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Filling gaps in the taxonomy of the *Phrynocephalus helioscopus* species complex (Reptilia, Squamata, Agamidae) with description of two new subspecies

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Abstract: *Phrynocephalus helioscopus* species complex have been thoroughly studied during recent years, but several lineages remained unassigned. Based on the morphological differences and divergence in COI (mtDNA) gene sequences, two new subspecies are described in the present article within the *Phrynocephalus helioscopus* species complex: *Ph. helioscopus karatauensis* **ssp. nov**. from the environs of Karatau Ridge in Kazakhstan and *Ph. saidalievi orlovae* **ssp. nov.** from the right bank of the Amu-Darya river in Fergana valley in Uzbekistan. The two new subspecies can be distinguished from other members of the species complex by a combination of several morphological features.

Keywords: Middle Asia, Kazakhstan, Uzbekistan, *Phrynocephalus helioscopus*, Karatau Ridge, *Phrynocephalus saidalievi*, Fergana Valley, DNA-barcoding, morphometrics, coloration

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INTRODUCTION

Members of the *Phrynocephalus helioscopus* species complex inhabit vast territory from Iran and Armenia in the west to western Mongolia in the east. Until recently, only two species were recognized within this complex, *Ph. helioscopus* (Pallas, 1771) and *Ph. persicus* De Filippi, 1863 (Barabanov, Ananjeva, 2007). But once the wave of usage of molecular phylogenetic methods started, many subspecies were described within both species (Solovyeva et al., 2011, 2012; Melnikov et al., 2013), with some of them later raised to full species status (Macey et al., 2018; Solovyeva et al., 2023). The latest assessment of *Phrynocephalus* diversity by Solovyeva et al. (2023) recognized up to 16 species-level units within the *Ph. helioscopus* species complex. Overall, the members of the *Ph. helioscopus* species complex are classified within the subgenus *Helioscopus* (Solovyeva et al., 2018).

Several lineages within the *Ph. helioscopus* species complex remain without taxonomic assignment. One of them includes populations of *Ph.* cf. *helioscopus* from the Karatau Ridge in southern Kazakhstan and was first reported by Solovyeva et al. (2011). In the study of Solovyeva et al. (2011), this lineage was represented by two sequences (JF769382 and JF769389) of the fragment of the cytochrome oxidase subunit I (COI) gene of mitochondrial DNA (hereafter, mtDNA), which formed a clade clearly distant

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from all the remaining lineages (with *p*-distances above 5.0%). The specimens from which these sequences were obtained included ZMMU R-12662 (from Kazakhstan, Zhambyl Province, outskirts of Suzak settlement; N44.133, E68.467) and ZMMU R-12165 (Kazakhstan, Zhambyl Province, surroundings of Lake Kyzylkol; N43.784, E69.553). According to the results of Solovyeva et al. (2011, 2023) these samples with moderate support were suggested as a sister lineage to *Ph. helioscopus cameranoi* Bedriaga, 1907, which inhabits the Ily River Valley in eastern Kazakhstan, ca. 900 km eastwards from the Karatau Ridge, and is geographically isolated from the other *Ph. helioscopus* subspecies. Meanwhile, the range extent of the geographically most closely distributed subspecies, *Ph. h. varius* Echiwald, 1931, which occurs in eastern Kazakhstan, remains unclear. Therefore, in the present paper we pay special attention to the morphological characteristics differing the Karatau Ridge population from *Ph. cameranoi* and *Ph. varius*.

In 2018, Macey et al. (2018), based on mtDNA and nuclear DNA (hereafter, nuDNA) sequences, suggested that the subspecies *Ph. helioscopus turcomanus* Dunayev, Solovyeva & Poyarkov, 2012 should be regarded as a full species *Ph. turcomanus*. The subsequent analyses of the COI barcoding region in *Phrynocephalus* by Solovyeva et al. (2023) supported the differentiation of the Karatau Ridge lineage and also demonstrated deep differentiation within *Ph. saidalievi* Sattorov, 1981 populations, inhabiting the Fergana Valley in western Uzbekistan. Specimens from the left and right banks of the Syrdarya River within the Fergana valley clustered in two reciprocally monophyletic lineages, demonstrating the need for additional studies of these populations. Solovyeva et al. (2023) suggested that deep genetic divergence within the *Ph. helioscopus* species complex might indicate the full species status of several geographically circumscribed lineages that were previously regarded as subspecies (Solovyeva et al., 2012). Overall, Solovyeva et al. (2023) proposed the updated taxonomy for the *Ph. helioscopus* complex, which included the following species: *Ph. helioscopus* s. str., *Ph. varius*, *Ph. turcomanus*, *Ph. cameranoi*, *Ph. sergeevi* Dunayev, Solovyeva & Poyarkov, 2012, *Ph. saidalievi*, and *Ph. meridionalis* Dunayev, Solovyeva & Poyarkov, 2012. Furthermore, three lineages *Phrynocephalus* spp. 5–7 within the complex were identified as putative candidate new taxa, including the lineages *Phrynocephalus* sp. 6 from Karatau Ridge, and *Phrynocephalus* sp. 7 from the left bank of the Syrdarya River. Further examination of the localities studied by Solovyeva et al. (2023) and the type specimens and the original description of *Ph. saidalievi* from "Tajikistan, Kanibadam" by T. Sattorov (1981) led us to the conclusion that, on the contrary, the specimens from the left bank of the Syrdarya River represent the true *Ph. saidalievi*, while the specimens from the right bank represent a currently undescribed lineage.

Recently, Wu et al. (2023) examined phylogenetic relationships within the *Ph. helioscopus* species complex based on examination of COI and ND2 mtDNA genes and genome-wide SNP-analyses. The authors supported the recognition of *Ph. meridionalis* and *Ph. saidalievi* as full species following the unified species concept (De Queiroz, 2008). At the same time, Wu et al. (2023) argued that the subspecies level is more appropriate for the other studied taxa (i.e., they recognized *Ph. helioscopus varius*, *Ph. helioscopus helioscopus*, *Ph. helioscopus cameranoi*, *Ph. helioscopus sergeevi*, and *Ph. helioscopus turcomanus*). Though there is an ongoing debate on usage of the subspecies category in taxonomy, and in herpetology in particular (e.g., Dufresnes et al., 2023), we generally agree with Wu et al. (2023) that recognizing subspecies might be a good solution for the fine-scale assessment of diversity in Central Asian lizards, including the members of the *Ph. helioscopus* species complex. It is important that Wu et al. (2023) analyzed one specimen of the Karatau Ridge population, and their analyses consistently supported it as a unique lineage clearly distinct from all other members of the *Ph. helioscopus* species complex. Therefore, Wu et al. (2023) concluded that there might be a cryptic species of the *Ph. helioscopus* complex in Karatau Ridge, thus repeating our earlier conclusions (Solovyeva et al., 2011, 2023). Moreover, the tree of Wu et al. (2023) strongly supported the Karatau Ridge lineage as a sister taxon of *Ph. helioscopus* cameranoi from the Ily River Valley.

In the present study, we follow the taxonomy proposed by Wu et al. (2023), as it was based on more integrative and extensive data than the single-locus analysis by Solovyeva et al. (2023). We analyze morphological and molecular differentiation of the Karatau Ridge population of *Ph. helioscopus* (lineage *Phrynocephalus* sp. 6 of Solovyeva at al., 2023) and the right bank population of *Ph. saidalievi* from the Fergana valley, and describe them as two new subspecies of their respective (paternal) species.

MATERIAL AND METHODS

Sampling. Tissue samples were taken from eleven *Ph. helioscopus* specimens from Karatau Ridge stored in the herpetological collection of the Zoological Museum of Lomonosov Moscow State University (ZMMU). 74 COI sequences of other representatives of *Ph. helioscopus* complex, including the sequences of specimens of *Ph. saidalievi* from the right and left banks of the Syrdarya River and one

additional sequence of *Ph. helioscopus* from Karatau Ridge, were retrieved from GenBank (they originate from our previous works, i.e., Solovyeva et al. 2011, 2023). The geographic distribution of samples is shown in Fig. 1. Details on museum IDs and localities of origin for each sample are summarized in Table 1.

Within the frameworks of the cooperation agreement with the Institute of Zoology Republic of Kazakhstan (IZ RK, Kazakhstan, Almaty), six specimens from environs of Karatau Ridge were obtained, collected in accordance with permit

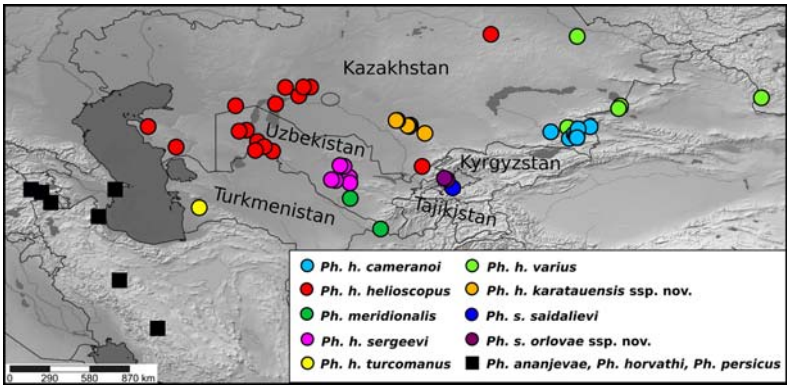

Fig. 1. Geographic location of samples used in the molecular analysis. Colors of symbols correspond to those in Fig. 3

Table 1. List of specimens used in molecular analysis

Subspecies	Voucher No.	Locality	N	E	GenBank No.	Source
1	2	3	4	5	6	7
Ph. anajevae	HCZ-1	Iran, Fars, Abadeh settl. env.	31.129	52.203	JF756687	Solovyeva et al., 2011
Ph. anajevae	HCZ-2	Iran, Fars, Abadeh settl. env.	31.129	52.203	JF756686	Solovyeva et al., 2011
Ph. h. cameranoi	ZMMU R-12669-1	Kazakhstan, Sugata Valley	43.45	78.9	JF756681	Solovyeva et al., 2011
Ph. h. cameranoi	ZMMU R-12661	Kazakhstan, SE Sugata Valley	43.45	78.9	JF756679	Solovyeva et al., 2011
Ph. h. cameranoi	ZMMU R-12668	Kazakhstan, Alma-Ata, Ili Depression, 3 km S from Tashkarasu settl.	43.733	79.467	JF769379	Solovyeva et al., 2011
Ph. h. cameranoi	ZMMU R-12665	Kazakhstan, Taldy-Kurgan, Ili Depression, sands on the right side of Zharkent – Khorgos Rd.	44.217	80.25	JF769380	Solovyeva et al., 2011
Ph. h. cameranoi	ZMMU R-12808	Kazakhstan, Alma-Ata, Ili Depression, Ulgen-Bogety Mts., Charyn-Borandysu Rd.	43.75	79.217	JF769372	Solovyeva et al., 2011
Ph. h. cameranoi	ZMMU R-12664	Kazakhstan, Alma-Ata, Ili Depression, Charyn River along of Kokpek Chundzha rout	43.6	79.317	JF769381	Solovyeva et al., 2011
Ph. h. cameranoi	ZMMU R-12812	Kazakhstan, Taldy-Kurgan, Ili Depression, Ili Riv., 10 km E from Aktau settl.	44.083	79.467	JF769378	Solovyeva et al., 2011
Ph. h. cameranoi	ZMMU R-12663	Kazakhstan, N Sugata Valley	43.51	79.4	JF756680	Solovyeva et al., 2011
Ph. h. cameranoi	ZMMU R-12669-2	Kazakhstan, Sugata Valley	43.45	78.9	JF756682	Solovyeva et al., 2011
Ph. h. cameranoi	ZMMU R-12782	Kazakhstan, Taldy-Kurgan, right board of Kapchagay reservoir	43.883	77.7	MK461350	Solovyeva et al., 2023
Ph. h. helioscopus	ZMMU R-12158	Kazakhstan, Aktyubinsk, Aral, Bolshiye Barsuki, Yuzhnoye vill.	46.18	58.4	JF769405	Solovyeva et al., 2011
Ph. h. helioscopus	ZMMU R-12160-2	Kazakhstan, Aktyubinsk, Aral, Akespe settl.	46.77	60.5	JF769403	Solovyeva et al., 2011
Ph. h. helioscopus	ZMMU R-13240-2	Kazakhstan, Aralsk town env.	46.794	62.133	JF769364	Solovyeva et al., 2011
Ph. h. helioscopus	ZMMU R-13241	Kazakhstan, Aralsk – Kamyshlybash road	46.228	61.367	JF769363	Solovyeva et al., 2011
Ph. h. helioscopus	ZMMU R-13242-2	Kazakhstan, Aralsk town	46.8	61.667	JF769370	Solovyeva et al., 2011
Ph. h. helioscopus	ZMMU R-13242-1	Kazakhstan, Aralsk town	46.8	61.667	JF769371	Solovyeva et al., 2011
Ph. h. helioscopus	ZMMU R-12519	Kazakhstan, Barsa-Kelmes island	45.7	59.867	JF756684	Solovyeva et al., 2011

