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DISTRIBUTION AND MORPHOLOGICAL VARIABILITY OF *Vipera berus* IN EASTERN EUROPE

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Keywords: Nikolsky's viper, common adder, Viperidae, *Vipera berus*, *Vipera nikolskii*, systematics, distribution, morphological analysis, hemipenes structure, Eastern Europe.

INTRODUCTION

The first the black viper inhabiting Southern Russia was described in 1771 by P. S. Pallas. This morph was cited under different names (*Coluber melanis*, *Vipera melanis*, *Coluber scytha*, *Vipera scytha*, *Vipera melaenis*, *Vipera melaenis* var. *scytha*, *Vipera berus* var. *prester*, *Vipera prester*, *Pelias prester*, *Coluber berus* morpha *prester*, *Pelias berus* var. *nigra*) for many years. Situation changed when V. N. Grubant, A. V. Rudaeva and V. I. Vedmederja (1973) proposed to distinguish the black forest-steppe adder as a full species *Vipera prester*. These authors listed morphological and ecological differences between this species and *Vipera berus*. In 1986 the same authors changed the proposed name and described a new taxon *Vipera nikolskii*. The specific status of *Vipera nikolskii* was accepted by most specialists and included in subsequent herpetological accounts (Golay et al., 1993; Nilson and Andrén, 1997; