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Morphological peculiarities and their possible bearing on the taxonomic status of the Crimean montane populations of the Steppe Viper, *Vipera renardi* (Christoph, 1861)

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Abstract. The external morphology of more than 1000 specimens of *Vipera renardi* (Christoph, 1861) from the Crimean peninsula and from the eastern and southern continental parts of Ukraine was examined and analyzed by statistical, multivariate methods. It turned out that, in contrast to central and northern Crimean as well as continental lowland populations, which correspond to the diagnosis of *V. renardi,* the South Crimean, montane populations have lower scale counts. According to the results of the multivariate analysis, the latter populations form a separate group, the level of divergence from the former being comparable with subspecies or even species-level differences within the *V. renardi* complex. The populations most distinct from typical *V. renardi* (s. str.) are those from the northern macroslope of the main range of the Taurian ridge. Compared with typical *V. renardi,* the montane populations are characterized by smaller size, lower numbers of circumocular and supralabial shields, ventral plates, intercanthal, parafrontal and loreal shields, a lighter body colouration and a less frequent colour pattern with fragmented zig-zag bands. These morphological peculiarities together with the partly isolated distribution of the Crimean montane population suggest that their subspecific recognition may be warranted.

Introduction

Data on the morphological variation of steppe vipers (*Vipera renardi*) in the Crimean peninsula are scanty and dispersed. The first paper devoted to the geographical variation of *V. renardi* in Crimea was published comparatively recently (Karmyshev 1999) and the data presented in this paper concern only the Sivash region populations (without separation of Crimean and South Ukrainian mainland material) and Kerch peninsula. Due to the low number of specimens, they do not reflect the peculiarities of variation in this species in Crimea. Comparison between steppe vipers from Crimea and Povolzhje (European Russia) shows that Crimean populations are characterized by lower ventral counts (Karmyshev, Tabachishchin, 2003). Before, Shcherbak (1966) had pointed out, that some Crimean specimens of *V. renardi* possess a low number of ventrals (min. 129). These researchers referred the Crimean steppe vipers to the widely distributed eastern Europe and Central Asian subspecies *V. ursinii renardi* (Christoph, 1861). In present time, this subspecies is considered as the nominotypic subspecies of the polymorphic species *V. renardi* (Kotenko et al. 1999; Nilson, Andrén 2001).

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In the last years, detailed morphological descriptions of some Crimean peripheral populations (Kukushkin 2004 b, 2005 a, 2005 b) were published, but attempts to summarize the available data have not been made.
Therefore, the aim of this paper is a general analysis of morphological variation in the steppe viper in Crimea based on extensive material. For the first time, data on the least known and the southernmost populations from Crimean mountains were used. Even the presence of steppe vipers there was uncertain for a long period. For instance, Brauner (1905) neglected the presence of steppe vipers in Crimean mountains, and for the first time it was found on the northern macroslope of the main range only in 1928 (Puzanov 1931). Only after the second half of the 20th century it was established, that *V. renardi* is comparatively widely distributed in the central and eastern parts of the northern macroslope of the main range (Shcherbak 1966; Kukushkin 2004 a).
Besides, we present data on the morphological variation of vipers from the Black sea coast of Kerch peninsula. The south-western part of Kerch peninsula is part of the alpine Crimean fold mountains and is presently considered as part of the Crimea Mountain (Atlas Krym, 2003), however its relief has a more hilly or even flat character.

Materials and Methods

25 morphological characters describing pholidosis, body proportions and coloration pattern, both previously used (Vedmederya 1989; Nilson, Andrén 2001) and proposed by us, were recorded from 1000 specimens of *V. renardi* from different populations of Crimea and

eastern and southern regions of mainland Ukraine and adjacent regions of Russia (Kursk, Belgorod) (Fig. 1). 23 characters were used in a multivariate analysis (Table 1). The morphology of the majority of the snakes, collected by the first author in 1992-2005 years in Crimea, in the Kujuk-Tuk island (Kherson region) and in the vicinities of Tokmak (Zaporizhzhja region) was studied in living specimens. Material from southern and eastern mainland regions of Ukraine in collections of the Museum of Nature at Kharkiv National University (MNKNU) was studied by the second author (Fig. 1).

The statistical treatment was performed using the software package Statistica 6.0. Patterns of geographical variation were investigated by principal component analysis (PCA) on 23 standardized characters, based on discrete, meristic and continuous variables (Table 1). The specimens were grouped on the basis of geographical origin and within the same habitats (see Fig. 1). Since *Vipera renardi* shows significant sexual dimorphism in many characters, the data from male and female specimens were analyzed separately in parallel analyses. All characters were standardized to zero mean and unit standard deviation.