Table 1. Continuation

1	2	3	4	5	6	7
Ph. h. helioscopus	ZMMU R-12151	Uzbekistan, Qoraqalpog`iston, Nukus, Bestube (Beshtube) settl.	42.63	59.67	JF769409	Solovyeva et al., 2011
Ph. h. helioscopus	ZMMU R-12155-2	Kazakhstan, Aktyubinsk, Northern Ust-Urt, Ozektyk settl.	45.58	57.27	JF769408	Solovyeva et al., 2011
Ph. h. helioscopus	ZMMU R-12153-1	Uzbekistan, Qoraqalpog`iston, Kungrad, Road from Ust-Urt mt.	43.991	57.972	JF769411	Solovyeva et al., 2011
Ph. h. helioscopus	ZMMU R-12155-1	Kazakhstan, Aktyubinsk, Northern Ust-Urt, Ozektyk	45.58	57.27	JF769407	Solovyeva et al., 2011
Ph. h. helioscopus	ZMMU R-12157	Kazakhstan, Karaganda, Aktau, 58 km of Aktau – Fort Shevchenko Rd.	44.23	51.6	JF769406	Solovyeva et al., 2011
Ph. h. helioscopus	ZMMU R-12160-1	Kazakhstan, Aktyubinsk, Aral, Akespe settl.	46.77	60.5	JF769402	Solovyeva et al., 2011
Ph. h. helioscopus	ZMMU R-13240-1	Kazakhstan, Aralsk town env.	46.794	62.133	JF769365	Solovyeva et al., 2011
Ph. h. helioscopus	IZIP Phh-003	Uzbekistan, Qoraqalpog`iston, Zhaslyk settl.	43.933	57.498	JF769413	Solovyeva et al., 2011
Ph. h. helioscopus	IZIP 0829	Uzbekistan, Qoraqalpog`iston, Kungrad, N from Kungrad, near Ravshan	43.259	58.691	JF769415	Solovyeva et al., 2011
Ph. h. helioscopus	ZMMU R-13242-3	Kazakhstan, Aralsk town	46.8	61.667	JF769369	Solovyeva et al., 2011
Ph. h. helioscopus	ZMMU R-12156	Kazakhstan, Aktyubinsk, Northern Aral, Akespe settl.	46.77	60.5	JF769404	Solovyeva et al., 2011
Ph. h. helioscopus	ZMMU R-12161-2	Kazakhstan, Shymkent, Kyzyl-Kiya, Kyzyl-Kiya settl.	41.64	69.36	JF769400	Solovyeva et al., 2011
Ph. h. helioscopus	ZMMU R-12150	Uzbekistan, Qoraqalpog`iston, Ravshan (Raushan) settl.	42.93	59.13	JF769414	Solovyeva et al., 2011
Ph. h. helioscopus	ZMMU R-13242-4	Kazakhstan, Aralsk town	46.8	61.667	JF769368	Solovyeva et al., 2011
Ph. h. helioscopus	ZMMU R-12161-1	Kazakhstan, Shymkent, Kyzyl-Kiya, Kyzyl-Kiya settl.	41.64	69.36	JF769399	Solovyeva et al., 2011
Ph. h. helioscopus	ZMMU R-12527	Kazakhstan, N Zhanakala settl.	50.217	73.817	JF756683	Solovyeva et al., 2011
Ph. h. helioscopus	ZMMU R-13240-3	Kazakhstan, Aralsk env.	46.794	62.133	JF769366	Solovyeva et al., 2011
Ph. h. helioscopus	ZMMU R-12152	Uzbekistan, Qoraqalpog`iston, Kungrad, SW from Kungrad settl.	42.683	58.55	JF769412	Solovyeva et al., 2011
Ph. h. helioscopus	ZMMU R-12525	Kazakhstan, Mangistau, Kenderli Kayassanskaya reserve zone	42.9	53.417	JF769387	Solovyeva et al., 2011
Ph. h. helioscopus	ZMMU R-12153-2	Uzbekistan, Qoraqalpog`iston, Kungrad, Road from Ust-Urt mt.	43.991	57.972	JF769410	Solovyeva et al., 2011
Ph. h. helioscopus	ZMMU R-12813	Uzbekistan, Kzyl-Orda, Aral, Vozrozhdeniya island	45.15	59.3	JF769388	Solovyeva et al., 2011
Ph. h. helioscopus	ZMMU R-12164	Kazakhstan, Aktyubinsk, Aral, Kulandy penninsula	46.04	59.28	JF769401	Solovyeva et al., 2011
Ph. h. helioscopus	ZMMU R-13242-5	Kazakhstan, Aralsk town	46.8	61.667	JF769367	Solovyeva et al., 2011
Ph. h. helioscopus	ZMMU R-12525-2	Kazakhstan, Mangistau, Kenderli Kayassanskaya reserve zone	42.9	53.417	KF691716	Solovyeva et al., 2014
Ph. horvathi	ZMMU R-13243-3	Armenia, near Gorovan vill.	39.917	44.733	GU657527	Solovyeva et al., 2011
Ph. horvathi	TLT-200602	Armenia, Armavir	40.067	44.05	JF769418	Solovyeva et al., 2011
Ph. horvathi	ZMMU R-13243-2	Armenia, near Gorovan vill.	39.917	44.733	GU657525	Solovyeva et al., 2011
Ph. horvathi	ZMMU R-13243-1	Armenia, near Gorovan vill.	39.917	44.733	GU657526	Solovyeva et al., 2011
Ph. horvathi	ZMMU R-13243-4	Armenia, near Gorovan vill.	39.917	44.733	GU657528	Solovyeva et al., 2011
Ph. horvathi	TLT-200601	Armenia, Armavir town	40.067	44.05	JF769419	Solovyeva et al., 2011

Table 1. Continuation

1	2	3	4	5	6	7
Ph. horvathi	ZMMU R-12322-1	Armenia, Armavir (Oktemberyan), 1 km SE Khandzan	40.15	44.033	JF769420	Solovyeva et al., 2011
Ph. horvathi	ZMMU R-3843-1	Armenia, Ararat, Ararat, Sands near Vedi settl. [vicinity of the type locality of *horvathi*]	39.933	44.717	JF769417	Solovyeva et al., 2011
Ph. horvathi	ZMMU R-12322-2	Armenia, Armavir (Oktemberyan) settl., 1 km SE Khandzan vill.	40.15	44.033	KF691715	Solovyeva et al., 2014
Ph. meridionalis	ZMMU R-12803	Uzbekistan, Bukhara, near Kagan town, Dzheyran farm	39.567	64.7	JF769376	Solovyeva et al., 2011
Ph. meridionalis	ZMMU R-12801-1	Uzbekistan, Surkhandaria, N from Aktash, in Pashchurt's direction [type locality of meridionalis]	37.583	66.667	JF769377	Solovyeva et al., 2011
Ph. persicus	FH-10-4	Iran, Ardebil town env.	38.393	48.368	JF756689	Solovyeva et al., 2011
Ph. persicus	FH_10_1, no. voucher	Iran, Markasi, Arak env.	34.24	49.75	JF756688	Solovyeva et al., 2011
Ph. persicus	ZMMU R-12466	Azerbaijan, Naxcivan, NW from Nachichevan city	39.283	45.283	JF769421	Solovyeva et al., 2011
Ph. persicus	ZMMU R-12786	Azerbaijan, Apsheron, near Sangachaly	40.15	49.467	JF769416	Solovyeva et al., 2011
Ph. s. saidalievi	ZMMU R-16885 (RAN-4431)	Kyrgyzstan, Batkent region, Kadamjay dist., near Sovetskiy vill.	40.25	71.34	OP970518	Solovyeva et al., 2023
Ph. s. saidalievi	ZMMU R-16886 (RAN-4432)	Kyrgyzstan, Batkent region, Kadamjay dist., near Sovetskiy vill.	40.25	71.34	OP970519	Solovyeva et al., 2023
Ph. s. saidalievi	ZMMU R-16887 (RAN-4433)	Kyrgyzstan, Batkent region, Kadamjay dist., near Sovetskiy vill.	40.25	71.34	OP970520	Solovyeva et al., 2023
Ph. s. saidalievi	ZMMU R-16888 (RAN-4434)	Kyrgyzstan, Batkent region, Kadamjay dist., near Sovetskiy vill.	40.25	71.34	OP970521	Solovyeva et al., 2023
Ph. s. saidalievi	ZMMU R-16889 (RAN-4435)	Kyrgyzstan, Batkent region, Kadamjay dist., near Sovetskiy vill.	40.25	71.34	OP970522	Solovyeva et al., 2023
Ph. h. sergeevi	ZMMU R-12286	Uzbekistan, Bukhara, near Kuldzhuktau Mts. and Dzhangyldy vil.	40.797	63.608	JF769391	Solovyeva et al., 2011
Ph. h. sergeevi	ZMMU R-12259-1	Uzbekistan, Navoi, Karakata Depression, 60 km NW from Zafarabad settl.	40.931	64.654	JF769394	Solovyeva et al., 2011
Ph. h. sergeevi	ZMMU R-12310	Uzbekistan, Bukhara, SW Kyzylkumy, Kuldzhuktau Mts.	40.783	63.483	JF769390	Solovyeva et al., 2011
Ph. h. sergeevi	ZMMU R-12166	Uzbekistan, Bukhara, Bukhara, Ayakagytma Lake environs	40.57	64.68	JF769396	Solovyeva et al., 2011
Ph. h. sergeevi	ZMMU R-12167	Uzbekistan, Qoraqalpog`iston, Central Kyzylkum, 10 km NE from Zarafshon settl.	41.65	64.3	JF769395	Solovyeva et al., 2011
Ph. h. sergeevi	ZMMU R-12264-1	Uzbekistan, Navoi, SE border TamdyTau Mts., 40 km from Zaravshan, between Tamdybulak and Yangitamdy [type locality of *sergeevi*]	41.702	64.033	JF769393	Solovyeva et al., 2011
Ph. h. sergeevi	ZMMU R-12281-1	Uzbekistan, Bukhara, near Kuldzhuktau Mts. 8 km W from Shuruk, near Desert Botanic Station	40.729	63.756	JF769392	Solovyeva et al., 2011
Ph. h. sergeevi	ZMMU R-12310	Uzbekistan, SW Kyzylkum, Kuldjuktau	40.78	63.48	MK461408	Solovyeva et al., 2023
Ph. h. turcomanus	ZMMU R-12789	Turkmenistan, Balkan, 70 km SE from Nebit-Dag [type locality of *turcomanus*]	38.967	54.917	JF769386	Solovyeva et al., 2011
Ph. h. varius	ZMMU R-12903-2	Mongolia, Hovd, Ikcher-Toli on the W from Bulgan town	46.1	91.35	JF769383	Solovyeva et al., 2011
Ph. h. varius	ZMMU R-12163-1	Kazakhstan, East Kazakhstan, Semey-Tau Mt., Scherbakovka settl. environs	50,08	79,41	JF769398	Solovyeva et al., 2011

Table 1. Continuation

1	2	3	4	5	6	7
Ph. h. varius	ZMMU R-12524	Kazakhstan, Zhalanashkol Lake env.	45.571	82.212	JF756685	Solovyeva et al., 2011
Ph. h. varius	ZMMU R-12163-1	Kazakhstan, East Kazakhstan, Semey-Tau Mt., Scherbakovka settl. environs	50.08	79.41	JF769397	Solovyeva et al., 2011
Ph. h. varius	ZMMU R-12903-1	Mongolia, Hovd, Ikcher-Toli on the W from Bulgan town	46.1	91.35	JF769384	Solovyeva et al., 2011
Ph. h. varius	ZMMU R-12810	Kazakhstan, Taldy-Kurgan, near Baschi and Kalinino settls.	44.167	78.783	JF769385	Solovyeva et al., 2011
Ph. h. varius	ZMMU R-13089-1	China, Xinjiang, Toli settl.	45,98	83,54	HQ543966	Solovyeva et al., 2014
Ph. h. varius	ZMMU R-12164	Kazakhstan, Border of Alma-Aty and E Kazakhstan provinces, Lake Zhalanashkol	45.4	82.09	MK461382	Solovyeva et al., 2023
Ph. h. karatauesnsis **ssp. nov**.	ZMMU R-12662	Kazakhstan, S Kazakhstan, Chimkent, N foothills of Karatau, near Suzak settl.	44.316	68.6	JF769382	Solovyeva et al., 2011
Ph. h. karatauesnsis **ssp. nov**.	ZMMU R-12165	Kazakhstan, Taraz, NE Karatau, Kyzylkol Lake	43.79	69.54	JF769389	Solovyeva et al., 2011
Ph. h. karatauesnsis **ssp. nov**.	ZMMU R-16120 (SEN-380)	Kazakhstan, near Karatau Ridge, Suzak environs	44.237	68.519	PP905305	this study
Ph. h. karatauesnsis **ssp. nov**.	ZMMU R-16121 (SEN-381)	Kazakhstan, near Karatau Ridge, Suzak environs	44.283	68.418	PP905306	this study
Ph. h. karatauesnsis **ssp. nov**.	ZMMU R-17944 (SEN-382)	Kazakhstan, near Karatau Ridge, Suzak settl.environs	44.283	68.418	PP905307	this study
Ph. h. karatauesnsis **ssp. nov**.	SEN-383	Kazakhstan, near Karatau Ridge	44.631	67.774	PP905308	this study
Ph. h. karatauesnsis **ssp. nov**.	SEN-384	Kazakhstan, near Karatau Ridge	44.631	67.774	PP905309	this study
Ph. h. karatauesnsis **ssp. nov**.	SEN-385	Kazakhstan, near Karatau Ridge, Suzak settl.environs	44.283	68.418	PP905310	this study
Ph. h. karatauesnsis **ssp. nov**.	SEN-386	Kazakhstan, near Karatau Ridge, Suzak settl. environs	44.283	68.418	PP905311	this study
Ph. h. karatauesnsis **ssp. nov**.	SEN-387	Kazakhstan, near Karatau Ridge, Suzak settl. environs	44.283	68.418	PP905312	this study
Ph. h. karatauesnsis **ssp. nov**.	ZMMU R-16123 (SEN-388)	Kazakhstan, near Karatau Ridge	44.624	67.671	PP908406	this study
Ph. h. karatauesnsis **ssp. nov**.	ZMMU R-17945 (SEN-389)	Kazakhstan, near Karatau Ridge	44.624	67.671	PP905313	this study
Ph. h. karatauesnsis **ssp. nov**.	ZMMU R-17946 (SEN-390)	Kazakhstan, near Karatau Ridge	44.624	67.671	PP905314	this study
Ph. s. orlovae **ssp. nov**.	ZMMU R-12678	Uzbekistan, Fergana Depression, 25 km N from Kokand, foothill adyrs to the north from the road Tashkent – Kokand	40.78	70.97	JF769375	Solovyeva et al., 2011
Ph. s. orlovae **ssp. nov**.	ZMMU R-12802	Uzbekistan, Namangan, Fergana Depression, Pabskaya Steppe, near Chodak and Koshmior settls.	40.88	70.8	JF769374	Solovyeva et al., 2011
Ph. s. orlovae **ssp. nov**.	ZMMU R-17935	Uzbekistan, Namangan, Fergana Depression, Pabskaya Steppe, near Chodak and Koshmior settls.	40.88	70.8	JF769373	Solovyeva et al., 2011
Ph. s. orlovae **ssp. nov**.	ZMMU R-17936	Uzbekistan, Namangan, Fergana Depression, Pabskaya Steppe, near Chodak and Koshmior settls.	40.88	70.8	KF691717	Solovyeva et al., 2014
Stellagama stellio	ZMMU R-11324	Israel, Rekhovat settl.	31.88	34.8	KF691700	Solovyeva et al., 2014
Paralaudakia caucasia	ZMMU R-12465	Azerbaijan, Lerik, Zuvand, Kelvyaz settl.	38.61	48.35	KF691701	Solovyeva et al., 2014
Paralaudakia lehmanni	ZMMU R-12248	Uzbekistan, Navoi, Nuratau, Kataich settl.	40.61	66.58	KF691702	Solovyeva et al., 2014
Paralaudakia microlepis	ZMMU R-12207	Iran, Khorasan, Birjant, Sedeh settl.	39.85	59.894	KF691703	Solovyeva et al., 2014

№ 27-3-16/2983-КЛХЖМ. According to Kazakhstan legislation, no permits are required to collect tissue samples without removing individuals from the wild. Bioethics permits № 63-1 and 147-a for fieldwork (samples, photos, and observation collections) were approved during the Bioethics Commission meetings of the Lomonosov Moscow State University № 86-o and 150-d. Samples in Uzbekistan were collected in accordance with the permit № 000034.

