cloacal region of *Eremias dzungarica* sp. nov. holotype (ZMMU R-12845); black dots indicate location of femoral pores. Scale bar equals 5 mm.

Recommended vernacular name. We recommend the following common name in English: *Dzungarian racerunner*. Recommended common name in Mongolian: *Züüngaryn güрvel*; in Russian: *Dzhungarskaya yaschurka*.

Description of holotype. An adult male preserved in 75% ethyl alcohol in a good state of preservation (Fig. 3); body robust and moderately depressed; a species of the subgenus *Pareremias* (Szczerbak 1974); tail long, ca. 1.5 times longer than body (SVL/TL ratio 0.77). Head relatively long (HL/SVL ratio 0.28) (Fig. 4), massive and wide (HW/HL ratio 0.57), head height slightly less than head width (HH/HW ratio 0.81). Limbs strong, hindlimbs longer than forelimbs (Pa/Pp ratio 0.67), hindlimbs comprise almost half of the body length (Pp/ SVL ratio 0.31). Nostrils not swollen nor raised, three pairs of nasals; subnasal not in contact with rostral shield and is located above first to third supralabials. Snout bluntly rounded, rostral broadly covers the anteriormost part of the dorsal surface of head, but not in contact with frontonasal. Occipital shield absent. Two large nasals and one small nasal in contact with rostral anteriorly, with first, second and third supralabials laterally, and with frontonasal and first loreal posteriorly. Frontonasal single, broader than long, its height less than its length, and laterally frontonasal in contact with first loreal and posteriorly with prefrontals. Two prefrontals contacting each other forming a longitudinal suture; each almost same size as frontonasal, notably longer than broad and laterally in contact with first and second loreals and posteriorly with frontal and a presubocular scale. The single frontal with distinct concavity,

slightly bluing, its maximal width in the anterior part ca. twice greater than width in the posterior part. Frontal broadened, much longer than prefrontal and frontonasal together, frontal length ca. two times greater than the distance from its anterior tip to the tip of snout. Frontal anteriorly in contact with prefrontals, posteriorly and laterally in contact with small presupraocular scale and supraoculars, but not separated from the latter by scales, nor by granules, and posteriorly with frontoparietals. Two frontoparietals almost as large as a single supraocular, laterally being in contact with the second supraocular and postsupraocular, and posteriorly with interparietal and parietals. Interparietal small and relatively diamond-shaped with well-pronounced bulging transparent pineal ocellus, surrounded by frontoparietals and parietals; two very large and plate-like parietals, slightly longer than broad, being in contact behind interparietal forming a suture which is ca. two times shorter than interparietal length. Two loreals, first one small, trapezoid-shaped, surrounded by third and fourth supralabials, subnasal, postnasal, frontonasal, prefrontal, and the second loreal which is distinctly large and has pentagonal shape. Two supraoculars of same size, anteriorly than the first supraocular a small presupraocular shield of triangular shape, followed by a series of 13–14 granular scales running posteriorly and separating supraoculars from 5–5 supraciliaries. Posteriorly than the second supraocular a postocular shield is present, it's broader than long, larger than presupraocular and in contact with second supraocular, frontoparietal and parietal medially and with postocular laterally, anteriorly surrounded by several granules; temporal region mostly covered by granular scales becoming larger towards the tympanal region and larger supratemporal shields (9 on each sides), two of them enlarged. Tympanic scale edging the dorsal edge of ear cavity, distinct and elongated obliquely, of semicrescent shape, almost the same size on both sides; tympanum vertically elongated, same size as the orbit. 8–8 supralabials, 6 of which on each side anteriorly to subocular; 6–8 supralabials in contact with subocular which does not border the mouth; the sixth supralabial enlarged of trapezoid shape. Subocular comparatively small, longer than broad with a distinct ridge being extensively in contact with the lower edge of orbit; anteriorly small presubocular shield; posteriorly large postsubocular shield; lower eyelids with a semitranslucent membrane made up of small scales. Gular scales comparatively large, 21 gulars from symphysis of chin shields to median gular, becoming slightly enlarged posteriorly; gular fold well-developed; collar well pronounced, not serrated, made up of 10 enlarged scales, collar scales of uneven size: the medial one the largest, lateral collar scales same size as the adjacent gulars. Five pairs of submaxillary shields, first two pairs in contact, the third to fifth pairs widely separated; the first pair of submaxillary shields somewhat larger than the fifth and in contact with mental anteriorly, with first and second infralabials laterally; each scale of the second submaxillary pair consists of two fused scales, partially divided by a transverse suture for one third of its width; the fifth submaxillary pair each in contact with the fourth pair anteriorly, being surrounded by 8 granular scales laterally and posteriorly and not in contact with infralabials; 7–7 infralabials. Up to 16 longitudinal and 31 transverse rows of almost squarish pectoral and ventral plates from collar to hindlimbs (Fig. 3, B); median ventral wider than long; dorsal scales smooth, granular, of almost same size along the dorsum, juxtaposed; 48 scales across the middle of dorsum, and about 112 scales in a single row from occiput to a point just above the vent; proximal caudals notably larger than posterior dorsals; caudals on dorsal surface of tail completely smooth, becoming large and elongate distally, arranged in distinct whorls, 24 scales in the 9–10th whorl behind the vent. Upper forearm covered dorsally by enlarged and almost diamond-shaped scales; lower forearm covered with granules; upper hindlimbs covered dorsally by granules, externally by large shields; tibia covered dorsally by granules, ventrally by large smooth plates, three plates in a transverse row; no fringes on the toes, claws light-colored. 22 uni- and bi-carinate lamellae under fourth toe arranged in a single row; 13/12 femoral pores in each side (Fig. 5), distal pores are notably smaller than median ones, almost reaching the knee joint (separated from the joint by a single scale on each side); the two femoral pore series separated anteriorly by a wide space consisting of 8–9 scales; the distance between the femoral pore series is ca. 2 times shorter than length of a single pore series. precloacal region encompassing polygonal shields, the three median ones being the largest; but almost not different from neighbouring scales in size; 6 plates in longitudinal row from the space between femoral pores to anterior edge of the vent.

Measurements and counts of holotype: SVL—65.0 mm; TL—85.0 mm; Ga—32.0 mm; HL—18.0 mm; HW—10.3 mm; HH—8.3 mm; NL—20.9 mm; Pa—20.0 mm; Pp—30.0 mm; HL/SVL—0.28; HW/HL—0.57; HH/ HW—0.81; Pa/SVL—0.31; Pp /SVL—0.46. Sq.—48; G.—21; Coll.—11; P.fm.—13/12; Ventr.—31; Ventr.Long.—16; Sq.c.cd.—24; Lam.subdig.—22; Lab.min.—6/6; Infralab.—7/7; Dist.P.fm.—2.0; Sq.dors.—112; Submax.—5/5, Submax.Cont.—2 (but the second and third pairs are almost fused).

Coloration and pattern. Scales on head dorsal surface dark grey-brown with unclear pattern of dark-brownish

blotches (Fig. 6); smaller dark spots scattered on head sides and in lateral parts of gular area. Ventral surface light beige; in the posterior part of belly—with rare bright yellow and black spots with on the most lateral ventrals. Dark blotches on body flanks forming two regular longitudinal rows. Dorsum uniformly greyish-brown; three longitudinal rows of dark spots in the medial part of dorsum converge in the scapular area forming two longitudinal stripes on the dorsal surface of neck. Two dorsolateral rows of large ocelli lasting from tympanum posteriorly; ocelli in the both rows with thick black edging; dorsal row of ocelli whitish to bluish; ventral row of ocelli bluish-green to grass-green in life. Temporal scales with contrasting pattern (dark brown blotches and light bluish background); posterior edges of upper hindlimbs and forelimbs with a bright greenish spot with black edging. Supralabials and supraoculars with vague dark pattern. The dorsal surface of tail with black spots; proximal upper surface of tail brown, distal part light brownish-grey.

Color in preservative. After 7 years in preservative, the general pattern of the holotype corresponds well to the pattern reported in life (Fig. 3). However warm tints in coloration fade, yellowish spots on ventrals completely disappeared, the ventral row of ocelli appear bluish instead of greenish in life; warmer background coloration of the holotype turned lighter and get bluish tint in preservative.

Variation. For the variation of paratypes see Table 3. The paratypes largely correspond with the description of the holotype (see Fig. 7). The juvenile paratypes (ZMMU R-12486-7–11) are much smaller than the adult paratypes (SVL = 26.5–38.0 mm, $n = 5$; SVL/TL = 0.62–0.70) and notably differ from the other types in coloration pattern (see Fig. 8): five interrupted dark nuchal stripes quickly disappear at neck in speckled or reticulated contrasting pattern, in some specimens light interrupted paravertebral stripes discernable, dorsum coffee-brown to dark beige in ground color; head dorsally lightly colored, with two well defined dark brown bands transversely above eyes; dorsolateral rows of ocelli yellowish-green, yellowish coloration also discernable at posterior surfaces of hindlimbs and lateral surfaces of tail; ventral surfaces of tail bright yellow. Despite previously reported morphological differences between highland (Saur and Saikan Mts.) and lowland (Aigyrkum Sands) populations of *E. dzungarica* **sp. nov.** from Eastern Kazakhstan (significant differences found in body size and head proportions, as well as in the relative length of hindlimbs, see Orlova 1995), the population from Mt. Ashutas (Eastern Kazakhstan) is not different from lowland Kazakh (Aigyrkum) and Mongolian populations in values of Sq. and also shares similar coloration pattern.

Sexual dimorphism. SVL does not significantly differ among sexes, but females have larger gleno-acetabular distance. Compared to males, females have slender head and body and duller coloration, bright dorsolateral ocelli well-pronounced in males (Fig. 9, A) are absent in females (Fig. 9, B). The relative head length in males is greater than in females (HL/SVL in males 0.23–0.25 vs. 0.20–0.23 in females).

Geographic variation. Racerunners from Mongolia collected at elevations above 2000 m a.s.l. are characterized by a bright contrasting coloration in males and quite narrow light vertebral stripe without dark pattern. Specimens of *E. dzungarica* **sp. nov.** collected in Eastern Kazakhstan (Aigyrkum sands, elevations under 1000 m a.s.l.) are characterized by the larger size of males (SVL up to 71.2 mm) and a quite broad light vertebral stripe; however they are similar to the Mongolian population in scalation characters and general coloration pattern (Orlova 1995).

Karyotype. The Uyench population of the new species has $2n = 38$ (36M + 2m), NF = 38; all chromosomes are acrocentric (Orlova & Terbish 1997).

Distribution. In Mongolia the “rock form” of multiocellated racerunner which we describe here as *E. dzungarica* is common in the foothills of Mongolian Altai (Mongolian Dzungaria), in close vicinity of Uyench Sum, Khovd Aimaq (Orlova & Terbish 1997: Fig. 54) (see Fig. 1, populations P.17–18). The new species was also reported from the upstreams of the Bulgan-gol River from the elevations above 2000 m a.s.l. We also recorded the new species in Khovd Aimaq, Bulgan Sum, Bayan-Mod, vicinity of Ikher-Toli (Fig. 1, population P.16). Outside Mongolia, *E. dzungarica* **sp. nov.**, previously identified as *E. multiocellata*, was recorded from Aigyrkum sands in East Kazakhstan Province (Ananjeva 1972). Later, the new species was recorded in from locality near to Buran settlement, East Kazakhstan Province (Prokopov 1978). Specimens of the new species deposited in the Zoological institute of Kazakh Academy of Sciences (Almaty) were collected from 20 km NW from Maikapchagai and 10 km SW from Ulken-Karatal (Brushko & Kubykin 1988; Brushko 1995). Tuniyev & Ananjeva (2010) report this species in Kyzylkum (Kulujun) sands on the left bank of Bukhtarma water reservoir and from Mt. Ashutas, where this species inhabits stony semidesert. The new species is also expected to inhabit the northern part of the Xinjiang Uyghur Autonomous Region north from Tian Shan Mountains (Chinese Dzungaria); the species is assumingly

reported for the Chinese herpetofauna as *E. multiocellata* (Zhao & Adler 1993); however, the precise taxonomic assignment of the Chinese populations would be possible only after a detailed molecular and morphological study.