Character	PC 1, males	PC 2, males	PC 1, females	PC 1, females
L. – body length, mm	-	-	-	-
L. cd. – tail length, mm	-	-	-	-
Vent. – number of ventral scales (including preventral)	0.219	0.249	0.299	-0.141
S. cd. – number of subcaudal scales	0.192	-0.016	0.175	-0.265
Gul. – number of gular scales	0.129	0.279	0.189	0.052
Sq. – number of scales around midbody	0.224	0.231	0.228	-0.126
Lab. – number of supralabial scales	0.247	0.192	0.281	-0.175
SLab. – number of sublabial scales	0.154	-0.087	0.081	0.229
Or. – number of scales around eye (without supraocular)	0.272	0.022	0.313	0.005
Ic. – number of scales between apical, canthal and frontal shields	0.097	-0.318	0.304	0.072
Pf. – number of parafrontal scales, in both sides together	0.286	-0.127	0.296	-0.141
S. sf. – number of scales in contact with frontal and supraocular shields simultaneously	-0.135	0.331	-0.029	0.199
Lor. – numer of loreal scales	0.259	-0.240	0.240	0.246
A2 – presence of two apical scales, in %	-0.060	-0.332	-0.116	-0.131
ON – presence of contact between upper preocular and nasal shields, in %	0.257	0.188	0.251	-0.200
S.pn. – number of small scales, touched to the posterior edge of nasal shield, not including upper preocular	0.297	0.084	0.067	-0.120
O.L. – number of subocular in contact with supralabial scales, (right+left)/2	-0.218	0.271	-0.288	-0.136
G.3/4 – presence of granule between third and fours supralabial and subocular row, in %	0.302	-0.013	0.262	0.258
G.4/5 – presence of granule between fourth and fifth supralabial and subocular row, in %	0.161	-0.325	0.139	0.192
Fpr. – presence of fragmented parietal scales	0.271	-0.019	0.260	-0.232
Fr.-Par. – break of normal contact between frontal and parietals shields, in %	-0.061	-0.134	0.028	-0.398
FZ – cases of fragmentation of ventral stripe (break at least in one point), in %	0.232	0.071	-0.088	-0.331
Inf. – number of sublabial scales in contact with the first mandible scale, (left+right)/2	0.201	-0.043	0.069	0.344
Scr. – presence of small keels on lateral (adjacent with belly) row of body scales, in %	-0.037	0.321	-0.041	-0.175
ZW – number of zigzag band windings	0.133	0.134	0.188	0.136

Table 1. Characters and their eigenvector coefficients in relation to the first and second principal components of the male and female PCAs.

Results

The principal component analysis gives similar results for males and females. The ordinations of sample means along the first two principal components, resulting from analyses using 23 characters are shown in Fig. 2. The ordination plots show an indication of geographical variation, with southern populations from mountainous regions of Crimea (Low Mountains, Chatyrdag) and Kerch peninsula (Chauda) having the lowermost first component scores. The highest scores have samples from north-western pre-Siwash parts of Crimea (N. Sivash), Kujuk-Tuk island in Sivash and continental steppe populations from Zaporizhzhja region (Tokmak). Populations from central parts of Crimea and from steppe and forest-steppe territories of Ukraine have intermediate scores. The second principal component differentiates Low Mountain and mainland steppe populations (Steppe) in females against all the rest populations, and all continental populations against all Crimean populations in males. Eigenvector coefficients given in Table 1 show, that the list of characters responsible for this separation slightly differ between males' and females' PCAs (listed according descending

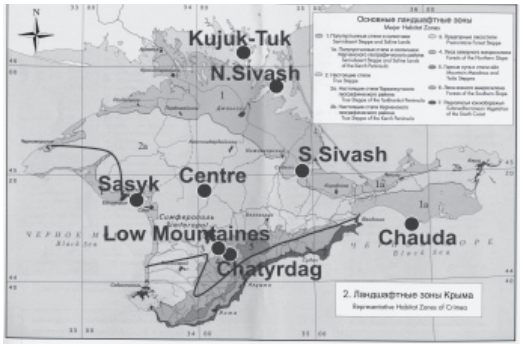

Figure 1. Localities of samples: "Forest-Steppe" (not shown), Kharkiv and Poltava regions, Ukraine; Kursk and Belgorod regions, Russia; "Steppe" (not shown), Kharkiv, Kherson, Zaporizhzhja, Dnipropetrovs'k, Donets'k regions, Ukraine; "Tokmak" (not shown), Tokmak vicinities, Zaporizhzhja region; "Kujuk-Tuk", Kujuk-Tuk island, Kherson region; "Nothern Sivash", nothern pre-Sivash part of Crimea, Dzhankoy and Krasnoperekopsk districts; "Southern Sivash", South-eastern part of pre-Sivash part of Crimea, Nizhnegorsk, Sovetsky and Kirovskoe districts; "Centre", Krasnogvardejsky district; "Sasyk", western coast of Crimea, Sasyk lake, Saki district; "Chauda", Cape Chauda, Kerch peninsula, Leninsky district; "Low Mountains", Low mountains of the northern macroslope of the main range of Taurian ridge, Simferopol district; "Chatyrdag", Middle mountains of the northern macroslope of the main range of Taurian ridge, northern slopes of Chatyrdag jajla, Simferopol district.