Molecular analysis. Molecular analysis was carried out in the laboratory of the Vertebrate Zoology Department of the Biological Faculty of the Lomonosov Moscow State University. We analyzed the 655 b.p. (base pair)-long fragment of the COI gene (cytochrome oxidase c subunit I) of mtDNA. Muscle and skin tissues were incubated with Proteinase K, and total genomic DNA was extracted using a standard phenol-chloroform extraction protocol followed by ethanol precipitation of DNA (following the protocol of Sambrook et al., 1989).

Polymerase chain reaction (PCR) amplification was performed using MyCycler Bio Rad under the conditions described by Ivanova et al. (2006). Two standard pairs of primers were used for PCR and sequencing: VF1d (5'-TTCTCAACCAACCACA-ARGAYATYGG-3') and VR1d (5'-TAGACTTCT-GGGTGGCCRAARAAYCA-3'), or Rep-COI-F (5'-TNTTMTCAACNAACCACAAAGA-3') and Rep-COI-R (5'-ACTTCTGGRTGKCCAAARAATCA-3') (Ivanova et al., 2006; Nagy et al., 2012). Amplification was performed in 22 μL reaction volumes containing 2 μL DNA, 4 μL of Evrogen HS-Screen mix, and 1 μL of each primer (10 pmol/μL). All stages of the extraction process included a blank as a negative control run in parallel. PCR products were visualized using a 1% agarose gel. PCR products were sequenced at the Evrogen laboratory using an ABI PRISM 3500xl sequencer with BigDye Terminator Chemistry v. 3.1 (Applied Biosystems, Foster City, CA, USA) using PCR primers.

The length of the obtained fragments was about 655 bp. The sequence of Stellagama stellio KF691700 was used as an outgroup. Sequences were aligned and checked using BioEdit Sequence Alignment Editor 7.1.3.0 (Hall, 1999). All sequences were deposited in GenBank (see Table 1 for all voucher information, with corresponding GenBank accession numbers).

To estimate the phylogenetic relationships within the Ph. helioscopus complex, we reconstructed phylogenetic trees under Bayesian criteria (BI) and using the maximum likelihood approach (ML). The optimum partitioning schemes for Bayesian Interference analysis for the COI fragment were taken from the previous works on the barcoding of the genus *Phrynocephalus* (Solovyeva et al., 2023); HKY+G model was applied for all codon positions separately. BI-analysis was performed using MrBayes v3.2.7a (Ronquist, Huelsenbeck, 2003) with two simultaneous runs, each with four chains, for five million generations. We checked the convergence of the runs and that the effective sample sizes (ESS) were all above 200 by exploring the likelihood plots using TRACER v.1.5 (Rambaut, Drummond, 2007). The initial 10% of trees were discarded as burnin. Confidence in tree topology was assessed by posterior probability (PP) (Huelsenbeck, Ronquist, 2001). The ML trees were generated using IQtree software (Nguyen et al., 2015) with ultrafast bootstrap = 10000 (UFBoot, Minh et al., 2013). The best-fit model of DNA evolution was selected using ModelFinder software (Kalyaanamoorthy et al., 2017); HKY+F+I+G4 was suggested as the best fit according to BIC.

Morphological analysis. Head coloration of 149 specimens of *Ph. helioscopus* complex was studied from photographs: 18 specimens of *Ph. helioscopus* ssp. from Karatau Ridge; 63 specimens of *Ph. h. cameranoi*; 22 specimens of *Ph. h. varius*; 7 specimens of *Ph. meridionalis*; 9 specimens of *Ph. saidalievi* sensu stricto; and 9 specimens of *Ph. sergeevi*. Part of the photographs ($N = 21$) were taken during the field trip to Kazakhstan in May, 2023 by Solovyeva E. N., the remaining photographs were taken during the previous field trips ($N = 75$; starting from 2008) by Solovyeva E. N., two photos by Lisachev A. P. and from the iNaturalist database (https://www.inaturalist.org/) ($N = 54$); in the latter case only the photographs where the head coloration was obvious were included in analysis. In this analysis, we did not distinguish the populations of *Ph. saidalievi* from the left and right banks of the Syrdarya River.

The following characteristics of head coloration were examined: the prevailing background head color (olive or gray); the presence of red dots (yes or no); the presence of dark dots (yes or no); the presence of the 8-shaped dark marking (yes or no); the degree of head coloration contrast (estimated as: not contrasting = 0; medium contrast = 1; highly contrasting = 2). The schematic representation of these characteristics is shown in Figure 2*, a–c*. The dark spots (sometimes underlined by red dots) in a row forming a line over the eye (see Fig. 2) were not taken into account, they were recorded in all studied specimens of *Ph. helioscopus*.

Thirteen measurements and nine scalation meristic characters were taken for the specimens from Karatau Ridge in Kazakhstan and the Fergana Valley in Uzbekistan and Kyrgyzstan to compare with the previously examined specimens (Solovyeva et al., 2012). Morphometric characters included: *SVL* – body length; *TL* – tail length; *SVL*/*TL* ratio; *Int. N* – dis-

a ***b*** ***c***

Fig. 2. Features of the head coloration in the *Phrynocephalus helioscopus* species complex members: *a* – 8-shape spot of *Ph. helioscopus karatauensis* **ssp. nov**., *b* – red dots and dark spots of *Ph. helioscopus varius*, *c* – dark spots and a row over the eye of *Ph. horvathi*

tance between nostrils; *T* – length of tibia; *LFL* – length of forelimb; *LHL* – length of hindlimb; *HH* – head hight (on the level of the middle of the eye); *HL* – head length; *HW* – head width; *CW* – 'cap' width (cap – a group of enlarged flat scales in the occipital region of the *Phrynocephalus* lizards); *P-N* – distance from parietal shield to nostril; *N-eye* – distance between nostril and preorbital fold. Meristic characters included: *N-N* – number of scales between nasal shields; *D. lab*. – number of upper labial scales; *V. lab*. – number of lower labial scales; *Slab-eye* – number of scales between the upper labials and the eye; *C* – number of scales across the cap from eye to eye; Par-snas – number of scales from central parietal to upper nasal; I – number of scales on the underside of the finger I of the hind limb (excluding the claw); IV – number of scales on the underside of the finger IV of the hind limb (excluding the claw); V – number of scales on the underside of the finger V of the hind limb (excluding the claw). The resulting dataset included morphological data for 129 specimens from eight taxa (see Table 2): "helioscopus sensu stricto", "cameranoi", "meridionalis", "saidalievi", "sergeevi", "varius", "Karatau", "Right bank of the Syrdarya River in the Fergana Valley". The following abbreviations were used to describe statistics: "*p*-value" for statistical significance, "df" for degrees of freedom, and "χ^2" for chi-square score.

Table 2. List of specimens used in morphological analysis (measurements and pholidosis counts)

Subspecies	*N*	Voucher no. ZMMU	Locality
1	2	3	4
Ph. h. helioscopus	12	R-8720	Kazakhstan, Aralsk env.
Ph. h. helioscopus	5	R-8726	Kazakhstan, Aralsk env.
Ph. h. helioscopus	3	R-8718	Kazakhstan, Barsa-Kelmes island
Ph. meridionalis	15	R-6817	Turkmenistan, Kugitang mts.
Ph. meridionalis	5	R-5902	Turkmenistan, Begiarelan mt.
Ph. h. cameranoi	4	R-5945	Kazakhstan, Sugata Valley
Ph. h. cameranoi	8	R-12669	Kazakhstan, 25 km W Kokpek settl.
Ph. h. cameranoi	5	R-12668	Kazakhstan, Tashkarasu env.
Ph. h. cameranoi	1	R-12528	Kazakhstan, SE Sugata Valley, Bartagoy settl.
Ph. h. cameranoi	2	R-12664	Kazakhstan, left bench of Charyn River, on the road to Ily River
Ph. h. cameranoi	10	R-12665	Kazakhstan, Khorgos env.
Ph. h. varius	6	R-12810	Kazakhstan, Taldy-Kurgan settl.
Ph. h. varius	6	R-5932	Kazakhstan, Alakol basin, 15 km N Zhalanashkol lake
Ph. h. varius	1	R-617	Kazakhstan, Berl-Baygai settl., Balkhash lake
Ph. h. varius	2	R-12809	Kazakhstan
Ph. h. varius	2	R-5931	Kazakhstan, Alakol basin, Tasti River Valley, 5 km SE Zharbulak vill.
Ph. h. varius	1	R-12384	Kazakhstan
Ph. h. varius	1	R-12383	Kazakhstan
Ph. h. varius	1	R-8731	Kazakhstan, Buran env., near Black Irtysh River
Ph. s. saidalievi	1	R-17310 (RAN-4895)	Kyrgizstan, Batkent region, Kadamjay dist., near Sovetskiy vill.
Ph. s. saidalievi	1	R-17311 (RAN-4896)	Kyrgizstan, Batkent region, Kadamjay dist., near Sovetskiy vill.
Ph. s. saidalievi	1	R-17312 (RAN-4897)	Kyrgizstan, Batkent region, Kadamjay dist., near Sovetskiy vill.
Ph. s. saidalievi	1	R-17313 (RAN-4898)	Kyrgizstan, Batkent region, Kadamjay dist., near Sovetskiy vill.
Ph. s. saidalievi	1	R-17314 (RAN-4899)	Kyrgizstan, Batkent region, Kadamjay dist., near Sovetskiy vill.
Ph. s. saidalievi	1	R-17315 (RAN-4901)	Kyrgizstan, Batkent region, Kadamjay dist., near Sovetskiy vill.

Table 2. Continuation

1	2	3	4
Ph. s. saidalievi	1	R-17316 (RAN-4902)	Kyrgizstan, Batkent region, Kadamjay dist., near Sovetskiy vill.
Ph. s. saidalievi	1	R-16885 (RAN-4431)	Uzbekistan, Fergana Valley, vicinity of Pavelgan settl.
Ph. s. saidalievi	1	R-16886 (RAN-4432)	Uzbekistan, Fergana Valley, vicinity of Pavelgan settl.
Ph. s. saidalievi	1	R-16887 (RAN-4433)	Uzbekistan, Fergana Valley, vicinity of Pavelgan settl.
Ph. s. saidalievi	1	R-16888 (RAN-4434)	Uzbekistan, Fergana Valley, vicinity of Pavelgan settl.
Ph. h. sergeevi	1	R-10745	Uzbekistan, NW Nuratau, near Taldy water well
Ph. h. sergeevi	1	R-6147	Uzbekistan, S Kuldzhuktau, Shuruk vill. env.
Ph. h. sergeevi	1	R-11756	Uzbekistan
Ph. h. sergeevi	2	R-6596	Uzbekistan, 15 km N Navoi settl.
Ph. h. sergeevi	4	R-7282	Uzbekistan, Kuldzhuktau foothills, 10 km W Shuruk vill.
Ph. h. sergeevi	1	R-10967	Uzbekistan, Central Kyzylkum Desert, 15 km NW Zarafshon settl.
Ph. h. karatauensis ssp. nov. (“karatau”)	1	R-16120	Kazakhstan, near Karatau Ridge
Ph. h. karatauensis ssp. nov. (“karatau”)	1	R-17944	Kazakhstan, near Karatau Ridge
Ph. h. karatauensis ssp. nov. (“karatau”)	1	R-16121	Kazakhstan, near Karatau Ridge
Ph. h. karatauensis ssp. nov. (“karatau”)	1	R-16125	Kazakhstan, near Karatau Ridge
Ph. h. karatauensis ssp. nov. (“karatau”)	1	R-16123	Kazakhstan, near Karatau Ridge
Ph. h. karatauensis ssp. nov. (“karatau”)	1	R-17945	Kazakhstan, near Karatau Ridge
Ph. h. karatauensis ssp. nov. (“karatau”)	1	R-17946	Kazakhstan, near Karatau Ridge
Ph. s. orlovae ssp. nov. (“right bank”)	1	R-12802	Uzbekistan, Namangan, Fergana Depression, Pabskaya Steppe, near Chodak and Koshmior settls.
Ph. s. orlovae ssp. nov. (“right bank”)	8	R-17935-17942	Uzbekistan, Namangan, Fergana Depression, Pabskaya Steppe, near Chodak and Koshmior settls.
Ph. s. orlovae ssp. nov. (“right bank”)	1	R-12678	Uzbekistan, Fergana Depression, 25 km N from Kokand, foothill adyrs to the north from the road Tashkent – Kokand
Ph. s. orlovae ssp. nov. (“right bank”)	1	R-17943	Uzbekistan, Fergana Depression, 25 km N from Kokand, foothill adyrs to the north from the road Tashkent – Kokand

For nominal discrete (qualitative) data, Multiple Correspondence Analysis (MCA) was performed in R using packages FactoMineR (Lê et al., 2008) and Factoshiny (Vaissie et al., 2024). Pearson’s chi-squared test for independence was calculated in Factoshiny. This test assesses the association between qualitative traits and the origin of specimens or species taxonomic assignment.