FIGURE 6. Holotype of *Eremias dzungarica* **sp. nov.** (ZMMU R-12845) in life in lateral (A) and dorsolateral (B) views.

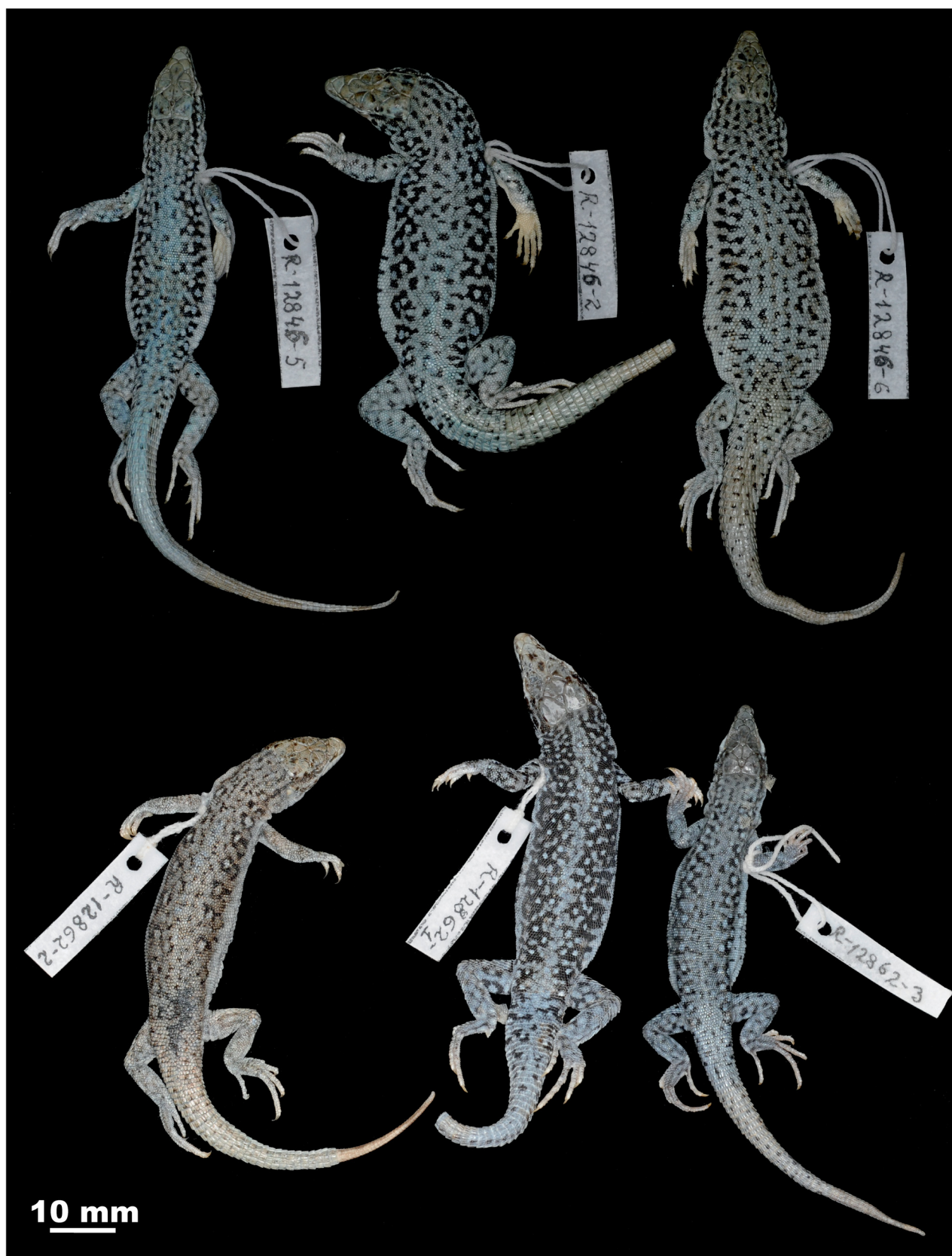


FIGURE 7. Paratype series of *Eremias dzungarica* **sp. nov.** (adults; ZMMU R-12846; R-12862) in preservative in dorsal view. Scale bar equals 10 mm.

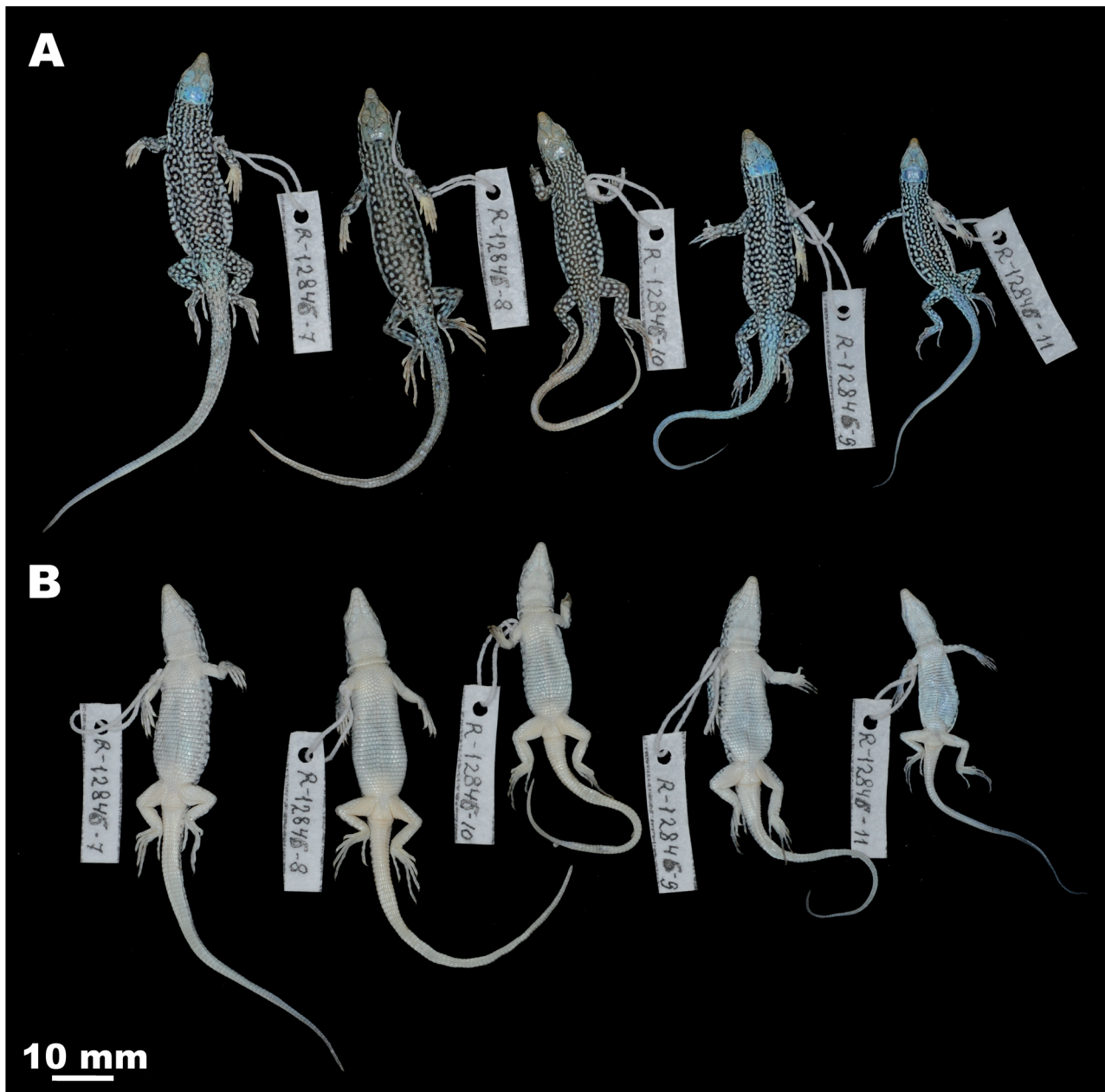


FIGURE 8. Paratype series of *Eremias dzungarica* **sp. nov.** (juveniles; ZMMU R-12846) in dorsal (A) and ventral (B) views. Scale bar equals 10 mm.

Ecological notes. In Mongolian Dzungaria, *E. dzungarica* **sp. nov.** inhabits elevations up to 2400–2600 m a.s.l., preferring rocky semi-desert or mountain desert habitats with occasional vegetation: *Haloxylon* (Amaranthaceae), *Caragana* (Fabaceae), *Nitraria* (Nitrariaceae), *Reaumuria* (Tamaricaceae) and Poaceae (Fig. 10, A; see Orlova & Terbish 1997, described as the “rock form” of *E. multiocellata*). In the vicinity of Uyench Sum, Khovd Aimaq, the new species is found in sympatry with the “sand form” of *E. multiocellata* sensu stricto (populations P.17 and P.56 respectively, see Appendix II); however the two species appear to be ecologically isolated with *E. multiocellata* preferring lowland desert habitats with loose sands and dunes at the foothills (Fig. 10, B; see Orlova & Terbish 1997, described as the “sand form” of *E. multiocellata*), while *E. dzungarica* **sp. nov.** inhabits hilly areas, rocky slopes and outcrops and ravines. In Eastern Kazakhstan, however, in Aigyrkum Sands *E. dzungarica* **sp. nov.** is found in lower elevations (usually at 400–600 m a.s.l.) and exclusively in sandy areas and on small dunes; whereas at Ashutas Mt. (1000 m a.s.l.) the new species was recorded on clay soils with gravel and occasional rocky outcrops.

Racerunners appear after the hibernation when temperature rises above 18° C (usually, end of April) and are

usually active until the end of September—early October (Orlova & Terbish 1997). Breeding takes place from end of April to early May; the population in Mongolian Dzungaria is reported to have ovoviviparity; from 1 to 4 newborns appear in middle-end of July (Orlova & Terbish 1997). Before bearing, pregnant females were observed to move to lower sandy areas with denser *Artemisia* (Asteraceae) vegetation, which probably provide a better habitat for newborns, where they were observed in the same biotopes with the “sand form” of *E. multiocellata* sensu stricto



FIGURE 9. *Eremias dzungarica* sp. nov. in life *in situ* showing sexual variation in coloration: adult male (A) and adult female (B).



FIGURE 10. Type locality of *Eremias dzungarica* **sp. nov.** in vicinity of Uyench Sum, Khovd Aimaq, western Mongolia: rock outcrops, typical habitat of *Eremias dzungarica* **sp. nov.** (the “rock form”) (A); sand dunes, typical habitat of the “sand form” of *E. multiocellata* (B).