of absolute value of Eigenvector coefficient character and first PC axis: males – G.3/4, S.pn., Pf., Or., Fpr., Lor., ON, Lab., FZ, Sq., Vent., O.L., Inf., etc.; females – Or., Ic., Vent., Pf., O.L., Lab., G.3/4, Fpr., ON, Lor., Sq., etc.).

Data on the morphology of some Ukrainian mainland and Crimean populations of steppe vipers are presented in Table 2. In comparison with typical *V. renardi*, occupying continental Ukraine and the western part of the Crimean coast of Sivash lagoon, vipers from the southern part of Crimea are characterized by rather small size (L. ♂ < 500 mm, L. ♀ < 600 mm; L. cd. ♂ < 70 mm, L. cd. ♀ < 60 mm), less number of ventral, orbital, supralabial, intercanthal, parafrontal and loreal scales, frequent absence of contact between upper preocular scale and nasal shield and not fragmented parietal shields. Thus, the pholidosis of steppe viper populations from southern Crimea is oligomerized. The most prominent differences in almost all characters exist between viper samples from the southernmost population Chatyrdag mountain massif and Kujuk-Tuk island, which corresponds with the diagnosis of *V. renardi* according to Nilson and Andrén (2001).

The body coloration of the steppe viper in the investigated territory is rather variable. In continental Ukraine and pre-Sivash region of Crimea specimens with typical coloration of *V. renardi* prevail. They have sand-gray ground colour of dorsum and dark-brown or black zigzag bands. In the mountainous forest territory of Crimea the percentage of specimens with pale yellow-brown dorsal coloration and bright-brown or light-brown zigzag bands is increased, while greenish-gray coloured specimens, which are present in small numbers in almost all the remaining populations, are absent. More than a half of all snakes in the Chauda population possess a pronounced yellowish or reddish shade of dorsal coloration. The general tone of coloration can frequently be yellowish-gray with ochre, citric, yellowish-olive or reddish shade. In southern Crimea the frequency of specimens with fragmented zigzag is significantly lower, in particular if compared with the Kujuk-Tuk island population. In all populations studied, most individuals have dark bellies with light dots, but in the southern populations of Crimea the belly is lighter, and there are also no black-bellied individuals, which in turn form a rather large part of continental Ukraine populations (up to 53 % males and 14 % females). Only in the mountainous forest zone (Low Mountains, Chatyrdag) and in Cape Chauda isolated specimens with a light pink-gray and black-white (without dots) belly could be found.

Discussion

The originality of the montane Crimean population (Chatyrdag) and their edge position in the range of *V. renardi* allow to speculate about the existence of an undescribed subspecies of the steppe viper in this region. Similarities of several pholidosis and coloration features of montane Crimean *V. renardi* with Caucasian species of the *Vipera ursinii* group – *Vipera lotievi*