For continuous (quantitative) data, we calculated box-and-whiskers-plots and basic descriptive statistics using R (R Core Team, 2021) and performed Principal Components Analysis (PCA) using FactoMineR (Lê et al., 2008) and Factoshiny (Vaissie et al., 2024).

Also, we checked several diagnostic features used in our previous work on the *Ph. helioscopus* species complex (Solovyeva et al., 2012) for the specimens from Karatau Ridge and the Fergana Valley, such as the presence and position of a group of enlarged scales between the anterior edges of the eyes; displaced scales in the postorbital scale rows; the number of scales between the enlarged anterior supraorbital and nasal shields; the presence of the enlarged scales among the posterior supralabials; the shape of the scales surrounding the remnants of the umbilical opening; the presence of the enlarged spiny scales on the shoulder; the presence of a number of pointed scales above the neck spots.

RESULTS

Phylogenetic analysis. The results of phylogenetic analysis are presented in Fig. 3. BI and ML produced trees that show essentially similar topologies. All previously recognized lineages were highly supported (comparing to Solovyeva et al., 2023), including the clade of *Ph. saidalievi* from the right bank of the Syrdarya River (100/1, hereafter the node support values are given for BS/PP) and the clade of *Ph. helioscopus* from Karatau Ridge (99/1). Phylogenetic relationships between *Ph. saidalievi* from left and right banks of the Syrdarya River and *Ph. meridionalis* have low resolution, the rest lineages, excluding *Ph. persicus*, comprise a clade. Relationships within this clade mostly have good support. First, the clade divides into two clades. The first one includes *Ph. h. cameranoi* and *Ph. helioscopus* populations from Karatau Ridge environs (*Ph. helioscopus* ssp.) as a sister lineage to it. Second, we see a group with temperate to low support (84/0.68) consisting of *Ph. h. sergeevi*, *Ph. h. varius*. *Ph. h. helioscopus* and *Ph. h. turcomanus*, relationships of the last three species are not resolved.

Clade of *Ph. saidalievi* from the right bank of the Syrdarya River shows very slight topological structure: samples from Pabskaya Steppe cluster together (98/0.77) and a sample from 25 km N to Kokand branches from them, clade of *Ph. saidalievi* from the

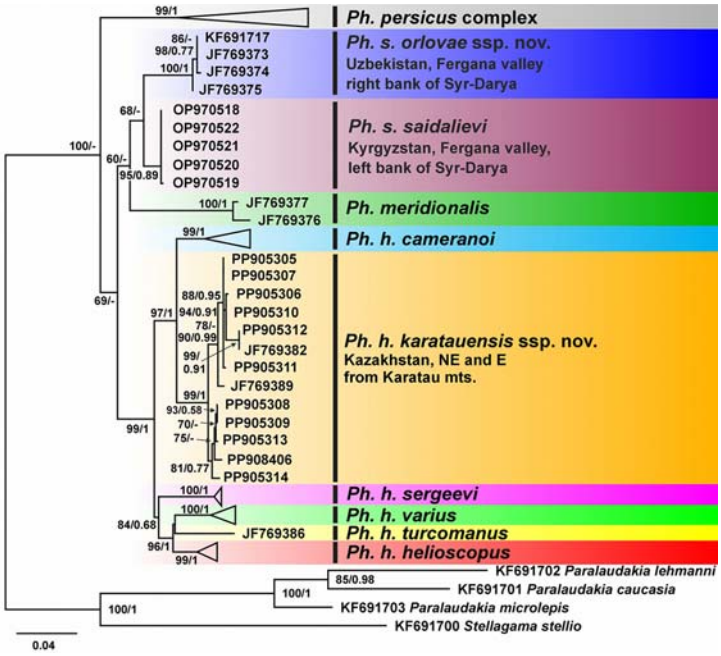

Fig. 3. ML-inferred phylogenetic tree showing the genealogical relationships of the Phrynocephalus helioscopus species complex based on the analysis of 655 b. p. fragment of COI gene (mtDNA). Numbers at the tree nodes show Maximum Likelihood Bootstrap Support/Bayesian Posterior Probabilities

left bank of the Syrdarya River doesn't show topological structure. Meanwhile, clade of *Ph. helioscopus* from Karatau Ridge has very clear branching into three main groups with temperate support (88/0.95 and 81/0.77) coinciding with the three main collection localities. These are specimens from Suzak environs (points 1 and 2 on the map, see Fig. 1), one specimen from the Kyzylkol lake (point 3 on the map, see Fig. 1) and the rest from the localities to the NW from Suzak (points 4 and 5 on the map, see Fig. 1).

Uncorrected *p*-distances within *Ph. helioscopus* sensu stricto lineages differ from 3.94 to 11.13% (Table 3). Distances between specimens from Karatau Ridge environs and others vary from 5.08% (with *Ph. h. cameranoi*) to 10.51% (with *Ph. meridionalis*), exceeding 13.05% with *Ph. persicus* lineages. Specimens from the right bank of the Syrdarya River differ less, their distances vary from 3.94% with *Ph. saidalievi* to 6.67% (with *Ph. h. helioscopus*) and up to 11.89% with *Ph. persicus* lineages.

Morphological analysis. A. Color pattern of the head. The occurrences of the values of the studied morphological features of the head pattern are represented in Tables 4, 5 and Fig. 2, *a–c*. According to the obtained results, the prevailing color of the cap of the toad-headed agamas from Karatau Ridge is gray in 88.89%, there are no red or dark dots in 94.44%, the 8-shaped spot occurs in 72.22% and the coloration has medium contrast in 61.11%. The main color of the cap can differ Karatau Ridge populations from *Ph. h. helioscopus*, *Ph. meridionalis* and *Ph. h. sergeevi*: gray cap in 88.89% of Karatau Ridge specimens versus olive cap in 85.71 to 100% for above mentioned species. The combination of two characteristics can be used as a diagnostic feature – the presence of 8-shaped spot together with the absence of red dots (see Fig. 2, 4, Table 5). The position of red and dark spots on the scales differs. Red pigment occupies the basal part of the scale, while black pigment concentrates at the top of the scale, thus the same scale can host both types of dots.

Results of MCA analyses are shown on Fig. 5. Confidence ellipses for *Ph. helioscopus* ssp. and

Table 3. Uncorrected *p*-distances (percentage) between and within the groups of *Ph. helioscopus* s.l. complex. Distances between groups are shown under the diagonal row; standard error values are given above the diagonal row, distances within groups are shown at the diagonal row

Subspecies	*helioscopus*	*cameranoi*	*meridionalis*	*saidalievi*	*sergeevi*	*karatauensis* **ssp. nov.**	*orlovae* **ssp. nov.**	*turcomanus*	*varius*	*persicus* s.l.
helioscopus	**0.42**	1.11	1.47	1.38	1.01	1.1	1.22	1.07	0.87	1.92
cameranoi	6.29	**1.37**	1.65	1.35	1.11	0.94	1.25	1.21	1.13	2.01
meridionalis	9.35	11.13	**1.4**	1.4	1.7	1.56	1.31	1.65	1.63	1.94
saidalievi	8.01	7.73	8.36	**0.24**	1.51	1.52	0.9	1.53	1.5	2.01
sergeevi	5.36	6.33	11.11	9.14	**0.16**	1.29	1.35	1.31	1.15	1.91
karatauensis **ssp. nov.**	5.84	5.08	10.51	8.83	7.13	**1**	1.28	1.28	1.12	1.87
orlovae **ssp. nov.**	6.67	7.22	7.46	3.94	7.6	7.32	**0.06**	1.3	1.31	1.74
turcomanus	5.61	7.1	10.7	9.02	7.61	7.13	7.07	**-**	1.05	2.01
varius	4.47	6.41	10.57	8.57	6.49	6.07	7.19	5.51	**1.19**	2.11
persicus s.l.	13.64	14.42	13.99	13.86	13.36	13.05	11.89	14.3	14.94	**6.33**

Table 4. Occurence of the diagnostic features of the head pattern within *Ph. helioscopus* sensu lato, %

N	Subspecies	Cap colour		Red spots		Dark spots		8-shape		Contrast		
		olive	grey	-	+	-	+	-	+	0	1	2
	All											
63	*cameranoi*	34.92	65.08	38.1	61.9	46.03	53.97	65.08	34.92	17.46	57.14	25.4
21	*helioscopus*	95.24	4.76	100	0	71.43	28.57	100	0	52.38	47.62	0
7	*meridionalis*	85.71	14.29	85.71	14.29	57.14	42.86	85.71	14.29	57.14	28.57	14.29
9	*saidalievi*	44.44	55.56	44.44	55.56	66.67	33.33	55.56	44.44	33.33	33.33	33.33
9	*sergeevi*	100	0	100	0	88.89	11.11	100	0	77.78	22.22	0
18	*karatauensis* **ssp. nov.**	11.11	88.89	94.44	5.56	94.44	5.56	27.78	72.22	16.67	61.11	22.22
22	*varius*	22.73	77.27	27.27	72.73	77.27	22.73	59.09	36.36	40.91	27.27	31.82
	Males											
34	*cameranoi*	26.47	73.53	35.29	64.71	41.18	58.82	70.59	29.41	2.94	61.76	35.29
7	*helioscopus*	85.71	14.29	100	0	57.14	42.86	100	0	14.29	85.71	0
3	*meridionalis*	100	0	100	0	33.33	66.67	100		66.67	33.33	0
2	*saidalievi*	0	100	0	100	0	100	0	100	0	50	50
1	*sergeevi*	100	0	100	0	100	0	100	0	100	0	0
7	*karatauensis* **ssp. nov.**	14.29	85.71	85.71	14.29	100	0	14.29	85.71	14.29	42.86	42.86
8	*varius*	25	75	25	75	75	25	50	50	25	25	50
	Females											
14	*cameranoi*	28.57	71.43	21.43	78.57	57.14	42.86	50	50	28.57	42.86	28.57
3	*helioscopus*	100	0	100	0	33.33	66.67	100	0	33.33	66.67	0
2	*meridionalis*	50	50	50	50	50	50	50	50	0	50	50
2	*saidalievi*	50	50	0	100	50	50	50	50	0	50	50
0	*sergeevi*	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
8	*karatauensis* **ssp. nov.**	0	100	100	0	100	0	37.5	62.5	25	62.5	12.5
4	*varius*	0	100	0	100	100	0	75	25	50	25	25

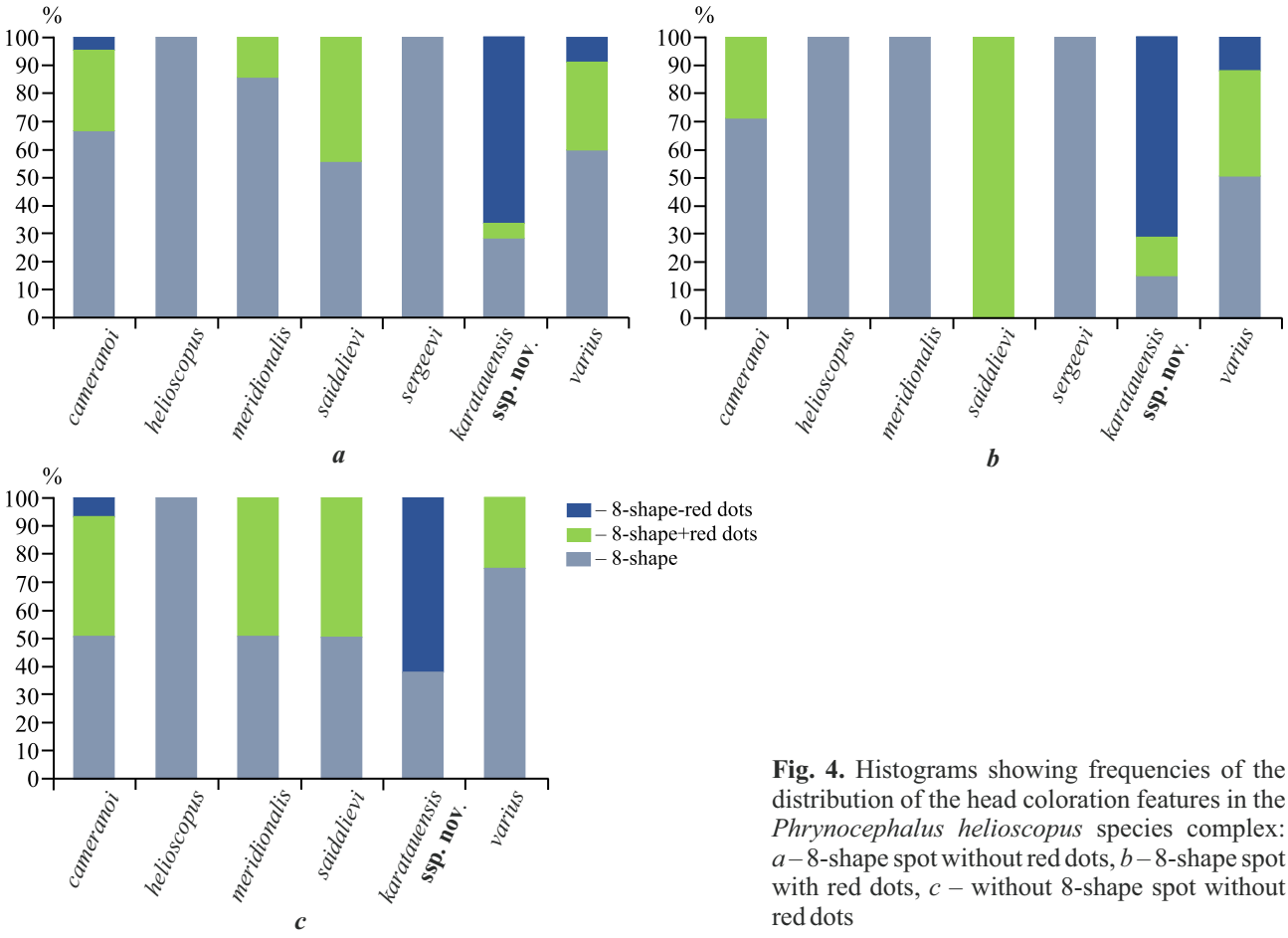

Fig. 4. Histograms showing frequencies of the distribution of the head coloration features in the *Phrynocephalus helioscopus* species complex: *a* – 8-shape spot without red dots, *b* – 8-shape spot with red dots, *c* – without 8-shape spot without red dots