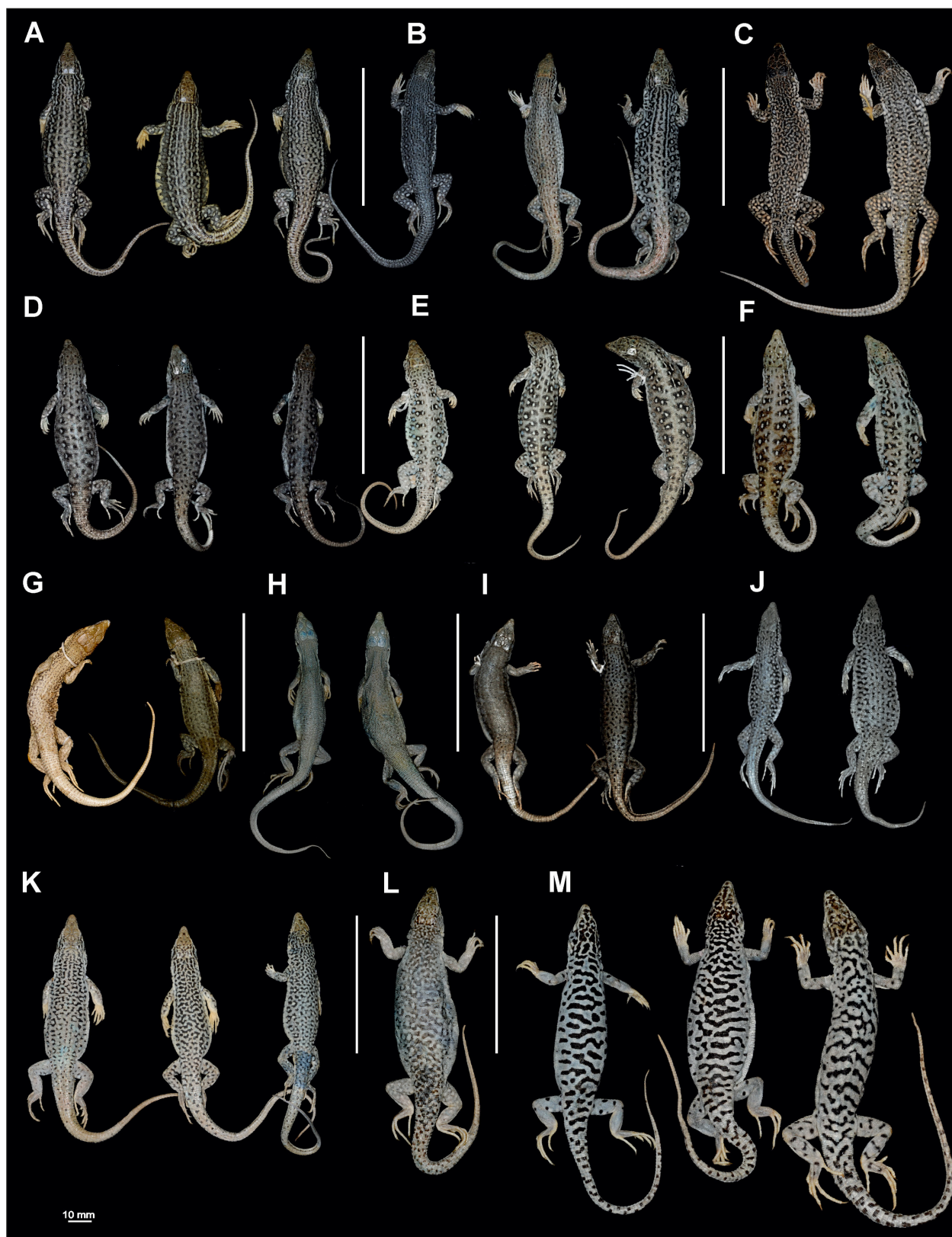


FIGURE 11. Dorsal patterns of *Eremias multiocellata*—*E. przewalskii* complex members (in scale): A—*E. multiocellata*; sand form A (ZMMU R-12841); B—*E. multiocellata*; sand form B (ZMMU R-13215); C—*E. multiocellata*; sand form B (ZMMU R-13206); D—*E. szczyrbaki* (ZMBPI R-000657; 635; 655); E—*E. stummeri* (ZMMU R-14335); F—*Eremias* sp. 1 (ZMMU R-14330); G—*E. yarkandensis* (types BMNH 1917.3.6.28; 1917.3.6.29); H—*E. buechneri* (ZISP-9131); I—*E. yarkandensis* (ZMMU R-14344); J—*E. dzungarica* **sp. nov.** (ZMMU R-12846); K—*E. cf. reticulata* (ZMMU R-12855); L—*E. przewalskii* (ZMMU R-13214); M—*E. przewalskii* (ZMMU R-13209).

In Mongolian Dzungaria, the new species coexists sympatrically with *E. arguta* and *E. multiocellata* sensu stricto. No morphological or genetic evidence of hybridization between *E. dzungarica* **sp. nov.** and *E. multiocellata* sensu stricto in the sympatric population P.17 = 56 (see Appendix II) were recorded (9 and 5 specimens examined, respectively).

Comparisons. *E. dzungarica* **sp. nov.** is both most morphologically and molecularly similar to the members of *E. multiocellata*—*E. przewalskii* species complex from Central and Middle Asia (subgenus *Pareremias*); comparison with *Eremias* species inhabiting this region, as well as with other members of the subgenus *Pareremias* appear to be the most pertinent.

Differences from sympatric and closely distributed *Eremias* species. From sympatric *E. arguta* (subgenus *Eremias* sensu stricto) the new species is differentiated by smaller size (SVL up to 65.5 vs. maximum SVL 88 mm in *E. arguta*), slender body and longer tail (SVL/TL ratio 0.61–0.75 in the new species vs. 0.86–1.26 in *E. arguta*), and dorsal pattern (brightly colored ocelli are absent in *E. arguta*; in Mongolia this species shows dorsal pattern of large dark transverse spots and blotches on light greyish background color of dorsum).

From *E. vermiculata* (subgenus *Rhabderemias*), also found in south-western Mongolia (but no cases of sympatry with *E. dzungarica* reported), *E. dzungarica* **sp. nov.** can be distinguished by more robust body, shorter tail, presence of bright ocelli on dorsum and body flanks (vs. absent in *E. vermiculata*), absence of thin dark vermiculations on dorsum (vs. present in *E. vermiculata*) and absence of a complete row of granules, separating supraorbitals from frontal and frontoparietals (vs. present in *E. vermiculata*).

From *E. argus* (subgenus *Pareremias*), mostly recorded from central and eastern Mongolia, no cases of sympatry with the new species were reported) the new species can be diagnosed by a more robust body, relatively longer tail (SVL/TL ratio 0.61–0.75 vs. 0.77–1.03 in *E. argus*) and longer hindlimbs (Pp/SVL ratio 0.43–0.56 vs. 0.38–0.54), dorsal coloration (rows of brightly colored ocelli absent in *E. argus*), presence of a single frontonasal (vs. paired frontonasal in *E. argus*).

Differences from other members of the *E. multiocellata*—*E. przewalskii* species complex. From sympatric “sand form” of *E. multiocellata* sensu stricto (Fig. 11, A) from localities in vicinity of Uyench Sum (Khovd Aimaq) the new species can be distinguished by larger size (maximal SVL 65.5 mm vs. 57 mm in *E. multiocellata* sensu stricto), relatively longer tail (SVL/TL ratio 0.61–0.75 in the new species vs. 0.73–0.98 in *E. multiocellata* sensu stricto) and relatively longer hindlimbs (Pp/SVL ratio 0.43–0.56 in the new species vs. 0.39–0.55 in *E. multiocellata* sensu stricto). The two species can be also reliably differentiated by dorsal coloration: in *E. multiocellata* sensu stricto dorsal light sandy background color is covered by sparse small black spots forming irregular longitudinal lines (Fig. 11, A–C); males have small light ocelli and a single dorsolateral row of bluish ocelli with thin dark edging (vs. 2–3 rows of large bluish or greenish ocelli with thick black edging in the new species). Though subjected to significant geographic variation, most scalation characters in the new species show lower values than in *E. multiocellata* sensu stricto (Sq. = 43–52, average 47.75 (n = 20) in *E. dzungarica* **sp. nov.** vs. Sq. = 50–60, average 54.80 (n = 30) in *E. multiocellata* sensu stricto; for details see Orlova & Terbish 1997: Table 42).

From *E. cf. reticulata* (in Mongolia distributed in Gobi-Altai Aimaq between the ranges of *E. multiocellata* in Dzungar Gobi and *E. przewalskii* in Trans-Altai Gobi; see Fig. 11, J) *E. dzungarica* **sp. nov.** can be differentiated by a more robust body with similar body size, shorter tail, smaller number of scales around 9–10th tail ring (21–28 in the new species vs. 23–31 in *E. cf. reticulata*) and by dorsal coloration. Though both species have bright ocelli with dark edging, in *E. cf. reticulata* they are found in both sexes, whereas in *E. dzungarica* **sp. nov.** only in males; the dorsal pattern of *E. cf. reticulata* (Fig. 11, J) is resembling that of *E. przewalskii* (Fig. 11, L, M); pterygoid teeth are less developed in the new species, than in *E. cf. reticulata* (see Orlova & Dunaev 1992).

The allopatric mountain population of Tsagan-Bogd Uul, described as *E. m. tsaganbogdensis* (Munkhbayer & Borkin 2010), can be differentiated from the new species by larger body size (maximal SVL 68 mm in *E. m. tsaganbogdensis* vs. 64.5 in *E. dzungarica* **sp. nov.**), comparatively longer hindlimbs Pp/SVL ratio 0.57 ± 0.01 (0.54–0.62; n = 4, males) and 0.56 ± 0.01 (0.53–0.59; n = 6, females) in *E. m. tsaganbogdensis* vs. 0.52 ± 0.01 (0.48–0.56; n = 10, males) and 0.48 ± 0.01 (0.43–0.50; n = 6, females) in the new species. *E. dzungarica* **sp. nov.** has lower number of Sq. = 47.7 ± 0.39 (43–52) vs. Sq. = 54.29 ± 0.63 (47–59) in *E. m. tsaganbogdensis*, and P.fm. = 11.5 ± 0.23 (9–15) vs. P.fm. = 12.45 ± 0.24 (11–15) in *E. m. tsaganbogdensis*. Diagnostic characters of scalation include: the fifth submaxillary shield is not divided in the new species (vs. paired in most specimens of *E. m. tsaganbogdensis*); dorsal tail scales always smooth in *E. dzungarica* **sp. nov.** (vs. tail scales notably keeled in 85%

of examined specimens of *E. m. tsaganbogdensis*, see Munkhbayar & Borkin 2010); and lower number of ventrals 30.7 ± 0.26 (28–32; $n = 28$) in *E. dzungarica* **sp. nov.** (vs. relatively greater number of ventrals 33 ± 0.24 ; 25–38; $n = 10$ in *E. m. tsaganbogdensis*).

From *E. przewalskii* (Fig. 11, L, M) the new species can be diagnosed by a smaller size (maximal SVL = 65 mm vs. maximal SVL = 84.7 mm for Mongolian and 97 mm for Chinese populations of *E. przewalskii*), smaller number of Sq. (43–52 in the new species vs. 47–71 in *E. przewalskii*) and smaller number of G. (18–28 in *E. dzungarica* **sp. nov.** vs. 24–41 in *E. przewalskii*); and by dorsal coloration (*E. przewalskii* has reticulated (Fig. 11, L) or zebra-like (Fig. 11, M) contrasting dorsal pattern and lacks bright ocelli on dorsum). *E. przewalskii* has well-developed pterygoid teeth (1 to 6 teeth on each pterygoid), whereas in *E. dzungarica* **sp. nov.** pterygoid teeth are usually absent or may be underdeveloped (see Orlova & Dunaev 1992).