	Sample											
Character	**Forest-steppe**		**Kujuk-Tuk**		**Nothern Sivash**		**Chauda**		**Low Mountains**		**Chatyrdag**	
	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀
L. max	463	600	561	595	527	637	434	537	467	543	441	541
L. cd. max	64	65	76	67	77	63	61.5	52	69.5	52	63	54
Vent.	(24)	(30)	(28)	(31)	(28)	(78)	(29)	(43)	(10)	(10)	(25)	(15)
	137-147	139-151	137-147	142-151	138-147	139-150	136-146	139-149	139-146	140-146	134-142	137-142
	141.3±0.5	144.4±0.6	144.2±0.3	147±0.3	141.8±0.5	144.5±0.3	140.9±0.5	143.0±0.4	141.2±0.1	142±0.6	138.4±0.4	139.7±0.4
S. cd.	(25)	(29)	(35)	(31)	(28)	(62)	(27)	(44)	(10)	(10)	(24)	(15)
	28-38	20-29	32-42	24-31	32-39	24-31	31-37	22-28	33-38	26-29	33-37	24-27
	34.0±0.5	25.7±0.3	36.3±0.3	28.2±0.3	36±0.3	26.5±0.2	33.6±0.3	25.0±0.2	34.6±0.5	27.3±0.3	34.8±0.2	25.3±0.30
Or.*	(25)	(30)	(65)	(60)	(36)	(93)	(29)	(47)	(10)	(10)	(24)	(15)
	8.5-11	8-10.5	7-10.5	8-11	8.5-11	8-11	8-11	7.5-12	7-9	8-9.5	7.5-9	8-9.5
	9.4±0.1	9.0±0.1	9.5±0.08	9.8±0.1	9.6±0.1	9.6±0.1	9.2±0.1	9.2±0.1	8.9±0.2	8.8±0.1	8.3±0.1	8.5±0.1
Lab.*	(25)	(30)	(30)	(23)	(30)	(75)	(29)	(42)	(10)	(9)	(24)	(15)
	9-10	8.5-10	8-10	8-10.5	8.5-11	7.5-10	8.5-9.5	8-9.5	7-9	8.5-9.5	8-9	8-9
	9.2±0.1	9.1±0.1	9±0.08	9.3±0.1	9.1±0.1	9.1±0.04	8.8±0.17	8.9±0.1	8.9±0.1	9±0.1	8.6±0.1	8.6±0.1
Ic*	(25)	(29)	(64)	(60)	(36)	(91)	(29)	(46)	(10)	(10)	(24)	(15)
	3-8	2-9	3-9	3-12	3-10	3-11	2-7	2-9	3-7	3-5	2-7	2-5
	4.2±0.3	5.3±0.3	4.4±0.2	5.3±0.2	4.8±0.3	5.5±0.2	4.2±0.3	4.7±0.2	4.3±0.4	3.8±0.3	4.3±0.2	3.7±0.2
Pf	(25)	(29)	(62)	(57)	(33)	(95)	(27)	(47)	(10)	(10)	(25)	(15)
	2-11	3-9	4-15	4-19	3-14	3-18	3-10	2-13	2-10	4-11	2-8	2-8
	5.8±0.5	6.2±0.3	7.8±0.3	10.2±0.4	7.2±0.5	8.4±0.6	5.7±0.4	6.8±0.4	5.5±0.7	6.8±0.8	4.7±0.3	4.7±0.5
Lor.*	(25)	(30)	(55)	(55)	(32)	(74)	(28)	(45)	(10)	(10)	(23)	(14)
	3-6	2-7	3-7	3-8	4.5-8	2.5-7.5	2.5-6	2.5-7	2-5	2.5-6	2-6	4-5.5
	4.1±0.1	4.5±0.2	4.9±0.1	5.5±0.1	5.5±0.2	5.5±0.1	4.4±0.2	5.2±0.1	3.5±0.4	3.6±0.3	4.2±0.2	4.6±0.1
Sq.	(25)	(32)	(62)	(54)	(53)	(106)	(30)	(50)	(10)	(10)	(24)	(15)
	21-22	17-23	19-22	21-24	20-23	21-23	20-21	20-21	20-21	21	19-21	21-22
Fpr. %	(50)	(58)	(168)	(168)	(114)	(232)	(80)	(100)	(18)	(20)	(50)	(36)
	14.0±4.9	27.6±5.9	18±3.0	38.1±3.8	11.4±3.0	33.6±3.1	2.5±1.8	10±3.0	0	20±8.9	0	0
FZ. %	(21)	(25)	(88)	(79)	(61)	(116)	(40)	(46)	(10)	(10)	(26)	(17)
	42.9±10.8	26.1±8.8	62.5±5.2	50.6±5.6	52.5±6.4	17.2±3.5	15±5.7	15.2±5.3	10.0±9.5	0	30.8±9.05	0
A2. %	(58) 1.8±1.7		(161) 5.6±1.8		(178) 18.5±2.9		(95) 3.2±1.8		(20) 20.0±8.9		(42) 14.3±5.4	
ON. %	(112) 63.4±4.5		(348) 84.8±1.9		(320) 85.3±2.0		(188) 41±3.6		(38) 60.5±7.9		(84) 42.9±5.4	

Table 2. Morphology of some Ukrainian populations of *V. renardi* (n; lim.; X+Sx). * – (left+right)/2

Table 3. Climatic characteristics of the *V. renardi* localities in Crimea and Ukraine (Andrienko et al. 1977, Vazhov 1977, Marynych 1982, Podgorodetskiĭ 1988, Atlas Krym 2003). *KH – coefficient of moistening Ivanov-Vysotsky (relation annual precipitation and annual evaporation).