Table 5. Occurence of the chosen combination of diagnostic features of the head pattern within *Ph. helioscopus* sensu lato, %

N	Subspecies	8-shape+ red dots	8-shape	-
	All			
63	*cameranoi*	28.57	4.76	66.67
21	*helioscopus*	0	0	100
7	*meridionalis*	14.29	0	85.71
9	*saidalievi*	44.44	0	55.56
9	*sergeevi*	0	0	100
18	*karatauensis* **ssp. nov.**	5.56	66.67	27.78
22	*varius*	31.82	9.09	59.09
N	Subspecies	8-shape+ red dots	8-shape	-
	Males			
34	*cameranoi*	29.41	0	70.59
7	*helioscopus*	0	0	100
3	*meridionalis*	0	0	100
2	*saidalievi*	100	0	0
1	*sergeevi*	0	0	100
7	*karatauensis* **ssp. nov.**	14.29	71.43	14.29
8	*varius*	37.5	12.5	50
N	Subspecies	8-shape+ red dots	8-shape- red dots	-
	Females			
14	*cameranoi*	42.86	7.14	50
3	*helioscopus*	0	0	100
2	*meridionalis*	50	0	50
2	*saidalievi*	50	0	50
8	*karatauensis* **ssp. nov**.	0	62.5	37.5
4	*varius*	25	0	75

Ph. h. varius overlap almost completely in analysis of all 5 qualitative features for all studied taxa (see Fig. 5, *a*), while confidence ellipses for Ph. helioscopus ssp. and *Ph. h. cameranoi* don't overlap at all. In the analysis of 3 main qualitative features (red dots, dark spots, 8-shape) (see Fig. 5, *b*) for all studied taxa, *Ph. helioscopus* ssp. has only a little overlap with *Ph. meridionalis*. Analysis of all 5 qualitative features for 3 taxa (*Ph. h. varius*, *Ph. h. cameranoi* and *Ph. helioscopus* ssp.) showed separated confidence ellipses (see Fig. 5, *c*).

Pearson's chi-squared test rejected independence for all studied qualitative characteristics (Table 6): df for 6 under p-value = 0.05 is 12.592 and df for 12 = = 21.026, while all calculated χ^2 are higher.

B. Analysis of measurements. The results of analyses of measurements are represented in Figures 6–8. As the MCA analysis showed the difference between measurements of females and males (see Fig. 6, *b*) we assessed data for them separately. On the rest of the MCA graphs (see Figs. 6, *a*, *c*, *d*) *Ph. saidalievi* has the most distant and separated confidence ellipse from the others, but specimens from the right bank of the Syrdarya River and specimens from the environs

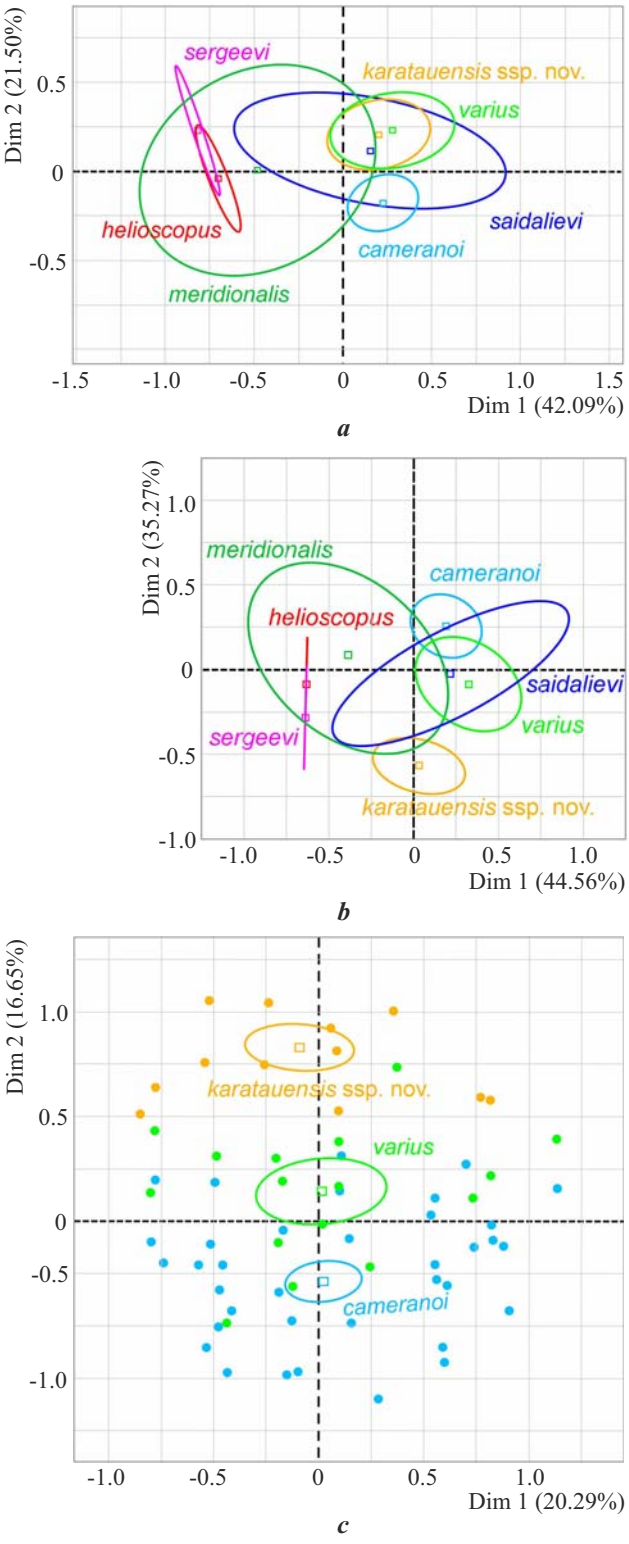

Fig. 5. MCA analysis of the head coloration characters in the *Phrynocepahlus helioscopus* species complex: *a* – of all 5 head coloration features (cap color, contrast, red dots, dark spots, 8-shape); *b* – of 3 head coloration features (red dots, dark spots, 8-shape); *c* – of 3 head coloration features (red dots, dark spots, 8-shape) for 3 lineages (*Ph. h. cameranoi*, *Ph. h. varius*, *Ph. helioscopus* ssp. "Karatau"). In *a*, *b* only confidence ellipses shown, in *c* both individual dots and confidence ellipses shown

Table 6. Results of Pearson's chi-squared test: χ^2 – chi-square score, df – degrees of freedom, *p*-value – statistical significance

Feature	χ^2	df	*p*-value
Cap color	52.301	6	0.000000001622
Contrast	30.937	12	0.002014
Red dots	53.328	6	0.000000001008
Dark spots	20.944	6	0.001878
8-shape	29.721	6	0.00004441

of Karatau Ridge have or don't have only small overlaps with confidence ellipses of other lineages. Due to the box-and-whiskers plots (Figs. 7, 8). There are no meaningful differences in measurements between specimens from Karatau Ridge and other studied lineages, values overlap either for females or males. On the contrary, *Ph. saidalievi* and specimens from the right bank of the Syrdarya River have some slight differences to the other *Ph. helioscopus* s.s. representatives in measurements both for males and females. *SVL*/*TL* (snout-vent length/tail length) for males <0.8 for both lineages from Fergana Valley and >0.8 for other lineages, for females this is <0.85 and >0.85 accordingly; *TL* for Fergana Valley lineages is more than 60 mm in females and 65 mm in males and less in other lineages. Five features slightly differ the right bank specimens from *Ph. saidalievi*: *LHL* (length of hind limb) in males from the right bank is usually 38.8–39.6 mm vs. 40–43 mm in *Ph. saidalievi* and in females 37.3–40.8 mm vs. 41–43 mm, *T* (length of tibia) is usually 10.91–12.77 mm vs. 14–15 mm in males and 10.53–13.27 mm vs. 13–14 mm in females, Int. *N* (distance between nostrils) 1.7–1.9 mm vs. 1.8–2.2 mm in males and 1.9–2.9 mm vs. 1.8 mm in females, and *P*–*N* (distance from parietal shield to nostril) 5.2–6.7 mm vs. 6.4–7.7 mm in males and 6.4–7.52 mm vs. 5.5–6.5 mm in females. But such meristic features can be unreliable due to the severe changes and damages that often happen to specimens in ethanol because of dehydration.

C. Analysis of scalation counts. The results of analyses of measurements are represented in Fig. 9, 10. As the PCA analysis showed no difference between measurements of females and males (see Fig. 9, *b*) we assessed data for them together. Again, *Ph. saidalievi* has the most distant and separated confidence ellipse,

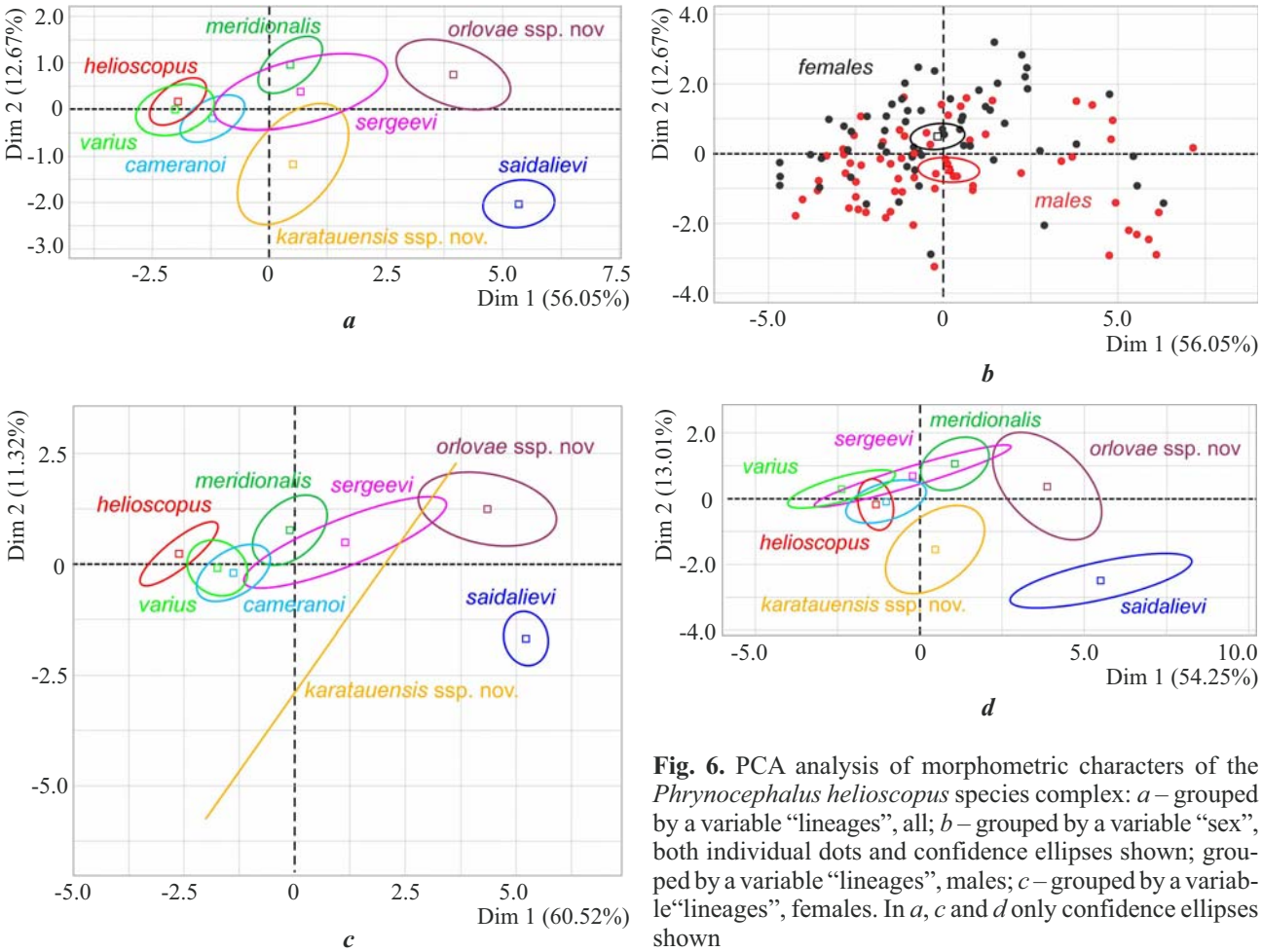

Fig. 6. PCA analysis of morphometric characters of the *Phrynocephalus helioscopus* species complex: *a* – grouped by a variable "lineages", all; *b* – grouped by a variable "sex", both individual dots and confidence ellipses shown; grouped by a variable "lineages", males; *c* – grouped by a variable"lineages", females. In *a*, *c* and *d* only confidence ellipses shown