From *E. yarkandensis* (Fig. 11, G, I) the new species can be distinguished by a more robust habitus (vs. comparatively slender head and body in *E. yarkandensis*), by subocular being not in contact with mouth edge (vs. subocular shield touching mouth edge in *E. yarkandensis*); by having dorsal tail scales always smooth in *E. dzungarica* **sp. nov.** (vs. tail scales notably keeled in types of *E. yarkandensis*); and by coloration pattern consisting of 3 rows of bright ocelli with thick black edging (vs. occasional small light ocelli in 1–2 dorsolateral rows with thin dark edging in *E. yarkandensis*).

From phylogenetically closely related *E. buechneri* (Fig. 11, H) from Kashgaria (southern Xinjiang, China) the new species can be distinguished by much more robust body habitus and massive head (vs. slender body and narrow head in *E. buechneri*); by relatively smaller number of Sq. (43–52 in the new species vs. 47–60 in *E. buechneri*); by much smaller number of G. (18–28 in *E. dzungarica* **sp. nov.** vs. 23–37; average 29.49 in *E. buechneri*); and lower number of ventrals 30.7 ± 0.26 (28–32; $n = 28$) in *E. dzungarica* **sp. nov.** (vs. relatively greater number of ventrals 32.2 ± 0.18 ; 30–36; $n = 55$ in *E. buechneri*); by length of the suture between frontal and frontoparietals being less than the double length of the posterior edge of mental shield (vs. the suture between frontal and frontoparietals being twice the length of the posterior edge of metal shield in *E. buechneri*); and by dorsal pattern with contrasting bright ocelli with black edging and dark spots on dorsum in *E. dzungarica* **sp. nov.** (vs. uniformly greyish dorsum without clear pattern or ocelli in *E. buechneri*).

Genetic differences. The new species is clearly different from all other congeners included in the present phylogenetic analysis with average uncorrected genetic *p*-distances varying from 3.20% (between *E. dzungarica* **sp. nov.** and the *E. cf. buechneri* from S Xinjiang, China) to 11.10% (between the new species and *E. cf. multiocellata* from Gansu Province, China) (see Table 2).

Discussion

From many forms of *Eremias* described between XIX–XX centuries as a result of the Central Asian expeditions carried out by Nikolay Przewalski and his followers, the comprehensive monograph of Szczerbak (1974) recognized as valid species only *E. multiocellata*, *E. przewalskii*, *E. buechneri*, *E. quadrifrons* from Central Asia and *E. argus* and *E. brenchleyi* from Eastern Asia. In his monograph, Szczerbak (1974) discriminated *Eremias* taxa mostly using mean character values for large sample sizes grouped *a priori* to geographic populations and thus many local variations remained unnoticed in his analysis (Poyarkov *et al.* 2014). However, even morphologically “good” species in Central Asian *Eremias* are often difficult to diagnose due to high ecological and geographic variation of characters and presence of numerous “intermediate” forms and populations. As was noted by Jaque v. Bedriaga (Bedriaga 1912: p. 589) “the slightest attempt to undertake a certain discrimination of some of these forms for compilation of differential diagnoses should be impossible due to the insurmountable difficulties. The clear differentiation of even quite well-established and well distinct species, such as *E. multiocellata* and *E. przewalskii*, represents a truly difficult task”.

Until recently, *E. multiocellata* was regarded as a monotypic species or as a single species with a number of subspecies (Szczerbak 1974; Orlova & Terbish 1997), of which only *E. m. yarkandensis* was reported for the territory of the former Soviet republics (now eastern Kyrgyzstan and Kazakhstan) (Szczerbak 1974). Further detailed morphological and karyological studies (Eremchenko *et al.* 1985, 1992; Eremchenko & Panfilov 1999), revealed that Kyrgyz populations of the species complex represent a number of distinct forms of assumingly specific status, clearly differentiated from each other. On the basis of morphological analysis some of the Kyrgyz populations were later assigned to the species inhabiting neighbouring areas of China (*E. yarkandensis* or *E.*

buechneri), or subsequently described as independent species (*E. stummeri*, *E. szczerbaki* and *E. kokshaaliensis*) (Eremchenko *et al.* 1992; Eremchenko & Panfilov 1999; Szczerbak 2003). Trueller *et al.* (1994) in an allozyme study also provided evidences for full species status of *E. stummeri*. However, up to now the taxonomic status of these populations remained questionable due to the lack of comprehensive studies joining both morphological and genetic variation of the species complex across Central Asia.

Our study represents a first attempt to apply DNA COI-barcoding methods for scrutinizing taxonomic diversity of the *E. multiocellata*—*E. przewalskii* species complex. The combination of mtDNA and morphological data allowed us to clarify taxonomic status and distribution ranges of species complex members, however further progress in phylogeny and taxonomy of the *E. multiocellata*—*E. przewalskii* species complex depends on adding additional genetic markers to the analyses and additional populations, particularly from the territory of China, where our sampling is rather incomplete (especially from Xinjiang, Gansu and Qinhai Provinces).

In particular, our study supported proposed specific status of Kyrgyz members of *E. multiocellata*—*E. przewalskii* species complex. The Issyk-Kul racerunner, *E. stummeri* (Fig. 11, E), inhabits Chu—Issyk-Kul basin and penetrates to northern slopes of Tian Shan Mountains in Almaty Province of Kazakhstan, while Szczerbak's racerunner, *E. szczerbaki* (Fig. 11, D), is found in the inner Tian Shan Mts., inhabiting the basin of Naryn River; the two species are well-differentiated both morphologically and genetically and form a clade (Fig. 2, group II). The populations of *E. stummeri* from Kegen and Tekes river valleys in Almaty Province of Kazakhstan (Figs. 1, 2; populations 18, 19), which were initially identified as *E. multiocellata* (Dujsebajeva *et al.* 2009), show no significant differences from the topotypic *E. stummeri* population of Issyk-Kul Lake basin both in morphology and in mtDNA sequences. In the Kegen population (population P.19, Fig. 1) we found two unique mtDNA haplotypes (haplotypes 19–20, see Fig. 2, Appendix II), slightly divergent from COI haplotypes of *E. stummeri* from the Kyrgyz populations of this species (*p*-distance = 1.0%); however one of Kyrgyz haplotypes (haplotype 21) was also recorded in Kegen (see Fig. 2). Another population of *E. stummeri* from Almaty Province of Kazakhstan (population P.20, haplotype 21) was indistinguishable from Kyrgyz *E. stummeri* populations in sequences of COI gene.

The Yarkand racerunner, *E. yarkandensis* Blanford 1875 was described from Tarim Basin in Chinese Kashgaria (southern Xinjiang), and was reported to penetrate to Kyrgyzstan in Eastern Alai (Eremchenko *et al.* 1992; Eremchenko & Panfilov 1999). Examination of the types of *E. yarkandensis* (Fig. 11, G) confirms the assignation of the Osh *Eremias* population (Fig. 1, Appendix II, population 27) to this species; phylogenetically it is nested in one clade with *E. przewalskii* and allied taxa (Fig. 2, group III).

All the forms of the *E. multiocellata* species complex in Kyrgyzstan appear to have allopatric distribution ranges. The Kokshaal racerunner, *E. kokshaaliensis* is easily distinguished from other Kyrgyz *Eremias* and the Chinese species *E. buechneri* by its slender body habitus, small head and mottled dorsal pattern; after discovery by Yakovleva (1964), this species was regarded as *E. buechneri* (Eremchenko *et al.* 1985, 1992) until it was recognized as an independent species by Eremchenko & Panfilov (1999). In our study, the population from southern Xinjiang (Kashgaria) corresponding to the type description of *E. buechneri*, forms a distinct lineage, which is a sister-species to the “rock form” of *E. multiocellata*, described as *E. dzungarica* **sp. nov.** herein. Unfortunately we failed to collect *E. kokshaaliensis* samples for genetic analysis and its phylogenetic position has to be clarified in further studies. Since *E. kokshaaliensis* is described from Kyrgyz-Chinese border, it is assumed that this species can be recorded in the neighbouring areas of China. However, the *Eremias* populations from the neighbouring area of Aksu (Xinjiang, China) examined in this study have the similar body size as the typical *E. kokshaaliensis*, but are morphologically distinct from the latter by body habitus and dorsal pattern (Fig. 11, F). These populations (Fig. 1, populations P.29–32) form a well-differentiated clade; their taxonomic status requires further clarification and studies.

As it has been shown by previous morphological studies, the most part of Mongolia (southern, central and western parts) with adjacent areas of Tuva Republic in Russia are inhabited by the “sand form” of *E. multiocellata*, which is morphologically distinct from the “rock form”, found from Dzungarian Gobi in westernmost Mongolia to Eastern Kazakhstan (Orlova & Terbish 1997), with a narrow zone of sympatry of the two forms reported from the vicinity of Uyench Sum (Khovd Aimaq). Our study confirms that these “forms” are phylogenetically distant and represent different taxa: the “sand form” (corresponding to the nominative *E. multiocellata* *sensu stricto*) is grouped with other sand-dwelling multiocellated racerunners from central China (Fig. 2, group I), whereas the “rock form” is assigned to one group with *E. przewalskii* and *E. buechneri* (Fig. 2, group III).

The “rock-form” of the multiocellated racerunner, described herein as *E. dzungarica* **sp. nov.**, inhabits Dzungaria—an area from Eastern Kazakhstan to westernmost Mongolia. In Zaisan valley in Kazakhstan several localities of this species are known to date with comparatively lowland populations from Aigyrkum sands and mountain populations from Ashutas, Saikan and Aktal Mts. showing certain morphological and ecological differences (Prokopov 1978, 1997; Orlova 1995). Our study confirms the conspecificity of Mongolian and Kazakh populations of *E. dzungarica* **sp. nov.** with comparatively low intraspecific genetic differentiation (0.50%, see Table 2). The extent of distribution of the new species in Chinese Xinjiang has yet to be evaluated.

Eremias multiocellata sensu stricto forms a compact clade (see Fig. 2, clade A” “sand form A”) of comparatively small-sized sand-dwelling lizards (see Fig. 11, A) distributed from the desert areas of central, southern, western Mongolia northwards to the Ubsu-Nuur valley in northern Mongolia and Tuva Republic, Russia (see Fig. 1). The type locality of *E. multiocellata* Günther, 1872 is on the “road from Sume to Tola (= Tuul)”, it fits well within the range of the “sand form A” in our sampling (see Fig. 1, type locality 1). Previously, populations from Tuva and northern Mongolia were assigned to the subspecies *E. m. bannikowi* (Szczerbak 1974); however in our analysis populations from Tuva Republic (Figs. 1, 2; population P.43) do not show any significant differences in mtDNA sequences from the nominative “sand form” of *E. multiocellata* from central and western Mongolia. The validity of *E. m. bannikowi* was also questioned by Dely (1979, 1980) on the basis of a thorough comparative morphological study of large collections from Mongolia. He noted that all diagnostic morphological characters are subjected to significant clinal variation in *E. multiocellata*. These results were later confirmed by Orlova & Terbish (1997). Since no stable morphological differences allow distinguishing between Tuva and central Mongolian populations, we assume that *E. m. bannikowi* should be regarded as a junior synonym of the nominate form of *E. multiocellata*. At the same time, dorsal patterns in *E. multiocellata* populations show considerable variation depending on ecological conditions, like the type of substrate: populations inhabiting sandy dunes show almost uniform light coffee-brown dorsal coloration with minute dark mottling and small dorsolateral ocelli (Uyench), whereas in populations inhabiting gravelly substrates (Boon-Tsagaan Nur) racerunners have contrasting dorsal coloration with bright bluish ocelli.