Climatic characters	**Region of Crimea (altitude, m above sea-level)**				
	South of forest-steppe, Eastern Ukraine (50-200) (Forest-steppe and Steppe)	Northern pre-Sivash region (< 20) (Northern Sivash)	Kerch Black sea bank (< 120) (Chauda)	Western bank (< 20) (Sasyk)	Mid Mountains of Main range (600 – 1100) (Chatyrdag)
Average temperature, °C:					
July (August)	20 – 21	22.5 – 23.2	23.3 – 23.4	22.1 – 23.2	15.4 – 17.0
January (February)	-6.0 -8.0	-3.0 -1.7	+0.3 +0.8	-0. . +1.0	-3.7 -3.0
Whole year	6.0 – 7.0	10 – 10.3	10.6 – 11.5	11 – 11.5	6.4 – 8
Annual precipitation, mm	400-500	339 – 370	329 – 376	342 – 358	595 – 960
*KH**	0.6-1.4	0.38 – 0.40	0.38 – 0.40	0.40 – 0.46	0.80 – 1.80
Length of period with positive temperature, days	150-160	170 – 193	214 – 227	220 – 230	147 – 165

Nilson, Tuniev, Orlov, Höggren et Andrén, 1995 and *Vipera erivanensis* (Reuss, 1933) can be explained with high probability as convergent adaptation to mountainous conditions. But, at least basing on general external morphology, these populations are most closely related to the western group of *V. renardi*.

Populations of low Mountains and Kerch peninsula (Chauda) together with populations of the southern part of steppe Crimea (Southern Sivash, Sasyk) are less distinct from typical *V. renardi* and in some cases demonstrate an intermediate position between it and the southern Crimean populations (Table 2, Fig. 2). In our opinion, such situation could be the result of at least two stages of colonization of Crimean peninsula by steppe vipers and their subsequent intergradation: a relict, which remained in the mountains and the southern part of plain Crimea during the Neopleistocene, and *V. r. renardi*, which according to Shcherbak (1966) came to Crimea from the north during the "xerothermic" stage of the Holocene. Introgressive hybridization is widely represented in small European vipers, in particular in the *V. kaznakovi* (Orlov, Tuniyev 1990) and *V. berus* complexes (Milto, Zinenko 2005). Under laboratory conditions, *V. renardi* is successfully hybridized with related Caucasian species – *V. erivanensis* and *V. lotievi* (Shyriaev 2005).

Gradually increasing differences in a southward direction from typical *V. renardi* can hardly be considered as clinal variation. The high level of similarity between Main range populations (Chatyrdag, Low Mountains) and southern Crimean steppe populations (Chauda, Sasyk) is impossible to explain by climatic or other habitat parameters, as the investigated populations live under very contrasting ecological conditions (Table 3). In the Main range region (Chatyrdag, Low Mountains) vipers occur in bushes (*Pyrus eleagnifolia*, *Prunus stepposa*, *Crataegus* sp., *Rubus* sp., *Juniperus oxycedrus*), in the open sites in broadleaved forest (*Quercus petraea* + *Carpinus betulus*, *Fraxinus exselsior* + *Acer campestre*, *C. betulus* + *Fagus orientalis*), in stony forest-steppe near mountain plateaus with dominance of European-Mediterranean, Fore Asian, Crimean-Caucasian and endemic Crimean elements (*Quercus pubescens*, *Carpinus orientalis*, *Sorbus graeca*, *Cornus mas*, *Cotinus coggygria*, *Acer steveni*, *Cotoneaster tauricus*, *Ligustrum vulgare*, *Spiraea hypericifolia*, *Jasminum fruticans*, *Juniperus hemispherica*, *J. foetidissima*, *Asphodeline taurica*, *Cerastium bibersteinii*, *Thymus tauricus*, *Stipa lithophila*, etc.), in mountain-meadow steppe (*Festuca rupicola* + *Carex humilis*) up to 900-1100 m above sea level, but do not go further then 1 km into mountain plateaus. Morphologically similar with mountainous populations, the Kerch population of Cape Chauda inhabits semidesert and meadow steppes with dominance of *Artemisia taurica*, *A. lerchiana, Festuca valesiaca*, *Lynosiris villosa*, *Limonium meyeri*, *Achillea nobilis, Ferula caspica*, *Malabaila graveolens* and little participation of the Mediterranean species (*Capparis spinosa*) and climatically more similar to habitats of pre-Sivash populations (Table 3). In the pre-Sivash and Western regions of Crimea *V. renardi* occupies typical habitats: lowland semidesert steppes and halophytic meadows, more rarely – psammophytic steppes.