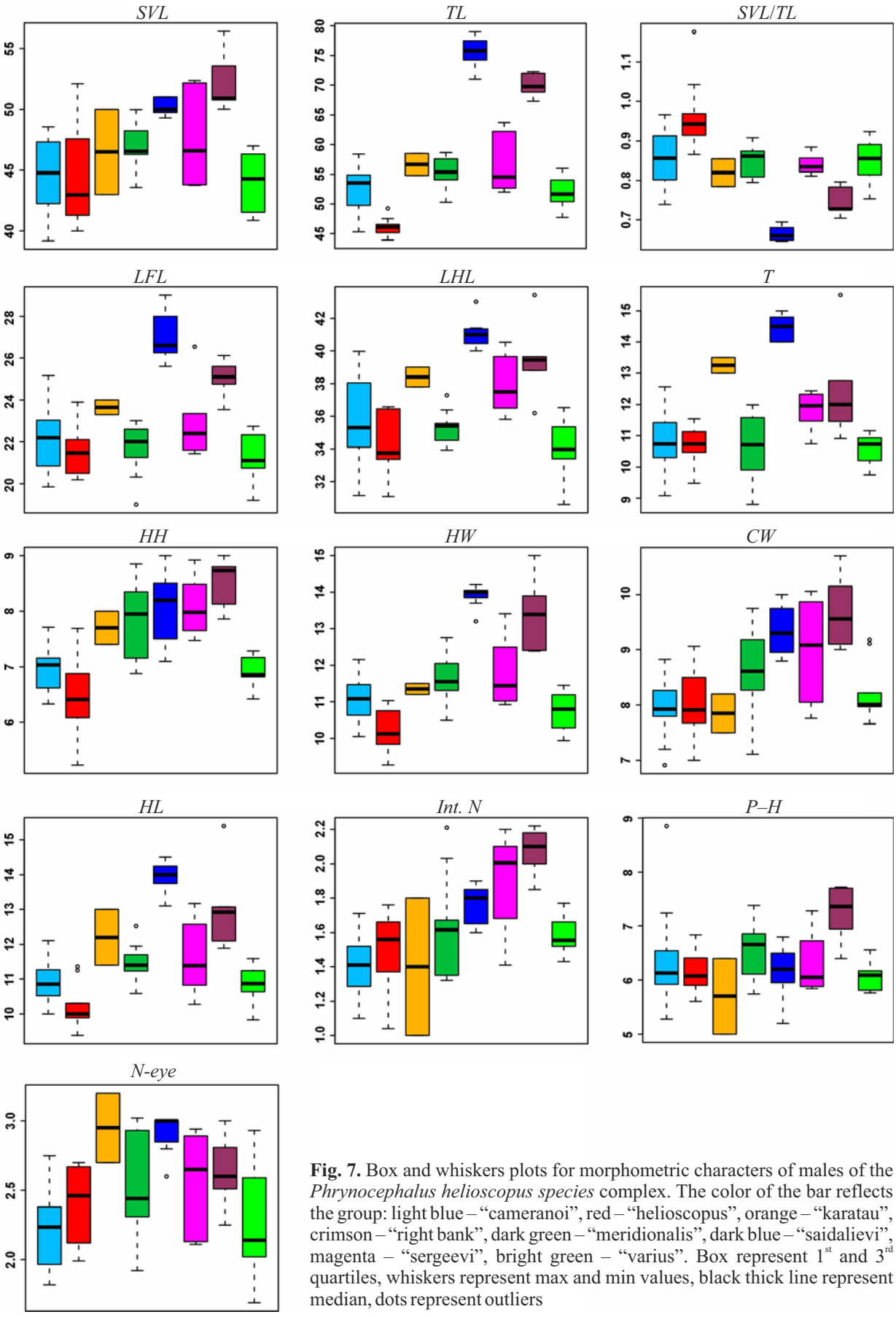

Fig. 7. Box and whiskers plots for morphometric characters of males of the *Phrynocephalus helioscopus species* complex. The color of the bar reflects the group: light blue – "cameranoi", red – "helioscopus", orange – "karatau", crimson – "right bank", dark green – "meridionalis", dark blue – "saidalievi", magenta – "sergeevi", bright green – "varius". Box represent 1st and 3rd quartiles, whiskers represent max and min values, black thick line represent median, dots represent outliers

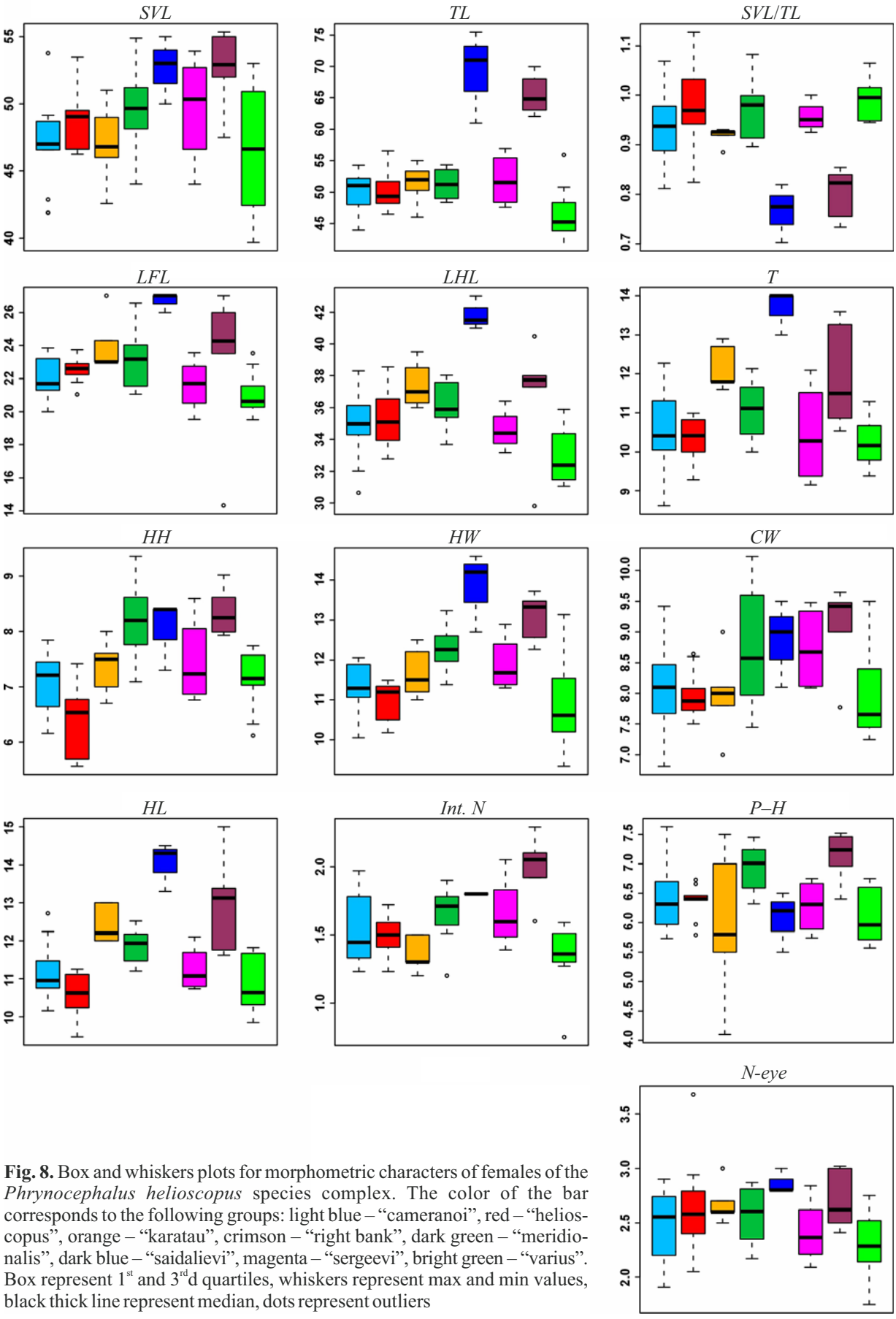

Fig. 8. Box and whiskers plots for morphometric characters of females of the *Phrynocephalus helioscopus* species complex. The color of the bar corresponds to the following groups: light blue – "cameranoi", red – "helioscopus", orange – "karatau", crimson – "right bank", dark green – "meridionalis", dark blue – "saidalievi", magenta – "sergeevi", bright green – "varius". Box represent 1st and 3rd quartiles, whiskers represent max and min values, black thick line represent median, dots represent outliers

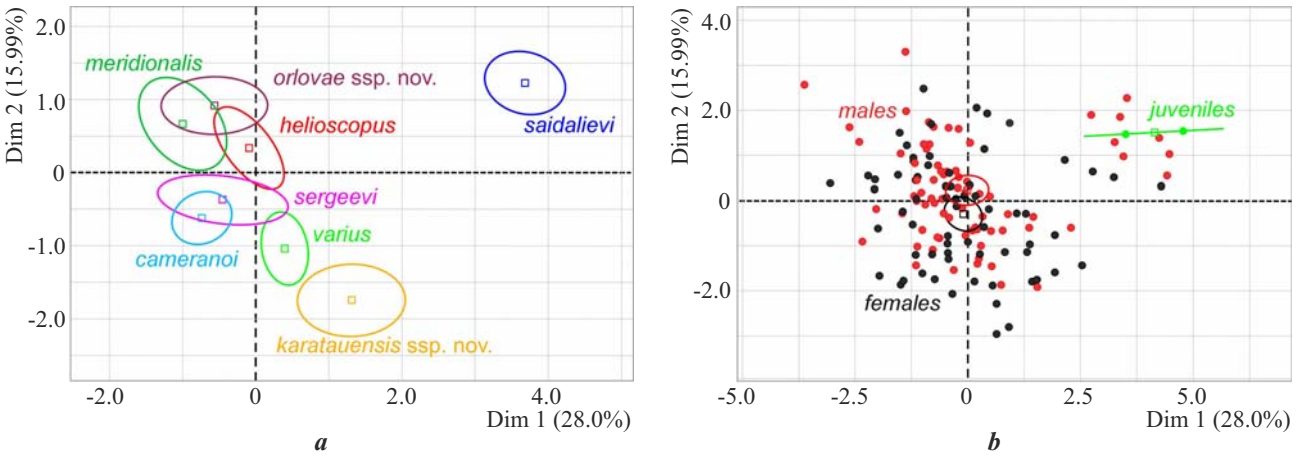

Fig. 9. PCA analysis of scalation characters of the *Phrynocephalus helioscopus* species complex members: *a* – grouped by a variable "lineages", males and females together, *b* – grouped by a variable "sex". In *a* only confidence ellipses are shown, in *b* both individual dots and confidence ellipses are shown

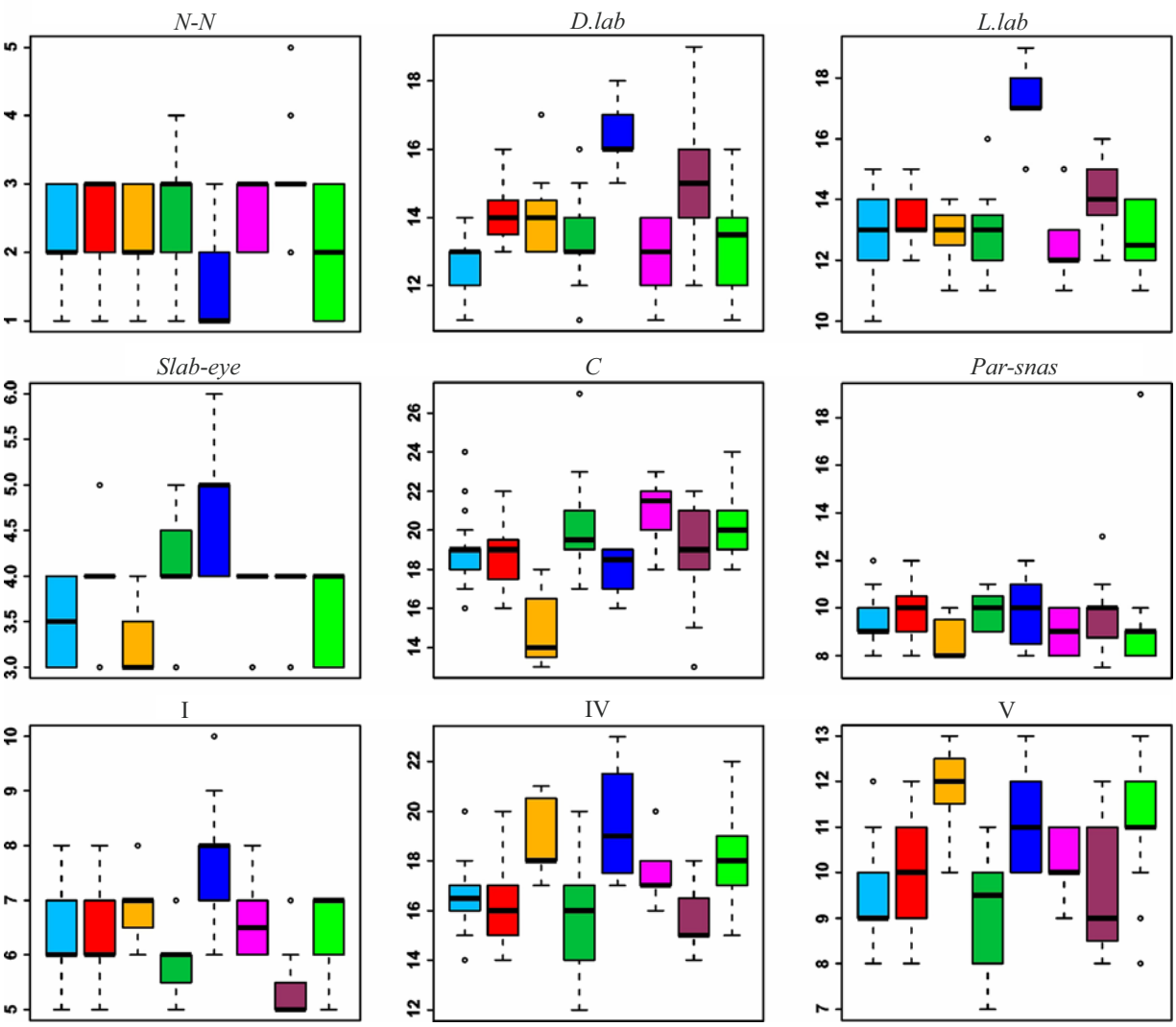

Fig. 10. Box and whiskers plots for scalation counts. The color of the bar corresponds to the following groups: light blue – "cameranoi", red – "helioscopus", orange – "karatau", crimson – "right bank", dark green – "meridionalis", dark blue – "saidalievi", magenta – "sergeevi", bright green – "varius". Box represent 1st and 3rd quartiles, whiskers represent max and min values, black thick line represent median, dots represent outliers

while specimens from the right bank of the Syrdarya River have significant overlap of confidence ellipse with other lineages (see Fig. 9, *a*). Specimens from Karatau Ridge environs are less distant than Ph. saidalievi, but their confidence ellipse doesn't overlap with other lineages. According to box-and-whiskers plots (see Fig. 10), only two features were more or less different for specimens from Karatau Ridge environs: *C* (number of scales across cap from eye to eye) usually less than in other lineages, 13–18 vs. 15–22, and V (number of scales on the underside of the V finger of the hind leg) usually more, 10–13 vs. 7–13. There is no significant difference in features between specimens from the right bank of the Syrdarya River and other *Ph. helioscopus* s.s. specimens, excluding *Ph. saidalievi*. But there are several features differing the right bank specimens from *Ph. saidalievi*: *V.lab* (number of lower labial scales) 12–16 vs. 17–19 accordingly, I (number of scales on the underside of the I finger of the hind leg) 5–6 vs. 6–9 and IV (number of scales on the underside of the IV finger of the hind leg) 14–18 vs. 17–22.