The recently described subspecies *E. m. tsaganbogdensis* represents an isolated morphologically distinct mountain-dwelling population inhabiting a small isolated mountain ridge Tsagan Bogdo Uul Mountains in the southernmost part of Mongolia near the Chinese border. This form inhabits elevations from 1500 to 2480 m a.s.l. and is isolated from the nearest known populations of *E. multiocellata* sensu stricto by a distance of 100–150 km (Munkhbayar & Borkin 2010). Our preliminary phylogenetic data indicate that this is more closely related to *E. przewalskii* than to *E. multiocellata* sensu stricto (p -distance = 2.3%); phylogenetically this population is close to lowland populations of southern Mongolia which we identify as *E. cf. reticulata*. However further studies of larger sampling and additional genetic and morphological characters are required for clarification of *E. m. tsaganbogdensis* taxonomic status.

Morphologically and genetically different sand-dwelling racerunners (see Fig. 2, clade B, “sand form B”) inhabit Dornogovi Aimaq in eastern Mongolia (Fig. 1, populations P.33–34). These lizards are larger than the nominative form: SVL = 59.93 ± 1.17 (55.3–63.0; $n = 20$) and are all characterized by dorsal pattern with light longitudinal stripes and slight dark mottling (Fig. 11, B) and presence of 1-2 additional shields between the prefrontal shields (present in 6 of 9 specimens; Sainshand Sum, Domogovi; a detailed morphological description see in Orlova & Terbish 1997: Tables 41, 42). Presence of additional scales was reported in other species of *Eremias* as well, this feature is often recorded in marginal isolated populations in *E. arguta* (Tsaruk 1986) and *E. multiocellata* (Orlova & Terbish 1997; Orlova *et al.* 2012). The same clade B includes populations of *E. multiocellata* from Ordos and Alashan deserts in central China (Fig. 1, populations P.35–41); they are larger than Mongolian populations, lack additional scales anterior to prefrontal shields and have variable dorsal pattern, mostly light-brown background with slight dark mottling or reticulated pattern (Fig. 11, B). The genetic and morphological differences between the two clades of *E. multiocellata* are quite significant; however their taxonomic value still has to be evaluated using multiple lines of evidence.

One of the most enigmatic Central Asian *Eremias* species is *E. quadrifrons* described from Alashan desert (Fig. 1, type locality 8) (Strauch 1876), known only from a single holotype specimen; despite numerous attempts other specimens of this species were not recorded during consequent surveys (Szczerbak 1974). Szczerbak (1974) assumed that there is a possibility that *E. quadrifrons* description was based on an abnormal specimen of *E. multiocellata*. Our sampling includes several populations in vicinity of the type locality of *E. quadrifrons* (Fig. 1, populations P.37, P.38); some of them show striped dorsal pattern similar to that described for *E. quadrifrons* (Fig.

11, B). However further studies including fieldwork in the environs *E. quadrifrons* type locality are required to clarify taxonomic status of this species and its phylogenetic relationships with *E. multiocellata* species complex. The taxonomic status of *E. multiocellata kozlowi* (Fig. 1, type locality 10) also remains unclear due to lack of sampling from the area of its distribution and requires further research. Morphologically this form appears to be closely related to the nominative form *E. (m.) multiocellata*; however preliminary chromosome studies suggest some unrecognized diversity in the area of Bei Shan (Inner Mongolia, China) (Gong *et al.* 1992). Our study reports presence of a divergent mtDNA lineage of *E. cf. multiocellata* in Gansu Province of China (Figs. 1, 2; population 42; lineage C); taxonomic status of this population has to be evaluated upon availability of voucher materials for examination.

Within *E. przewalskii* two subspecies were traditionally recognized: the nominative form *E. p. przewalskii* inhabiting southern Mongolia and China and *E. przewalskii tuvensis* Szczerbak 1970, which was described from Tuva Republic in southern part of Siberia, and is supposed to inhabit Ubsu-Nuur Valley and adjacent parts of north-western Mongolia (Szczerbak 1974). However, in our analysis we found no differences in mtDNA sequences between Tuva population and the rest of species range, Tuva population shares the same haplotype with populations P.4–6 from central Mongolia (Fig. 1, population P.8), corresponding to *E. przewalskii tuvensis*, and the nominative populations from southern Mongolia and Chinese Alashan desert (type locality of *E. przewalskii*). Morphological characters chosen by Szczerbak (1970) for recognition of *E. przewalskii tuvensis* as a separate taxon are subjected to significant clinal variation from north to south (Dely 1979; 1980; Orlova 1992); thus there is no basis for recognition of *E. przewalskii tuvensis* as a valid subspecies and we propose to regard it as a synonym of a monotypic *E. przewalskii*.

Several forms described from China were traditionally regarded as junior synonyms of *E. przewalskii*, differentiated mostly by coloration patterns and minor scalation characters: *E. brachydactyla* (dorsal pattern: dark network), *E. kessleri* (with rather large, irregular black spots) and the nominative form (the black spots confluent into irregular cross-bars; head with large black spots) (Boulenger 1921; Szczerbak 1974). Orlova (1992) reviewed morphological variation *E. przewalskii* and noted that despite the huge range of the species in Mongolia, in a single locality only one dorsal pattern type is recorded; whereas in China specimens with two dorsal pattern types can coexist in a single habitat (ZISP 6580–ZISP 6582; Chirgu-Bulak, China). The specimen ZISP 5145 collected by N.M. Przewalskii from “lower Tarim” from Chinese Dzungaria (Xinjiang) identified as “*E. kessleri*” is of peculiar interest; this specimen possess rows of bluish ocelli and the locality is situated in ca. 1000 km westwards from the main range of *E. przewalskii*: further studies on variation of *E. multiocellata*—*E. przewalskii* species complex in China are required to clarify this problem (Orlova 1992).

An interesting racerunner population from Altai Sum of Gobi-Altai Aimaq was listed as *E. multiocellata reticulata* in our recent publication (Orlova *et al.* 2014) and is preliminary identified in this study as *E. cf. reticulata*. After description of this form as *E. multiocellata* var. *reticulata* by Bedriaga (1912) from eastern Dzungaria (Fig. 1, type locality 11), it was listed as a junior synonym of *E. multiocellata*, or was regarded as a “transitional” form between *E. m. multiocellata*, *E. m. kozlowi* and *E. m. yarkandensis* (Szczerbak 1974). Morphologically this racerunner resembles both *E. multiocellata* and *E. przewalskii*, having large body size (SVL up to 72.5 mm), reticulated dorsal pattern and bright green or bluish ocelli with black edging present both in males and females. In previous allozyme study, Mongolian population of *E. cf. reticulata* formed a separate group, which was recovered as an intermediate lineage between *E. multiocellata* and *E. przewalskii* clades (Trueller *et al.* 1994; listed as *Eremias* sp.). However, in our analysis this population (Fig. 1, population P.9) was found to be a member of *E. przewalskii* group (Fig. 2, clade J-1) and is genetically most close to populations from mountains in Qinhai Province of China (Fig. 2, clade J-2; Fig. 1, populations P.12–13; elevations ca. 1700–2000 m a.s.l.) initially identified as *E. multiocellata*. Genetic distances between these lineages and true *E. przewalskii* are quite small (p -distances = 0.90%–2.30%, see Table 2); more detailed evaluation of the taxonomic status of these populations requires morphological examination of voucher materials from this part of China. It is remarkable that a number of previous studies on Chinese *Eremias*, reported genetic proximity or indistinguishability of *E. multiocellata* and *E. przewalskii* (Wan *et al.* 2007; Guo *et al.* 2011). Our study indicates that nominative *E. multiocellata* and *E. przewalskii* form two independent mtDNA clades (Fig. 2), however morphologically members of *E. przewalskii* clade show significant variation which could lead to misidentifications of certain populations. A thorough study of morphological and genetic variation of *E. multiocellata*—*E. przewalskii* species complex with reference to available type material is required for further progress in this question.

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APPENDIX I. List of recognized species of the genus *Eremias* Fitzinger with subgeneric allocation.

Subgenus *Aspidorhinus* Eichwald (previously referred to as *Dimorphea* Eremchenko or as *Eremias* sensu stricto sensu Szczerbak 1974):

- E. afganistanica* Böhme & Szczerbak—Afghan [highland] Racerunner
E. lalezhari Moravec—Lalezhar Racerunner
E. montana Rastegar-Pouyani & Rastegar-Pouyani—Mountain Racerunner
E. strauchi Kessler—Strauch's Racerunner
E. nigrolateralis Rastegar-Pouyani & Nilson—Black-sided Racerunner [considered as a junior synonym of *E. persica* by Rastegar-Pouyani *et al.* 2010]
E. novo Rastegar-Pouyani & Rastegar-Pouyani—Zagros Racerunner [considered as a junior synonym of *E. montanus* by Rastegar-Pouyani *et al.* 2010]
E. nikolskii Bedriaga—Kyrgyz Racerunner
E. papenfussi Mozaffari, Ahmadzadeh & Parham—Teheran Racerunner
E. persica Blanford—Persian Racerunner
E. isfahanica Rastegar-Pouyani, Hosseini, Rafiee, Kami, Rajabizadeh & Wink—Isfahan Racerunner
E. kopetdaghica Szczerbak—Kopetdagh Racerunner (until recently considered as a subspecies of *E. strauchi*, but recognized as valid species by Rastegar-Pouyani *et al.* 2016)
E. regeli Bedriaga—Tajik Racerunner
E. suphani Basoglu & Hellmich—Suphan Racerunner
E. velox (Pallas)—Rapid Racerunner

Subgenus *Eremias* sensu stricto (previously referred to as *Ommateremias* Lantz):

- E. arguta* (Pallas)—Steppe-runner or Steppe Racerunner
E. aria Anderson & Leviton—East-Afghan Racerunner
E. intermedia (Strauch)—Aralo-Caspian Racerunner
E. nigrocellata Nikolsky—Black-Ocellated Racerunner

Subgenus *Pareremias* Szczerbak:

- E. argus* Peters—Mongolian Racerunner
- E. brechleyi* Günther—Ordos Racerunner
- E. buechneri* Bedriaga—Kashgar Racerunner
- E. dzungarica* **sp. nov.**—Dzungar Racerunner
- E. kokshaalensis* Eremchenko & Panfilov—Kokshaal Racerunner
- E. multiocellata* Günther—Multi-ocellated Racerunner
- E. przewalskii* (Strauch)—Gobi Racerunner
- E. quadrifrons* (Strauch)—Alashan Racerunner
- E. stummeri* Wettstein—Issyk-Kul Racerunner
- E. szczerbaki* Eremchenko & Panfilov—Szczerbak's Racerunner
- E. yarkandensis* Blanford—Yarkand Racerunner

Subgenus *Rhabderemias* Lantz:

- E. andersoni* Darevsky & Szczerbak—Anderson's Racerunner
- E. cholistanica* Baig & Masroor—Cholistan Racerunner
- E. fasciata* Blanford—Sistan Racerunner
- E. lineolata* (Nikolsky)—Striped Racerunner
- E. pleskei* Bedriaga—Pleske's or Transcaucasian Racerunner
- E. scripta* (Strauch)—Sand Racerunner
- E. vermiculata* Blanford—Variegated or Central Asian Racerunner

Subgenus *Scapteira* Wiegmann:

- E. acutirostris* (Boulenger)—Point-snouted Racerunner
- E. grammica* (Lichtenstein)—Reticulate Racerunner
- E. aporosceles* (Alcock & Finn)—Pore-less Racerunner [considered as a junior synonym of *E. acutirostris* by Szczerbak 1974 but valid fide Anderson 1999]
- E. kavirensis* Mozaffari & Parham—Kavir Racerunner

APPENDIX II. List of specimens and populations of *Eremias multiocellata* — *E. przewalskii* species complex examined in phylogenetic part of this study. Names of localities and countries of origin are given; numbers appointed to populations correspond to those in Fig. 1. GenBank accession numbers are given.