It should be mentioned, that in the northern macroslope of Main range of Crimean mountains, together with *V. renardi,* two other endemic species of Caucasian origin

dominate in the herpetocenosis: *Lacerta agilis tauridica* Suchow, 1927 (sensu Kalyabina et al. 2004) and *Darevskia lindholmi* (Lantz et Cyrén, 1936) (Shcherbak 1966, Kalyabina-Hauf et al. 2004, Kalyabina-Hauf, Ananyeva 2004). It is supposed, that *Emys orbicularis* L., 1758 from Mountainous Crimea and Kerch peninsula is also represented by an endemic form (Kotenko et al. 2005).

It is interesting, that the geographical variation of the sand lizard, which is syntopic with the steppe viper in Crimea, shows the same tendencies: oligomerization of the pholidosis in south-western direction, low levels of differences between mountainous populations and northern Crimean and southern Ukrainian populations as compared with differences between other subspecies or species in the complex, intermediate character states between *L. a. exigua* (Eichwald, 1831) and *L. a. tauridica* in populations of pre-mountainous and southern plain parts of Crimea (Sviridenko, Kukushkin 2005; Peskov, Brovko 2005). It is rather probable, that stages of colonization of Crimea and its routes in *L. agilis* and *V. renardi* were similar.

The evidence presented here suggests a late Pleistocene origin of the steppe viper populations of the mountainous and adjacent plain parts of Crimea. During the Wuerm glacial on Crimean jajlas, only weak glaciation was developed (Ena et al. 1991), however, reptile populations could survive and persist cold periods in refuges on slopes and in southern parts of the plains. Remains of relict termophilic vegetation (*Juniperus excelsa*, *Taxus baccata*) in gorges of the eastern slope of Chatyrdag confirm such assumption. However, further analyses of possible correlations between morphology and habitat parameters have to be carried out, which could alternatively explain the observed interpopulational differences, before taxonomic conclusions can be drawn; a molecular genetic approach seems indispensable.

References

Andrienko, T.L., Bilyk, G.I., Bradis, E.M., Golubets, M.A., Makhaeva, L.V., Rubtsov, N.I., Tkachenko, V.S., Shelyag-Sosonko, Yu.R. (1977): Geobotanichne raĭonirovannya Ukrayins'koyi RSR [Geobotanical division of Ukrainian SSR]: Kŷyiv, Naukova dumka (in Ukrainian).

Atlas avtonomnoyi respubliki Krym [Atlas of the autonomous republic Crimea] (2003): Kŷyiv, Simferopol' (in Ukrainian).

Brauner, A.A. (1905): Predvaritel'noe soobshchenie o presmykayushchikhsya i zemnovodnykh Kryma, Kubanskoĭ oblasti, Volynskoĭ i Varshavskoĭ guberniĭ [Preliminary communication about reptiles and amphibians of the Crimea, Kubanskaya region, Volynskaya and Varshavskaya provinces]. In: Zapiski Novoross. obshchestva estestvoispytateleĭ **28**, p. 1-14. Odessa, Tipo-Litografia A. Shul'tse (in Russian).

Vazhov, V.I. (1977): Agroklimaticheskoe raĭonirovanie Kryma [Agroclimatic division of the Crimea]. Trudy Nikitskogo botanich. sada. **71**. Yalta, GNBS: 92-120 (in Russian).

Vedmederya, V.I. (1989): Gadyuki podroda *Pelias* [Adders of the subgenus *Pelias*]. In: Rukovodstvo po izucheniyu zemnovodnykh i presmykayushchikhsya, p. 35-39, Shcherbak, N., Eds., Kiev, Naukova Dumka (in Russian).

Ena, V.G., Kuznetsov, V.G., Lysenko, N.I. (1991): Okhrana prirodoproyavleniĭ pleistotsenovykh landshaftov Gornogo Kryma [Protection of the natural phenomenons of the Pleistocene landscapes of the Mountain Crimea]. In: Ékologicheskie aspekty okhrany prirody Kryma, p. 11-14. Kiev, UMK VO (in Russian).

Kalyabina-Hauf, S.A., Milto, K.D., Ananyeva, N.B., Joger, U., Kotenko, T.I., Wink, M. (2004): Reevaluation of the status of *Lacerta agilis tauridica* Suchov, 1926. Russ. Journ. of Herpetol. **11**, **1**: 65-72.

Kalyabina-Hauf, S.A., Ananyeva, N.B. (2004): Phylogeography and intraspecies structure of the widely distributed Sand Lizard, *Lacerta agilis* L., 1758 (Lacertidae: Sauria: Reptilia) (case study of mithochondrial cytochrome b gene). Trudy ZIN RAN. **302**. ZIN RAN, St. Petersburg: (in Russian).