D. Diagnostic features from Solovyeva et al. (2012). For specimens in environs of Karatau Ridge, the pointed scales in cervical region above the neck spots either absent or weakly expressed; enlarged spiny scale on the shoulder is rather present, than absent; there are no displaced scales in the rows of postorbital scales; large scales above the posterior upperlabials are usually absent; the elongated scales around the trace of the yolk sac are found and absent in equal measure, there are two scales between the large anterior supraorbital and nasal plates; between the anterior edges of the eyes there is a group of large scales that form two distinct longitudinal rows between the eyes.

For specimens from the right bank of the Syrdarya River, the pointed scales in cervical region above the neck spots are absent; enlarged spiny scale on the shoulder is absent; usually there are no displaced scales in the rows of postorbital scales, only rarely; large scales among the posterior upperlabials are absent; the elongated scales around the trace of the yolk sac are found and absent in equal measure; there are 2–4 scales between the large anterior supraorbital and nasal plates; between the anterior edges of the eyes there is a group of large scales that do not form two distinct longitudinal rows between the eyes.

Family Agamidae Gray, 1827
Genus *Phrynocephalus* Kaup, 1825
***Phrynocephalus helioscopus* (Pallas, 1771)**
***Phrynocephalus helioscopus karatauensis* ssp. nov.**
Solovyeva, Dunayev, Nazarov & Poyarkov

Chresonymy:
Phrynocephalus helioscopus – Brandt in Lehmann, 1852: 333 (partim); Nikolsky, 1915 (partim).
Phrynocephalus helioscopus – Solovyeva et al., 2011.
Phrynocephalus sp. 6 – Solovyeva et al., 2023.

Holotype: ZMMU R-16120 (adult male) (Fig. 11), collected by Solovyeva E. N., Lisachev A. P. from Kazakhstan, environs of Karatau Ridge, Suzak environs (N44.237, E68.519) on 25.05.2019.

Paratypes: ZMMU R-16121 (female), ZMMU R-16123 (female), ZMMU R-17944 (female), ZMMU R-17945 (female), ZMMU R-17946 (female), ZMMU R-16125 (male) (Fig. 12). ZMMU R-16121, R-17944 were collected Solovyeva E. N., Lisachev A. P. in Kazakhstan, near Karatau Ridge, Suzak environs (N44.283, E68.418) on 25.05.2019. ZMMU R-16123, R-17945-17946 were collected Solovyeva E. N., Lisachev A. P. in Kazakhstan, near Karatau Ridge

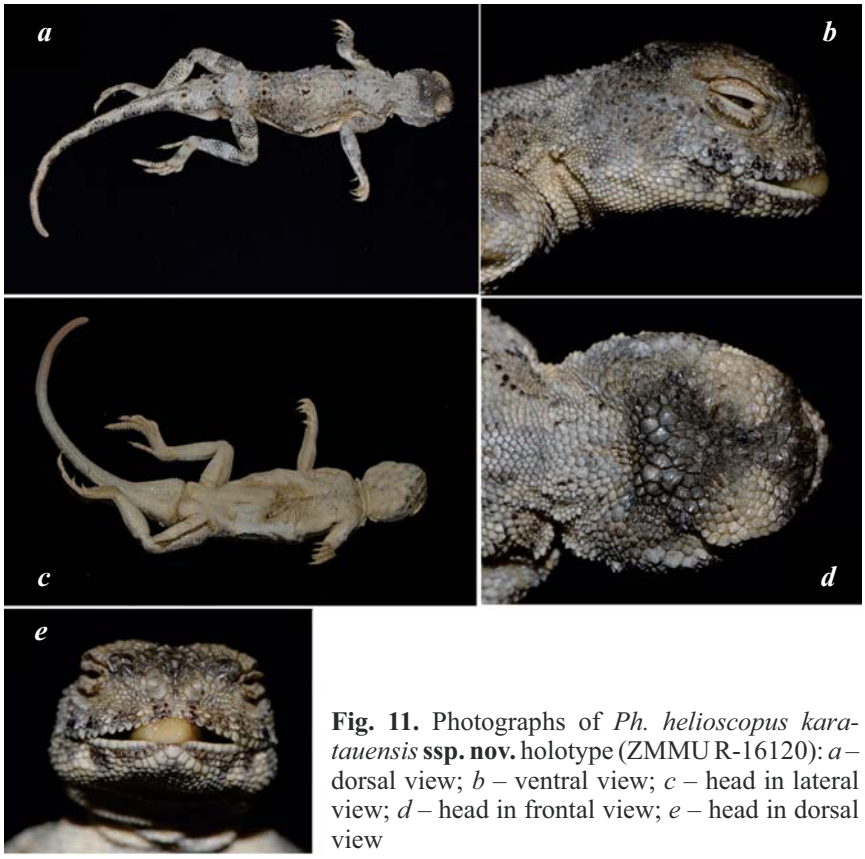

Fig. 11. Photographs of *Ph. helioscopus karatauensis* **ssp. nov.** holotype (ZMMU R-16120): *a* – dorsal view; *b* – ventral view; *c* – head in lateral view; *d* – head in frontal view; *e* – head in dorsal view

Fig. 12. Photographs of *Ph. helioscopus karatauensis* **ssp. nov**. type series: ZMMU R-16120, ZMMU R-16121, ZMMU R-17944, ZMMU R-16123, ZMMU R-17945, ZMMU R-17946, ZMMU R-12165

(N44.624, E67.671) on 26.05.2019. ZMMU R-12165 was collected in Kazakhstan, Taraz, NE Karatau Ridge, Lake Kyzylkol (N43.79, E69.54), date and collectors unknown.

Diagnosis. A member of the *Ph. helioscopus* complex based on the following combination of morphological attributes: (1) no enlarged scales with spines on the sides of the head and neck; no scales with highly developed white spines resembling a fringe on the posterior edge of the thigh and on the sides of the base of the tail, (2) on the upper surface of the neck, a transverse fold of skin clearly visible, a pair of pink or red spots with a blue border in the cervical region on the sides (Bannikov et al., 1977).

Phrynocephalus helioscopus karatauensis **ssp. nov**. can be distinguished from other subspecies of *Ph. helioscopus* by the following combination of two diagnostic morphological characteristics of the head: the presence of gray 8-shaped spot together with the absence of red dots.

Etymology. The name of the new subspecies *karatauensis* is a Latinized toponymic adjective, derived from Karatau, the name of the mountain ridge in the SE Kazakhstan, where the new subspecies was found. We suggest the "Karatau sun-watcher toad-headed agama" as a common name in English and "каратаусская такырная круглоголовка" as a common name in Russian.

Color of holotype in life (Fig. 13, according to A. S. Bondartsev (1954)). The overall background of the back ochre (pallido-ochraceus), ochre coated (ochraceus), mouse-gray (murinus), pale-gray (pallido-griseolus), dun (isabellinus), or sand (arenicolor). Often to the color of the soil.

The color of the cap and nasal area most often (84% of cases) bluish gray (cyaneo-griseus), less commonly mouse-gray (murinus), with the supraorbital area corresponding to the main shade of the back (lighter than cap).

In the cervical region, a pair of orange-pink (aurantico-roseus) or yellowish-red (flavido-rufus) small elongated spots surrounded at the outer edge by pale blue (pallido-caeruleus, caerucens) spots-stripes.

In the surface area between the shoulder and pale blue spots – a dark-sand (atro-arenicolor, cervinus), a yellow-brown (flavor-fuscus) stain bordered by a thin black line one scale thick.

In the suprascapular region, a pair of triangular spots, from yellow-brown (flavor-fuscus) to sordide-purple (sordide violaceus). Smaller spots of the same color located above the thighs and at the base of the tail. Sometimes fused or extended to each other by the angles of the base of the triangle. Above and below them – a pair of pale blue (pallido-caeruleus, caerulescens) specks with an area of 8–14 scales (sometimes they kind of frame the spot from above and below). The pale blue patch has different shapes, can be extended in the neck into a thin longitudinal area and in the middle of the back into a transverse strip. The same, but smaller (area of 3–5 scales) spots can be located chaotically («scattered» along the back).

In the middle of the back, a group of black (ater) or plum-black (prunicolor) groups of 4–8 scales in the center of a small red (fulvus, rufescens) spot bordered by a discontinuous thin line one-scale and pale blue spots.

Across the middle of the back can be up to four reddish spots in one line. Along the ridge can be up to eight pairs of pale blue spots.

Sometimes color spots (orange-pink and pale-blue) on the upper side of the body not expressed.

Thighs and tibia with transverse blackish or dark olive (atro-olivaceus) stripes and separate blackish scales.

Fig. 13. Photographs of *Ph. helioscopus karatauensis* **ssp. nov**. in life

The tail has the same spots going from the sides of the tail to the upper side, but they do not touch each other and the center line of the tail. Sometimes these spots from different sides can merge into a dark oblique stripe. The distal part of the tail dark, blackish.

Below the distal third (quarter) of the male's tail, rusty (ferrugineus), dark orange (atro-aurantiacus), brown-red (fuscato-rubidus). The basal part of the ventral side of the tail (before the preanal expansion) pale blue, often almost white. In females, the entire tail pale blue or blue (caeruleus) between the dark side patches that enter the lower side in a chess order.

The head gray (murinus, pale gray – pallido-griseolo-violaceus, gray-purple – griseoli-violaceus) with a «marble» pattern, usually the most pronounced in males.

The belly white, pale gray (pallid-griseolus), bluish-ash (caerulescenti-cinereus, caesius). On the chest of males is sometimes marked "tie" of gray specks (also found in females). The tie can reach the middle of the belly, or may be missing completely.

Variation of paratypes. Measurements and pholidosis counts of paratypes are shown in the Table 7. *SVL* 43.0–50.0 mm in males, 42.6–51.0 mm in females, *TL* – 54.8–58.5 mm in males and 50.3–55.0 in females. Length of tibia 11–14 mm in males and 11–14.3 mm in females. 13–18 scales located across the cap in different rows, nasal shields separated by 1–3 rows of longitudinally elongated scales. 17–21 subdigital plates on the fourth finger of the hind limb. The pointed scales in cervical region above the neck spots either absent or weakly expressed; enlarged spiny scale on the shoulder rather present, than absent; no displaced scales in the rows of postorbital scales; large scales among the posterior upperlabials absent; the elongated scales around the trace of the yolk sac are found and absent in equal measure, two scales between the large anterior supraorbital and nasal plates; a group of large scales that form two distinct longitudinal rows between the eyes situated between the anterior edges of the eyes.

Distribution. Kazakhstan, to the northeast and east from Karatau Ridge, in the areas of Kyzylkol Lake and Suzak settlement. It is unknown, is there a sympatry zone with *Ph. varius* or not, in the space between Karatau Ridge. and Balkhash lake (Fig. 14).

Comparisons with other subspecies. The new subspecies can be differentiated from other specimens of *Ph. helioscopus* complex by the combination of the presence of gray 8-shaped spot together with the absence of red dots on the head. If using the diagnostic key from Solovyeva et al. (2012), a new subspecies

Fig. 14. Natural habitat of *Ph. helioscopus karatauensis* **ssp. nov**. Kazakhstan, Karatau Ridge environs

has intermediate characteristics between *Ph. varius* and *Ph. cameranoi*.

Phrynocephalus saidalievi Sattorov, 1981 *Phrynocephalus saidalievi orlovae* ssp. nov. Solovyeva, Nazarov, Dunayev, Abduraupov & Poyarkov

Chresonymy:

Phrynocephalus helioscopus – Eichwald 1831: 186.

Phrynocephalus helioscopus saidalievi – Sattorov, 1981: 73.

Phrynocephalus saidalievi – Solovyeva et al., 2023

Holotype: ZMMU R-12802 (adult male) (Fig. 15), collected by Solovyeva E. N. and Dolotovskaya S. I. from Uzbekistan, Namangan, Fergana Depression, Pabskaya Steppe, near Chodak and Koshmior to the north from the road Tashkent–Kokand (N40.88, E70.8) on 31.05.2008.

Paratypes. ZMMU R-12678 (male), ZMMU R-12802 (male), ZMMU R-17935-17942 (3 males, 5 females) (Fig. 16). ZMMU R-12678 and ZMMU R-17943 were collected collected by Nazarov R. A., Zinenko N. V. in Uzbekistan, Fergana Depression, 25 km N from Kokand, foothill adyrs to the north from the road Tashkent–Kokand (N40.78, E70.97) in the end of October 2007. ZMMU R-12802 and ZMMU R-17935-17942 were collected collected by Solovyeva E. N. and Dolotovskaya S. I. in Uzbekistan, Namangan, Fergana Depression, Pabskaya Steppe, near Chodak and Koshmior (N40.88, E70.8) on 31.05.2008.

Diagnosis. A member of the *Ph. helioscopus* complex based on the following combination of morphological attributes: (1) no enlarged scales with spines on the sides of the head and neck; no scales with highly developed white spines resembling a fringe on the posterior edge of the thigh and on the sides of the base of the tail, (2) on the upper surface of the neck, a transverse fold of skin clearly visible, pair of pink or red spots with a blue border in the cervical region on the sides (Bannikov et al., 1977).