#	Population Code	Specimen ID	Haplotype	Genbank No.	Country	Locality	Coordinates	Reference
<i>Eremias przewalskii</i>								
1	P.1	no voucher	Hap1	KM507330	China	Gansu Prov., Minqin County, Wuwei	38.63 N; 103.11 E	Du <i>et al.</i> 2014
2	P.2	ZMMU R-13209	Hap2	KY366551	China	Inner Mongolia Prov., 30 km W from Bayanhhot	39.12 N; 101.27 E	this work
3	P.3	ZMMU R-13214	Hap3	KY366552	China	Inner Mongolia Prov., Alashan desert, 150 km W from Bayanmod	40.41 N; 105.59 E	this work
4	P.4	ZMMU R-12046-1	Hap4	KY366553	Mongolia	Bayankhongor Aimaq, Zhinst	45.62 N; 100.21 E	this work
5	P.5	ZMMU R-13038-1	Hap4	KY366554	Mongolia	Govi-Altai Aimaq, Biger valley	45.73 N; 97.40 E	this work
6	P.5	ZMMU R-13038-3	Hap4	KY366555	Mongolia	Govi-Altai Aimaq, Biger valley	45.73 N; 97.40 E	this work
7	P.5	ZMMU R-13038-4	Hap4	KY366556	Mongolia	Govi-Altai Aimaq, Biger valley	45.73 N; 97.40 E	this work
8	P.6	ZMMU R-12842-1	Hap4	KY366557	Mongolia	Govi-Altai Aimaq, 3 km W from Biger Sum	45.72 N; 97.15 E	this work
9	P.6	ZMMU R-12842-2	Hap4	KY366558	Mongolia	Govi-Altai Aimaq, 3 km W from Biger Sum	45.72 N; 97.15 E	this work
10	P.7	ZMMU R-12888-1	Hap5	KY366559	Mongolia	Govi-Altai Aimaq, Tsogt, Dzahuin-Govi, 10 km W Bayan-Toroo	45.67 N; 96.65 E	this work
11	P.7	ZMMU R-12888-2	Hap5	KY366560	Mongolia	Govi-Altai Aimaq, Tsogt, Dzahuin-Govi, 10 km W Bayan-Toroo	45.67 N; 96.65 E	this work
12	P.8	ZMMU R-13060-1	Hap4	KY366561	Russia	Tuva Republic, Ovyurskiy Distr., Tere-Khol lake, Tsuger-El's sands	50.68 N; 93.21 E	this work
13	P.8	ZMMU R-13060-2	Hap4	KY366562	Russia	Tuva Republic, Ovyurskiy Distr., Tere-Khol lake, Tsuger-El's sands	50.68 N; 93.21 E	this work
14	P.8	ZMMU R-13060-3	Hap4	KY366563	Russia	Tuva Republic, Ovyurskiy Distr., Tere-Khol lake, Tsuger-El's sands	50.68 N; 93.21 E	this work
15	P.8	ENS-T07-1 (no voucher)	Hap4	KY366564	Russia	Tuva Republic, Ovyurskiy Distr., Tere-Khol lake, Tsuger-El's sands	50.68 N; 93.21 E	this work
16	P.8	ENS-T07-2 (no voucher)	Hap4	KY366565	Russia	Tuva Republic, Ovyurskiy Distr., Tere-Khol lake, Tsuger-El's sands	50.68 N; 93.21 E	this work
<i>Eremias cf. reticulata</i> (including <i>E. m. tsaganbogdensis</i>)								
Clade J1								
17	P.9	MNUE-Em-5	Hap6	KY366566	Mongolia	Bayankhongor Aimaq, Tsagan Bogdo Uul (Mt.)	42.88 N; 98.82 E	this work
18	P.10	ZMMU R-12855-1	Hap7	KY366567	Mongolia	Gobi-Altai Aimaq, 4 km NW from Altai Sum, env. Danshig-Khuduk	44.64 N; 95.86 E	this work
19	P.10	ZMMU R-12855-2	Hap8	KY366568	Mongolia	Gobi-Altai Aimaq, 4 km NW from Altai Sum, env. Danshig-Khuduk	44.64 N; 95.86 E	this work
20	P.10	ZMMU R-12856-1	Hap8	KY366569	Mongolia	Gobi-Altai Aimaq, 4 km NW from Altai Sum, env. Danshig-Khuduk	44.64 N; 95.86 E	this work

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APPENDIX II. (Continued)

#	Population Code	Specimen ID	Haplotype	Genbank No.	Country	Locality	Coordinates	Reference
<i>Eremias cf. przewalskii</i>								
21	P.11	ZMMU R-12858-1	Hap9	KY366570 KY366571	Mongolia	Ömnögovı Aimaq, 8-10 km S from Bayandalai Sum	43.39 N; 103.45 E	this work
22	P.11	ZMMU R-12859-1	Hap10		Mongolia	Ömnögovı Aimaq, 8-10 km S from Bayandalai Sum	43.39 N; 103.45 E	this work
<i>Eremias sp. 2</i>								
23	P.12	no voucher	Hap11	KY366572 KY366573	China	Qinhai Prov., Delingha env.	37.35 N; 97.35 E	this work
24	P.13	no voucher	Hap12		China	Qinhai Prov., Gonghe (Qiabugia), Chekhov, env. of Kyiking (Chin-Kon)	36.20 N; 100.75 E	this work
<i>Eremias cf. buchneri</i>								
25	P.14	ZMMU R-8910-1a	Hap13	KY366574 KY366575	China	Xinjiang Prov., Qarqan (Chemo) Distr., Altintag Mt., Chinbulak, 60 km S from Tura	37.51 N; 86.05 E	this work
26	P.14	ZMMU R-8910-1b	Hap13		China	Xinjiang Prov., Qarqan (Chemo) Distr., Altintag Mt., Chinbulak, 60 km S from Tura	37.51 N; 86.05 E	this work
<i>Eremias dzungarica sp. nov. (rock form)</i>								
27	P.15	ZMMU R-11989-1	Hap14	KY366576 KY366577	Kazakhstan	East-Kazakhstan Prov., Aigyrkum sands, 5-7 km SW from Buran	47.98 N; 84.89 E	this work
28	P.15	ZMMU R-11989-2	Hap15		Kazakhstan	East-Kazakhstan Prov., Aigyrkum sands, 5-7 km SW from Buran	47.98 N; 84.89 E	this work
29	P.16	ZMMU R-12862-1	Hap16	KY366578 KY366579	Mongolia	Khovd Aimaq, Bulgan Sum, Bayan-Mod, 11 km W from Ikher-Toli	47.06 N; 92.91 E	this work
30	P.16	ZMMU R-12862-3	Hap16		Mongolia	Khovd Aimaq, Bulgan Sum, Bayan-Mod, 11 km W from Ikher-Toli	47.06 N; 92.91 E	this work
31	P.17	ZMMU R-12845-2	Hap16	KY366580 KY366581	Mongolia	Khovd Aimaq, 7 km SW from Uyench Sum (same locality as P.56)	46.93 N; 93.61 E	this work
32	P.17	ZMMU R-12845-4	Hap16		Mongolia	Khovd Aimaq, 7 km SW from Uyench Sum (same locality as P.56)	46.93 N; 93.61 E	this work
33	P.17	ZMMU R-12845-5	Hap17	KY366582 KY366583	Mongolia	Khovd Aimaq, 7 km SW from Uyench Sum (same locality as P.56)	46.93 N; 93.61 E	this work
34	P.17	ZMMU R-12845-6	Hap16		Mongolia	Khovd Aimaq, 7 km SW from Uyench Sum (same locality as P.56)	46.93 N; 93.61 E	this work
35	P.17	ZMMU R-12845-7	Hap16	KY366584 KY366585	Mongolia	Khovd Aimaq, 7 km SW from Uyench Sum (same locality as P.56)	46.93 N; 93.61 E	this work
36	P.17	ZMMU R-12845-8	Hap16		Mongolia	Khovd Aimaq, 7 km SW from Uyench Sum (same locality as P.56)	46.93 N; 93.61 E	this work
37	P.17	ZMMU R-12845-9	Hap16	KY366586 KY366587	Mongolia	Khovd Aimaq, 7 km SW from Uyench Sum (same locality as P.56)	46.93 N; 93.61 E	this work
38	P.17	ZMMU R-12845-10	Hap16		Mongolia	Khovd Aimaq, 7 km SW from Uyench Sum (same locality as P.56)	46.93 N; 93.61 E	this work
39	P.18	ZMMU R-12550-1	Hap18	KY366588	Mongolia	Khovd Aimaq, 24 km N from Uyench Sum	46.27 N; 92.05 E	this work

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APPENDIX II. (Continued)