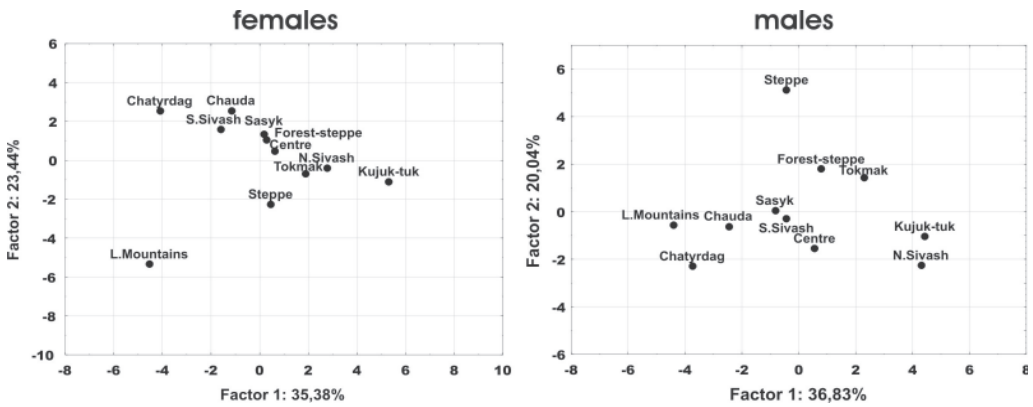

Figure 2. The ordination plots of the sample means along the first two principal components. Left – females, right – males. Sample names as in Fig. 1.

Karmyshev, Y.V. (1999): Rasprostranenie i morfologicheskaya izmenchivost' stepnoĭ gadyuki Kryma i sopredel'nykh territoriĭ [Distribution and morphological variability of the Steppe Viper of the Crimea and adjacent territories]. In: Problemy izucheniya fauny yuga Ukrainy, p. 54-59. Odessa, Astroprint, Melitopol', Branta (in Russian).

Karmyshev, Y.V. (2001): Rasprostranenie i taksonomicheskiĭ status stepnoĭ gadyuki (*Vipera ursinii*) na yuge Ukrainy [Distribution and taxonomyc status of the Steppe Viper (*Vipera ursinii*) in the south of Ukraine]. In: Voprosy gerpetologii, p. 117-119. Pushchino, Moscow. (in Russian).

Karmyshev, Yu.V., Tabachishchin, V.G. (2003): Ékologo-morfologicheskaya kharakteristika krymskikh i nizhnevolzhskikh populatsiĭ stepnoĭ gadyuki (*Vipera* (*ursinii*) *renardi*) [Ecocogical-morphological description of the Crimean and Lower Volga populations of the Steppe Viper (*Vipera* (*ursinii*) *renardi*)]. In: Zmei Vostochnoi Evropy, p. 26-29. Tol'yatti, IÉVB RAN (in Russian).

Kotenko, T.I., Morozov-Leonov, S.Y., Mezhzherin, S.V. (1999): Biochemical genetic differentiation of the Steppe Viper (*Vipera ursinii* group) in Ukraine and Romania. In: Abstracts of 10th Ord. Gen. Meet. S.E.H., p. 88-90. Irakleio.

Kotenko, T., Zinenko, O., Guicking, D., Sauer-Güerth, H., Wink, M., Fritz, U. (2005): First data on the geographic variation of *Emys orbicularis* in Ukraine: mtDNA haplotypes, coloration, and size. In: Herpetologia Petropolitana: Proceedings of 12th Ord. Gen. Meet. S.E.H., Ananyeva, N., Tsinenko, O., Eds., St. Petersburg – Moscow: 43-46.

Kukushkin, O.V. (2004a): Rasprostranenie, reproduktivnye osobennosti, razmerno-vozrastnaya struktura i sovremennoe sostoyanie populatsii stepnoĭ gaduki, *Vipera renardi* (Christoph, 1861), v Krymu [Distribution, reproductive peculiarities, size-ages structure and contemporary state of the populations of the Steppe Viper, *Vipera renardi* (Christoph, 1861), in the Crimea]. In: Karadag. Istoria, geologia, botanika, zoologia, kniga **1**. Simferopol', SONAT: 397-424 (in Russian).

Kukushkin, O.V. (2004b): Materialy k izucheniyu gerpetofauny Vostochnogo Kryma [Data on study of the herpetofauna of the Eastern Crimea]. In: Letopis' prirody Karadagskogo prirodnogo zapovednika NANU. **20**. Simferopol', SONAT: 191-215 (in Russian).