Etymology. The subspecific epithet orlovae is given in honor of Valentina Fedorovna Orlova (Zoological Museum of MSU, Moscow, Russia) in recognition of her many contributions to the studies of reptiles of arid areas of Central Asia. We suggest "Orlova's sun-watcher toad-headed agama" as a common name in English and "такырная круглоголовка Орловой" as a common name in Russian.

Color of holotype in life (Fig. 17, according to A. S. Bondartsev (1954)). The primary background color of the dorsal side of the lizard's torso ranges from mouse-gray (murinus) and smoky-gray (fumosus) to yellowish-brown (flavo-fuscus) and ochre (ochraceus).

Table 7. Measurements (mm) and pholidosis counts of adult *Ph. h. karatauensis* **ssp. nov.**

Specimen	*SVL*	*TL*	*SVL/TL*	*Int. N*	*T*	*LFL*	*LHL*	*HH*	*HL*	*HW*	*CW*	*P-N*	*N-eye*	*N-N*	*D.lab.*	*V.lab.*	*Slab-eye*	*C*	*Par-snas*	I	IV	V
№ R-16120 SE0380 male	50.0	58.5	0.86	1.8	14.0	24.0	39.0	8.0	13.0	11.5	8.2	6.4	2.7	3	13	14	3	17	10	6	18	13
№ R-16125 male	43.0	54.8	0.79	1.0	11.0	23.3	37.8	7.4	11.4	11.2	7.5	5.0	3.2	2	13	13	4	13	8	6	21	12
№ R-16121 SE0381 female	46.0	52.0	0.89	1.5	13.0	27.0	36.0	7.0	12.0	11.0	8.1	4.1	2.5	3	13	11	3	16	8	8	20	12
№ R-17944 SE0382 female	46.8	50.3	0.93	1.3	14.3	23.0	37.0	7.6	12.0	12.5	7.0	7.5	2.6	3	14	13	3	14	8	7	17	10
№ R-16123 SE0390 female	49.0	53.3	0.92	1.3	12.0	24.3	39.5	7.5	13.0	11.5	8.0	7.0	3.0	2	14	14	3	13	8	7	18	11
№ R-17945 SE0388 female	42.6	46.0	0.93	1.2	11.0	23.0	36.3	6.7	12.2	11.2	7.8	5.8	2.6	2	17	13	3	18	10	7	21	13
№ R-17946 SE0389 female	51.0	55.0	0.93	1.5	14.0	23.0	38.5	8.0	13.0	12.2	9.0	5.5	2.7	1	15	12	4	14	9	7	18	12

Note. For abbreviations, see Materials and Methods.

Fig. 15. Photographs of *Ph. saidalievi orlovae* **ssp. nov.** holotype (ZMMU R-12802): *a* – dorsal view; *b* – head in lateral view; *c* – ventral view; *d* – head in frontal view; *e* – head in dorsal view

It significantly depends on the color of the substrate, occasionally even appearing grayish-purple (griseolo-violaceus), salmon-colored (salmoneus), or bluish-green (glaucescens), and pale turquoise (pallid-callainus).

On the head, gray (or black) speckles and reddish-brown (rubiginosus) or brownish-red (fuscato-rubidus) stripes bordered by a black line, approximately one scale in width (which frames the eye areas from the inside).

In the cervical region, pairs of blood-red (sanguineus), red (ruber), or carmine-red (carminatus) spots with a blue (caeruleus), bluish (caerulescens), or pale blue (pallid-caeruleus) inner border.

Along the back and at the base of the tail, paired rusty (ferrugineus), red-brown (rubiginosus, fuscato-rubidus), sometimes even orange-red (aurantius), or chrome-orange (aurantiacus) spots, often with a black scale at the center.

On the sides of the torso, three pairs of dark or sometimes dirty-brownish-purple (sordid violaceus) spots of varying shapes (with the middle ones being less intense in color or absent).

On the sides of the tail, pairs of dark-brown (brunneus) spots or stripes arranged in a checkerboard pattern in the distal part of the tail, often with a lightening in the center of the spots.

Individual dark spots on the shins, thighs, and toes on the upper sides of the front and hind limbs. Individual white, bluish (caerulescens), or pale blue (pallid-caeruleus) speckles, each about 1–3 scales in size, may be on the thighs and upper side of the torso.

The underside of the torso white, and in males, the distal part of the tail blue (caeruleus). In females, the juvenile yellowish-green (flavor-virens, chlorinus) or greenish (viridulus, pallido-viriduls) coloration persists longer not only in the proximal but also in the distal part of the tail on the underside. The underside of the head often has grayish spots that typically blend into a marbled pattern, more distinctly expressed in males. They also often exhibit a "tie" on the chest – a longitudinally elongated spot between the front limbs across the chest area, consisting of small dark speckles whose intensity varies with the lizard's emotional state.

Variation of paratypes. Measurements and pholidosis counts of paratypes are shown in the Table 8. *SVL* 50.0–56.4 mm in males, 47.5–55.3 mm in fema-

Fig. 16. Photographs of *Ph. saidalievi orlovae* **ssp. nov.** type series: ZMMU R-12768, ZMMU R-17943, ZMMU R-12802, ZMMU R-17935-17942

Fig. 17. Photographs of *Ph. saidalievi orlovae* **ssp. nov**. in life

les, *TL* 62.1–72.3 mm in males and 50.3–69.9 in females, *SVL*/*TL* 0.7–0.8 in males and 0.73–0.84 in females. Length of tibia 10.9–15.5 mm in males and 10.5–13.6 mm in females. 13–22 scales located across the cap in different rows, nasal shields separated by 2–5 rows of longitudinally elongated scales. On the fourth finger of the hind limb 15–18 subdigital plates. The pointed scales in cervical region above the neck spots absent; enlarged spiny scale on the shoulder absent; usually no displaced scales in the rows of postorbital scales, only rarely; large scales among the posterior upperlabials absent; the elongated scales around the trace of the yolk sac found and absent in equal measure; 2–4 scales between the large anterior supraorbital and nasal plates; between the anterior edges of the eyes situated a group of large scales that do not form two distinct longitudinal rows between the eyes.

Distribution. Uzbekistan, Fergana Valley, right bank of the Syrdarya River (Fig. 18).

*Comparisons with other subspecie*s. The new subspecies can be differentiated from other specimens of *Ph. helioscopus* s.s. complex by the *SVL*/*TL* ratio, although not from *Ph. s. saidalievi*: in both *Ph. saidalievi* subspecies *SVL*/*TL* for males <0.8 and >0.8 for other lineages, for females this is <0.85 and >0.85 accordingly. *Ph. saidalievi* orlovae can be differentiated from *Ph. s. saidalievi* by *V. lab*. (number of lower labial scales): 12–16 in *Ph. saidalievi orlovae* vs. 17–19 in *Ph. saidalievi saidalievi*.

DISCUSSION

Our results show significant differentiation between populations of *Ph. helioscopus* from Karatau Ridge and other representatives of the *Ph. helioscopus* complex. According to Solovyeva et al. (2023), even the formal threshold of $p = 3.0\%$ in COI mtDNA gene suggests a significant differentiation of *Phrynoce-*

Table 8. Measurements (mm) and pholidosis counts of adult *Ph. s. orlovae* **ssp. nov.**

Specimen	*SVL*	*TL*	*SVL/TL*	*Int. N*	*T*	*LFL*	*LHL*	*HH*	*HL*	*HW*	*CW*	*P-N*	*N-eye*	*N-N*	*D.lab.*	*V.lab.*	*Slab-eye*	*C*	*Par-smas*	1	IV
№ R-12802 male	50.02	68.81	0.73	2.1	12.77	25.6	39.64	7.86	11.89	12.38	9	7.36	2.25	5	14	14	3	20	10	5	15
№ R-17935 male	50.75	69.75	0.73	2.22	12	24.76	39.44	8.13	12.1	12.4	9.1	6.94	2.81	3	15	15	3	21	13	5	14
№ R-17936 female	55.32	64.8	0.85	2.29	13.27	23.84	37.5	8.62	13.38	13.48	9.44	7.32	3.02	3	16	15	4	22	9	5	14
№ R-17937 female	52.82	69.96	0.76	1.6	11.55	24.7	37.97	8	11.62	12.26	9.65	6.96	2.41	4	14	14	4	18	8	5	15
№ R-17938 female	51.98	62.06	0.84	2	11.45	14.33	29.81	9.02	13.3	13.36	9	7.52	2.63	3	12	12	4	22	11	5	18
№ R-17939 male	50.89	72.27	0.7	2.18	10.91	23.54	36.19	8.8	13.07	13.39	10.15	7.7	2.6	3	15	14	4	18	10	6	15
№ R-17940 male	53.56	67.27	0.8	1.85	11.46	26.12	43.41	8.73	12.92	13.9	9.56	7.72	2.51	3	14	13	4	21	10	5	15
№ R-17941 female	47.5	64.78	0.73	2.1	10.53	26	40.48	7.99	12.95	13.73	9.48	7.46	2.61	3	16	16	4	19	10	5	16
№ R-17942 female	52.99	63.09	0.84	1.92	10.86	23.51	37.3	7.93	11.76	12.56	7.77	7.15	2.5	3	12	13	4	18	9	5	16
№ R-12678 male	56.4	72.0	0.78	2.0	15.5	25.1	38.8	9.0	15.4	15.0	10.7	6.4	3.0	3	19	16	4	15	7.5	7	18
№ R-17943 female	55.0	68.0	0.81	2.1	13.6	27.0	38.0	8.5	15.0	13.3	9.4	6.4	3.0	2	18	15	4	13	8.5	7	17

Note. For abbreviations, see Materials and Methods.

a

b

Fig. 18. Natural habitat of *Ph. saidalievi orlovae* **ssp. nov.** Pabskaya Steppe adyrs: *a* – the view from the hill, *b* – the plain in front of the adyrs

phalus taxa warranting taxonomic recognition; this level of divergence was more congruent with the traditional morphology-based species delimitation schemes in Phrynocephalus than higher divergence values. Our data agree with Solovyeva et al. (2023) and Wu et al. (2023) in recognizing *Ph. h. cameranoi* as a sister taxon of *Ph. helioscopus karatauensis* **ssp. nov**. from Karatau Ridge, while geographically closely distributed *Ph. varius* appears to be phylogenetically far rela-ted to the latter. The uncorrected *p*-distance in the COI gene between *Ph. helioscopus karatauensis* **ssp. nov**. and *Ph. h. cameranoi* is 5.1%, which is generally higher than the interspecific genetic distance observed in the genus *Phrynocephalus* (Solovyeva et al., 2023).

The Fergana Sunwatcher Toad-headed agama, *Ph. saidalievi* was described from the "...vicinity of the Kanibadam village (Tajik part of the Fergana Valley)" in Tajikistan (Sattorov, 1981; p. 7). Kanibadam village is situated approximately at 40º 17′ N, 70º 25′ E, on the left bank of the Syrdarya River, therefore, we assume that the type series of *Ph. saidalievi* was collected from the left bank of the river. *Phrynocephalus saidalievi orlovae* **ssp. nov**. was recorded in the Uzbeki part of the Fergana Valley on the right bank of the Syrdarya River. The samples of *Ph. saidalievi* used in our study were collected on the left bank of the Syrdarya River, though we lack specimens or sequences of *Ph. saidalievi* from the area close to the type locality in the Tajik part of the Fergana Valley. Therefore, further sampling across the Fergana Valley is required to obtain a better understanding of *Ph. saidalievi* differentiation and phylogeography. We argue that it is highly likely that the Syrdarya River valley might serve as a barrier separating the range of *Ph. saidalievi* in two geographic populations, corresponding to two subspecies: *Ph. s. saidalievi* on the left bank and *Ph. saidalievi orlovae* **ssp. nov**. on the right bank. It is remarkable that similar patterns were recently reported for other desert-associated species of reptiles in the Fergana Valley, for example in the *Alsophylax geckos* (Nazarov et al., 2023).

The morphological differences between *Ph. helioscopus karatauensis* **ssp. nov**., *Ph. saidalievi orlovae* **ssp. nov**., and other representatives of the *Ph. helioscopus* species complex may be sometimes slight and intermediate in the museum specimens, but some of the examined features appear to be good enough for identification of these taxa. Interestingly, the diagnostic key for identification of *Ph. helioscopus* species complex members proposed by Solovyeva et al. (2012), if applied to the Karatau Ridge population described herein as *Ph. helioscopus karatauensis* **ssp. nov**., leads to the dichotomy between *Ph. h. varius* and *Ph. h. cameranoi*. Indeed, when compared to these two taxa, the newly described subspecies *Ph. helioscopus karatauensis* **ssp. nov**. shows somewhat 'intermediate' state condition in the character of the presence of elongated scales surrounding the umbilical marking: some specimens have elongated scales around the umbilical marking, while others lack such scales. However, the large scales above the posterior supralabials are generally absent, which closely resembles the morphology observed in *Ph. varius*.

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ЗАПОЛНЕНИЕ ПРОБЕЛОВ В СИСТЕМАТИКЕ ТАКЫРНЫХ КРУГЛОГОЛОВОК: ОПИСАНИЕ ДВУХ НОВЫХ ПОДВИДОВ ВИДОВОГО КОМПЛЕКСА *PHRYNOCEPHALUS HELIOSCOPUS* (REPTILIA, SQUAMATA, AGAMIDAE)

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Аннотация. Комплекс видов *Phrynocephalus helioscopus* тщательно изучался в последние годы, однако несколько филогенетических линий оставались недостаточно изученными. На основании морфологических различий и дивергенции последовательностей генов COI (мтДНК) в настоящей статье в составе видового комплекса *Phrynocephalus helioscopus* описаны два новых подвида: *Ph. helioscopus karatauensis* **ssp. nov**. из окрестностей хребта Каратау в Казахстане и *Ph. saidalievi orlovae* **ssp. nov**. с правого берега р. Амударья в Ферганской долине в Узбекистане. Два новых подвида можно отличить от других представителей видового комплекса по сочетанию нескольких морфологических признаков.

Ключевые слова: Средняя Азия, Казахстан, Узбекистан, *Phrynocephalus helioscopus*, хребет Каратау, *Phrynocephalus saidalievi*, Ферганская долина, ДНК-штрихкодирование, морфометрия, окраска

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