#	Population Code	Specimen ID	Haplotype	Genbank No.	Country	Locality	Coordinates	Reference
<i>Eremias stummeri</i>								
40	P.19	ZMMU R-12551-1a	Hap19	Clade E	Kazakhstan	Almaty Prov., Rayimbek Distr., Ketmen Mts. foothills, 7-8 km E from Kegen	42.97 N; 79.32 E	this work
41	P.19	ZMMU R-12551-2	Hap20		Kazakhstan	Almaty Prov., Rayimbek Distr., Ketmen Mts. foothills, 7-8 km E from Kegen	42.97 N; 79.32 E	this work
42	P.19	ZMMU R-12551-2a	Hap19		Kazakhstan	Almaty Prov., Rayimbek Distr., Ketmen Mts. foothills, 7-8 km E from Kegen	42.97 N; 79.32 E	this work
43	P.19	ZMMU R-12551-3	Hap21		Kazakhstan	Almaty Prov., Rayimbek Distr., Ketmen Mts. foothills, 7-8 km E from Kegen	42.97 N; 79.32 E	this work
44	P.19	ZMMU R-12551-4	Hap19		Kazakhstan	Almaty Prov., Rayimbek Distr., Ketmen Mts. foothills, 7-8 km E from Kegen	42.97 N; 79.32 E	this work
45	P.19	ZMMU R-12551-5	Hap19		Kazakhstan	Almaty Prov., Rayimbek Distr., Ketmen Mts. foothills, 7-8 km E from Kegen	42.97 N; 79.32 E	this work
46	P.19	ZMMU R-12551-5a	Hap19		Kazakhstan	Almaty Prov., Rayimbek Distr., Ketmen Mts. foothills, 7-8 km E from Kegen	42.97 N; 79.32 E	this work
47	P.19	ZMMU R-12551-6	Hap19		Kazakhstan	Almaty Prov., Rayimbek Distr., Ketmen Mts. foothills, 7-8 km E from Kegen	42.97 N; 79.32 E	this work
48	P.19	ZMMU R-12551-7	Hap19		Kazakhstan	Almaty Prov., Rayimbek Distr., Ketmen Mts. foothills, 7-8 km E from Kegen	42.97 N; 79.32 E	this work
49	P.19	ZMMU R-12551-8	Hap19		Kazakhstan	Almaty Prov., Rayimbek Distr., Ketmen Mts. foothills, 7-8 km E from Kegen	42.97 N; 79.32 E	this work
50	P.19	ZMMU R-12551-10	Hap19	Clade E	Kazakhstan	Almaty Prov., Rayimbek Distr., Ketmen Mts. foothills, 7-8 km E from Kegen	42.97 N; 79.32 E	this work
51	P.19	ZMMU R-12495-1	Hap21		Kazakhstan	Almaty Prov., Rayimbek Distr., Ketmen Mts. foothills, 7-8 km E from Kegen	42.97 N; 79.32 E	this work
52	P.20	ZMMU R-12552-1	Hap22		Kazakhstan	Almaty Prov., Rayimbek Distr., Ketmen Mts. foothills, 7-8 km E from Kegen	42.97 N; 79.32 E	this work
53	P.20	ZMMU R-12552-2	Hap22		Kazakhstan	Mts., 15 km S from Tuzkol Lake, Zhabyrtau Mt.	42.92 N; 80.08 E	this work
54	P.20	ZMMU R-12552-4	Hap22		Kazakhstan	Almaty Prov., Rayimbek Distr., central Tian Shan Mts., 15 km S from Tuzkol Lake, Zhabyrtau Mt.	42.92 N; 80.08 E	this work
55	P.21	ZMMU R-14335-2	Hap28		Kyrgyzstan	Issyk-Kul Prov., E bank of Issyk-Kul lake, env. of Karakol	42.46 N; 78.36 E	this work
56	P.21	ZMMU R-14335-3	Hap27		Kyrgyzstan	Issyk-Kul Prov., E bank of Issyk-Kul lake, env. of Karakol	42.46 N; 78.36 E	this work
57	P.21	ZMMU R-14335-4	Hap27		Kyrgyzstan	Issyk-Kul Prov., E bank of Issyk-Kul lake, env. of Karakol	42.46 N; 78.36 E	this work
58	P.22	ZMMU R-14338-1	Hap24		Kyrgyzstan	Issyk-Kul Prov., 100 km SW from Karakol, Kaji-Say env.	42.16 N; 77.18 E	this work
59	P.22	ZMMU R-14338-2	Hap24		Kyrgyzstan	Issyk-Kul Prov., 100 km SW from Karakol, Kaji-Say env.	42.16 N; 77.18 E	this work

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APPENDIX II. (Continued)

#	Population Code	Specimen ID	Haplotype	Genbank No.	Country	Locality	Coordinates	Reference
60	P.23	ZMMU R-12427-1	Hap26	KY366609	Kyrgyzstan	Issyk-Kul Prov., NW bank of Issyk-Kul lake, 20-25 km N from Toru Aygyr, Kungei-Alatau Mts.	42.58 N; 76.41 E	this work
61	P.23	ZMMU R-12427-2	Hap26	KY366610	Kyrgyzstan	Issyk-Kul Prov., NW bank of Issyk-Kul lake, 20-25 km N from Toru Aygyr, Kungei-Alatau Mts.	42.58 N; 76.41 E	this work
62	P.24	ZMMU R-12556-1	Hap21	KY366611	Kyrgyzstan	Issyk-Kul Prov., env. of Balykchy, road to Akolen	42.35 N; 76.17 E	this work
63	P.24	ZMMU R-12556-2	Hap21	KY366612	Kyrgyzstan	Issyk-Kul Prov., env. of Balykchy, road to Akolen	42.35 N; 76.17 E	this work
64	P.24	ZMMU R-12557-1	Hap29	KY366613	Kyrgyzstan	Issyk-Kul Prov., env. of Balykchy, road to Akolen	42.35 N; 76.17 E	this work
65	P.24	ZMMU R-12557-2	Hap29	KY366614	Kyrgyzstan	Issyk-Kul Prov., env. of Balykchy, road to Akolen	42.35 N; 76.17 E	this work
66	P.25	ZMMU R-14339-1	Hap24	KY366615	Kyrgyzstan	Naryn Prov., Kochkor Distr., Kochkor	42.22 N; 75.75 E	this work
67	P.26	ZMMU R-14341-2	Hap23	KY366616	Kyrgyzstan	Naryn Prov., Kochkor Distr., S from Kochkor	42.08 N; 75.66 E	this work
68	P.26	ZMMU R-14341-3	Hap25	KY366617	Kyrgyzstan	Naryn Prov., Kochkor Distr., S from Kochkor	42.08 N; 75.66 E	this work
<i>Eremias szczerbaki</i>								
69	P.27	ZMMU R-14342-1	Hap30	KY366618	Kyrgyzstan	Naryn Prov., Naryn Distr., N from Naryn	41.48 N; 75.98 E	this work
70	P.27	ZMMU R-14342-2	Hap31	KY366619	Kyrgyzstan	Naryn Prov., Naryn Distr., N from Naryn	41.48 N; 75.98 E	this work
<i>Eremias yarkandensis</i>								
71	P.28	ZMMU R-14344-1	Hap32	KY366620	Kyrgyzstan	Osh Prov., vicinity of Nura	39.65 N; 73.87 E	this work
72	P.28	ZMMU R-14344-2	Hap32	KY366621	Kyrgyzstan	Osh Prov., vicinity of Nura	39.65 N; 73.87 E	this work
73	P.28	ZMMU R-14344-3	Hap32	KY366622	Kyrgyzstan	Osh Prov., vicinity of Nura	39.65 N; 73.87 E	this work
74	P.28	ZMMU R-14344-4	Hap32	KY366623	Kyrgyzstan	Osh Prov., vicinity of Nura	39.65 N; 73.87 E	this work
75	P.28	ZMMU R-14344-5	Hap32	KY366624	Kyrgyzstan	Osh Prov., vicinity of Nura	39.65 N; 73.87 E	this work
<i>Eremias sp. 1</i>								
76	P.29	ZMMU R-14327-1	Hap33	KY366625	China	Xinjiang Prov., 35 km NE from Aksu	41.40 N; 81.05 E	this work
77	P.30	ZMMU R-14329-1	Hap34	KY366626	China	Xinjiang Prov., 60 km NE from Aksu	41.54 N; 80.79 E	this work
78	P.31	ZMMU R-14330-1	Hap37	KY366627	China	Xinjiang Prov., 75 km NE from Aksu	41.74 N; 80.83 E	this work
79	P.31	ZMMU R-14330-2	Hap38	KY366628	China	Xinjiang Prov., 75 km NE from Aksu	41.74 N; 80.83 E	this work
80	P.31	ZMMU R-14330-3	Hap39	KY366629	China	Xinjiang Prov., 75 km NE from Aksu	41.74 N; 80.83 E	this work
81	P.32	ZMMU R-14328-1	Hap35	KY366630	China	Xinjiang Prov., 89 km NE from Aksu	41.56 N; 81.21 E	this work
82	P.32	ZMMU R-14328-2	Hap36	KY366631	China	Xinjiang Prov., 89 km NE from Aksu	41.56 N; 81.21 E	this work
83	P.32	ZMMU R-14328-3	Hap36	KY366632	China	Xinjiang Prov., 89 km NE from Aksu	41.56 N; 81.21 E	this work

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APPENDIX II. (Continued)

#	Population Code	Specimen ID	Haplotype	Genbank No.	Country	Locality	Coordinates	Reference
<i>Eremias multiocellata</i>; sand form B								
84	P.33	ZMMU R-12610-1a	Hap40	Clade B KY366633	Mongolia	Dornogovi Aimaq, Sainshand Sum, vicinity of Sainshand	44.89 N; 110.10 E	this work
85	P.33	ZMMU R-12610-1b	Hap40		Mongolia	Dornogovi Aimaq, Sainshand Sum, vicinity of Sainshand	44.89 N; 110.10 E	this work
86	P.34	ZMMU R-14523	Hap40		Mongolia	Dornogovi Aimaq, Sainshand Sum, ca. 100 km NE from Örgön	45.18 N; 111.79 E	this work
87	P.35	ZMMU R-13215	Hap47		China	Inner Mongolia Prov., 50 km S from Baotou	40.28 N; 110.00 E	this work
88	P.36	ZMMU R-13205	Hap41	KY366637	China	Inner Mongolia Prov., W Ordos, 30 km SW from Bayan-Uls	40.02 N; 108.50 E	this work
89	P.37	ZMMU R-13207	Hap42	KY366638	China	Inner Mongolia Prov., 120 km W from Wuhai	39.53 N; 105.45 E	this work
90	P.38	ZMMU R-13206	Hap44	KY366639	China	Inner Mongolia Prov., Alashan desert, 40 km S from Bayan-Hot	38.67 N; 105.62 E	this work
91	P.39	ZMMU R-13208	Hap43	KY366640	China	Inner Mongolia Prov., 80 km SW Bayan Nur	40.00 N; 103.87 E	this work
92	P.40	no voucher	Hap45	NC025304	China	Gansu Prov., Minqin County	38.63 N; 103.11 E	Tong <i>et al.</i> 2014
93	P.41	no voucher	Hap46	KJ64798	China	Gansu Prov., env. of Lanzhou, Baiyin	36.46 N; 104.21 E	unpublished
<i>Eremias multiocellata</i>								
94	P.42	no voucher	Hap48	KY366641	China	Gansu Prov., env. of Shandan	38.78 N; 101.08 E	this work
<i>Eremias multiocellata</i>; sand form A								
95	P.43	ZMMU R-13058-1	Hap49	Clade A KY366642	Russia	Tuva Republic, Erzín Distr., Ubsu-Nur valley, 12 km SE from Yamalyg Mt.	50.16 N; 94.79 E	this work
96	P.43	ZMMU R-13058-2	Hap50		Russia	Tuva Republic, Erzín Distr., Ubsu-Nur valley, 12 km SE from Yamalyg Mt.	50.16 N; 94.79 E	this work
97	P.43	ZMMU R-13058-3	Hap51		Russia	Tuva Republic, Erzín Distr., Ubsu-Nur valley, 12 km SE from Yamalyg Mt.	50.16 N; 94.79 E	this work
98	P.43	ZMMU R-13058-4	Hap52		Russia	Tuva Republic, Erzín Distr., Ubsu-Nur valley, 12 km SE from Yamalyg Mt.	50.16 N; 94.79 E	this work
99	P.43	ZMMU R-13059-1	Hap50	KY366646	Russia	Tuva Republic, Erzín Distr., Ubsu-Nur valley, 12 km SE from Yamalyg Mt.	50.16 N; 94.79 E	this work
100	P.44	ZMMU R-12952a	Hap53	KY366647	Mongolia	Dundgovi Aimaq, env. of Deren	46.59 N; 106.54 E	this work
101	P.44	ZMMU R-12952b (VOT-52-2)	Hap53	KY366648	Mongolia	Dundgovi Aimaq, env. of Deren	46.59 N; 106.54 E	this work
102	P.45	ZMMU R-12608-1	Hap54	KY366649	Mongolia	Dundgovi Aimaq, env. of Ölzit Sum	48.03 N; 102.51 E	this work
103	P.45	ZMMU R-12608-2	Hap54	KY366650	Mongolia	Dundgovi Aimaq, env. of Ölzit Sum	48.03 N; 102.51 E	this work
104	P.46	ZMMU R-12863-1	Hap55	KY366651	Mongolia	Ummugovi Aimaq, 102 km NW from Dalandzadagat, Tsogt-Ovu	44.42 N; 105.32 E	this work