Kukushkin, O.V. (2005a): O morfologicheskom svoeobrazii stepnoĭ gaduki (*Vipera renardi*) Krymskogo nagor'ya [On morhological originality of the Steppe Viper (*Vipera renardi*) of the Crimean upland]. In: Zapovedniki Kryma: zapovednoe delo, bioraznoobrazie, ékoobrazovanie, chast' 2, p. 148-153. Simferopol', Ékologia i mir (in Russian).

Kukushkin, O.V. (2005b): O stepnoĭ gaduyke (*Vipera renardi*) na zapadnom poberezh'e Kryma [About Steppe Viper (*Vipera renardi*) on the western coast of the Crimea]. In: Izuchenie i sokhranenie prirodnykh ékosistem zapovednikov lesostepnoĭ zony, p. 311-314. Kursk, Tsentral'no-Chernozëmnyĭ gos. zapovednik (in Russian).

Marynych, A.M., Lan'ko, A.I., Shcherban', M.I., Shyshchenko, P.G. (1982): Fysychna geografiya Ukrayins'koyi RSR [Physical geography of Ukrainian SSR]. Kŷyiv, Vyshcha shkola (in Ukrainian).

Milto, K.D., Zinenko, O.I. (2005): Distribution and morphological variability of *Vipera berus* in eastern Europe. In: Herpetologia Petropolitana: Proceedings of 12th Ord. Gen. Meet. S.E.H., Ananyeva, N., Tsinenko, O., Eds., St. Petersburg – Moscow: 64 – 73.

Nilson, G., Andrén, C. (2001): The Meadow and Steppe Vipers of Europe and Asia: the *Vipera (Acridophaga) ursinii* complex. Acta Zool. Acad. Sci. Hungaricae **47**, **2-3**: 87-267.

Orlov, N.L. and Tuniev, B.S. (1990): Three species in the *Vipera kaznakowi* complex (Eurosiberian group) in the Caucasus: their present distribution, possible genesis, and phylogeny. Asiatic Herpetol. Research **3**: 1-36.

Peskov, V.N., Brovko, A.Yu. (2005): Izmenchivost' meristicheskikh priznakov folidoza i morfologicheskaya differentsiatsia *Lacerta agilis* (Lacertidae, Sauria, Reptilia) na territorii Ukrainy [The variation of meristic traits of pholidose and morphological differentiation of the *Lacerta agilis* (Reptilia, Lacertidae) in the territory of Ukraine]. In: Materialy pershoyi konf. Ukrayins'kogo gerpetologichnogo tovarystva, p. 128-134. Kŷyiv, Zoomuzeĭ NNPM NANU (in Russian).

Podgorodetskiĭ, P.D. (1988): Krym: Pryroda [The Crimea: Nature]. Simferopol', Tavriya.

Puzanov, I.I. (1931): Predvaritel'nye itogi izucheniya fauny pozvonochnykh Krymskogo zapovednika [Preliminary results of the study of the vertebrates fauna of Crimean reserve]. In: Sbornik rabot po izucheniyu fauny Krymskogo gos. zapovednika, p. 5-39. Moscow – Leningrad, Gos. meditsinskoe izd-vo (in Russian).

Sviridenko, E.Yu., Kukushkin, O.V. (2005): K morfologicheskoĭ kharakteristike prytkoĭ yashcheritsy (*Lacerta agilis tauridica* Suchow, 1927) yugo-zapadnoi chasti Krymskogo nagor'ya [To the morphological description of the Sand Lizard (*Lacerta agilis tauridica* Suchow, 1927) of the southern-western part of the Crimean upland]. In: Izuchenie i sokhranenie prirodnykh ékosistem zapovednikov lesostepnoĭ zony, p. 348-352. Kursk, Tsentral'no-Chernozëmnyĭ gos. zapovednik (in Russian).

Shiryaev, K.A. (2005): New data on reproductive biology of Caucasian species of the genus *Vipera*. In: Herpetologia Petropolitana, p. 213-215. Proceedings of 12th Ord. Gen. Meet. S.E.H., Ananyeva, N., Tsinenko, O., Eds., St. Petersburg – Moscow.

Shcherbak, N.N. (1966): Zemnovodnye i presmykayushchiesya Kryma. Herpetologia Taurica [Amphibians and Reptiles of the Crimea. Herpetologia Taurica]. Kiev: Naukova Dumka: (in Russian).

Vyrabotka prioritetov: novyi podkhod k sokhraneniyu bioraznoobraziya v Krymu. Rezul'taty programmy „Otsenka neobkhodimosti sokhraneniya bioraznoobraziya v Krymu" [Priority-setting in conservation: a new approach for Crimea. Results of the programm „Valuation of necessity of the biodiversity conservation in the Crimea"] (1999). - Washington, Biodiversity Support Programm (in Russian).