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APPENDIX II. (Continued)

#	Population Code	Specimen ID	Haplotype	Genbank No.	Country	Locality	Coordinates	Reference
105	P.46	ZMMU R-12863-2	Hap56	KY366652	Mongolia	Umnugovi Aimaq, 102 km NW from Dalandzadagat, Tsogt-Ovu	44.42 N; 105.32 E	this work
106	P.47	ZMMU R-12045-1	Hap60	KY366653	Mongolia	Bayankhongor Aimaq, Zhinst	45.62 N; 100.21 E	this work
107	P.47	ZMMU R-12045-2	Hap60	KY366654	Mongolia	Bayankhongor Aimaq, Zhinst	45.62 N; 100.21 E	this work
108	P.48	ZMMU R-12841-1	Hap60	KY366655	Mongolia	Bayankhongor Aimaq, N bank of Bööntsagan Nuur Lake	45.67 N; 99.12 E	this work
109	P.48	ZMMU R-12841-2	Hap60	KY366656	Mongolia	Bayankhongor Aimaq, N bank of Bööntsagan Nuur Lake	45.67 N; 99.12 E	this work
110	P.49	ZMMU R-13039-1	Hap60	KY366657	Mongolia	Govi-Altai Aimaq, Delger	45.93 N; 98.05 E	this work
111	P.50	ZMMU R-12843-1	Hap59	KY366658	Mongolia	Govi-Altai Aimaq, Shargyn-Govi, 2 km SW from Khaliun Sum	45.93 N; 96.12 E	this work
112	P.50	ZMMU R-12843-2	Hap59	KY366659	Mongolia	Govi-Altai Aimaq, Shargyn-Govi, 2 km SW from Khaliun Sum	45.93 N; 96.12 E	this work
113	P.51	ZMMU R-12081-1	Hap57	KY366660	Mongolia	Govi-Altai Aimaq, Shargyn-Govi, 30 km S from Sharga Sum	46.36 N; 95.23 E	this work
114	P.52	ZMMU R-12844-1	Hap60	KY366661	Mongolia	Govi-Altai Aimaq, Junggar Govi, 4 km W from Bidzh	45.59 N; 93.58 E	this work
115	P.52	ZMMU R-12844-2	Hap60	KY366662	Mongolia	Govi-Altai Aimaq, Junggar Govi, 4 km W from Bidzh	45.59 N; 93.58 E	this work
116	P.53	ZMMU R-12853-1	Hap60	KY366663	Mongolia	Govi-Altai Aimaq, Junggar Govi, Bugat	45.22 N; 93.53 E	this work
117	P.53	ZMMU R-12853-2	Hap60	KY366664	Mongolia	Govi-Altai Aimaq, Junggar Govi, Bugat	45.22 N; 93.53 E	this work
118	P.54	ZMMU R-12848-1	Hap60	KY366665	Mongolia	Khovd Aimaq, 58 km SE from Altai Sum, E foothills of Sertengiyin-Khuvch-Ula	45.65 N; 92.98 E	this work
119	P.54	ZMMU R-12849-1	Hap58	KY366666	Mongolia	Khovd Aimaq, 58 km SE from Altai Sum, E foothills of Sertengiyin-Khuvch-Ula	45.65 N; 92.98 E	this work
120	P.54	ZMMU R-12849-2	Hap60	KY366667	Mongolia	Khovd Aimaq, 58 km SE from Altai Sum, E foothills of Sertengiyin-Khuvch-Ula	45.65 N; 92.98 E	this work
121	P.55	ZMMU R-12847-1	Hap59	KY366668	Mongolia	Khovd Aimaq, 1 km SW from Altai Sum	45.80 N; 92.25 E	this work
122	P.56	ZMMU R-13132-1	Hap60	KY366669	Mongolia	Khovd Aimaq, 7 km SW from Uyench Sum (same locality as P.17)	46.93 N; 93.61 E	this work
123	P.56	ZMMU R-13132-2	Hap60	KY366670	Mongolia	Khovd Aimaq, 7 km SW from Uyench Sum (same locality as P.17)	46.93 N; 93.61 E	this work
124	P.56	ZMMU R-13132-3	Hap60	KY366671	Mongolia	Khovd Aimaq, 7 km SW from Uyench Sum (same locality as P.17)	46.93 N; 93.61 E	this work
125	P.56	ZMMU R-13132-4	Hap60	KY366672	Mongolia	Khovd Aimaq, 7 km SW from Uyench Sum (same locality as P.17)	46.93 N; 93.61 E	this work
126	P.56	ZMMU R-13132-5	Hap60	KY366673	Mongolia	Khovd Aimaq, 7 km SW from Uyench Sum (same locality as P.17)	46.93 N; 93.61 E	this work

APPENDIX III. List of specimens and populations of *Eremias multiocellata*—*E. przewalskii* species complex examined in this study for morphological comparisons.

- E. multiocellata*: **ZMMU R-5409, R-5410** (n = 34) Mongolia, Bayan-Khongor Aimaq, about 15 km NE of Baitrag-Gol river delta; **ZMMU R-5411, R-5412, R-5415, R-5416, R-5417, R-5783, R-6414, R-6416** (n = 29) Mongolia, Khovd Aimaq, near Uench Sum; **ZMMU R-8630, R-8634** (n = 16) Mongolia, Gobi-Altai Aimaq, Tonkhil Sum; **ZMMU R-5782, R-8633** (n = 25) Mongolia, Khovd Aimaq, near Altai Sum; **ZMMU R-5265** (n = 26) Mongolia, Umnegov Aimaq, eastern Tsogt-Tsetsij; **ZMMU R-5408** (n = 16) Mongolia, Gobi-Altai Aimaq, Khairkhan; **ZMMU R-5734, R-5735** (n = 25) Mongolia, Bayan-Khongor Aimaq, Tsagan-Bogdo-Ula; **ZMMU R-7180, R-7181** (n = 15) Mongolia, Dundgov Aimaq; **ZMMU R-2681** (n = 7) Mongolia, Dornogov Aimaq, 20 km NW of Sain-Khuduk (Sain-Usu Khuduk).
- E. cf. reticulata*: **ZMMU R-8636** (n = 34), and **R-12855** (13 ad+ 5 juv.). Mongolia, Gobi-Altai Aimaq, near Altai Sum; **ZMB N38762** (n = 2) China, Western China; Yu-Min-Nan.
- E. przewalskii*: **ZMMU R- 7046** (n = 30). Mongolia, Khovd Aimaq, Northern coast of Char-Us-Nuur Lake, Urdgol Sum (= Chandman); **ZMMU R-5034** (n = 17). Mongolia, Gobi-Altai Aimaq, Lake Beger-Nuur; **ZMMU R- 5030** (n = 25). Mongolia, Gobi-Altai Aimaq, Lake Alag-Nuur; **ZMMU R-5402** (n = 20). Mongolia, Bayan-Khongor Aimaq, 35–40 km NE of Ba-Tsagan; **ZMMU R-5023, R-5029, R-5031** (n = 54). Mongolia, Umnegov Aimaq; Shavgijn-Uus, southern Chovuun (= Noen); Sain Khuduk Well; 6 km E from Obot-Khural; **ZMMU R-5614, R-5802** (n = 21). Mongolia, Dornogov Aimaq: 43°53' N, 108° 05' E; 60 km SSE of Dzun-Bayan; **ZISP 5145** (n = 1), **ZISP 6578** (n = 2), **ZISP 7047** (n = 4), **ZISP 6582** (n = 2), all from China, “Alashan Desert”; **ZISP 6574** (n = 2), **ZISP 6576** (n = 2) China, Chara-Morite; **ZISP 12426** (n = 4) China, Elken-khuduk (valley Goitszo); **ZISP 6610** (n = 2), **ZISP 6611** (n = 2), **ZISP 6616** (n = 2) China, Alashan Desert (as *Eremias kessleri*); **ZISP 6581** (n = 2), **ZISP 6583** (n = 2) China, Tschirgu-Bulyk (as *Eremias kessleri*); **ZISP 6584** (n = 1) China, Gansu (as *Eremias kessleri*); **ZISP 6580** (n = 2), **ZISP 12430** (n = 1) China, Ka-Tu-Chu (as *Eremias kessleri*).
- E. stummeri*: **NMW 15664** (n = 1) Kyrgyzstan, Issyk-Kul Lake, vicinity of Karakol (= Przhevalsk) (holotype, photo material); **ZMMU R-12551** (n = 10) Kazakhstan, Almaty Prov., Rayimbek Distr., Ketmen Mts. foothills, 7-8 km E from Kegen, **ZMMU R-12552** (n = 4) Almaty Prov., Rayimbek Distr., central Tian Shan Mts., 15 km S from Tuzkol Lake, Zhabyrtau Mt.; **R-14335** (n = 4) Kyrgyzstan, Issyk-Kul Prov., E bank of Issyk-Kul lake, env. of Karakol; **R-14338** (n = 2) Kyrgyzstan, Issyk-Kul Prov., 100 km SW from Karakol, Kaji-Say env., **R-14339** (n = 34) Kyrgyzstan, Naryn Prov., Kochkor Distr., Kochkor.
- E. scherzaki*: **ZMMU R-14342** (n = 2) Kyrgyzstan, Naryn Prov., Naryn Distr., N from Naryn; **Kyrgyzstan Institute of Biology and Soil Science, Herpetology Collection R 000635–000657** (n = 23) Kyrgyzstan, Naryn Prov., Naryn Distr.
- E. yarkandensis*: **BMNH(NHMUK) 1917.3.6.28–30** (n = 3) China, Yarkand (syntypes, photo material); **BMNH 1946.8.7.65–66** (n = 2) China, Kashgaria; **ZMB N38744** (n = 1) China, Turfan; **ZMMU R-14344** (n = 5) Kyrgyzstan, Nura, Osh Prov., vicinity of Nura.
- E. kokshaaliensis*: **ZMMU R-5302** (n = 4) Kyrgyzstan, Sary-Dzhaz; **ZMBPI R 000587–000591, R 000596, R 000599–000601** (n = 12) Kyrgyzstan, Sary-Dzhaz.
- E. buechneri*: **ZISP 7081** (n = 1) China, Kashgaria, Dol (holotype); **ZISP 8280** (n = 3) China, exact locality unknown (coll. 1891); **ZISP 8300** (n = 5: 3 ad+ 2 juv.) Between Yarkend and Toktakhun (coll. Pevzov, 1891); **ZISP 9131** (n = 2) Kashgar, riv. Tolan-Khodzha (coll. Roborowsky, 1890).
- Eremias dzungarica* sp. nov.: **ZMMU R-11989** (n = 2) Kazakhstan, East-Kazakhstan Prov., Aigyrkum sands, 5-7 km SW from Buran; **ZMMU R-12862** (n = 3) Mongolia, Khovd Aimaq, Bulgan Sum, Bayan-Mod, 11 km W from Ikher-Toli; **ZMMU R-12845** (n = 10) Mongolia, Khovd Aimaq, 7 km SW from Uyench Sum; **ZMMU R-12550** (n = 1) Mongolia, Khovd Aimaq, 24 km N from Uyench Sum.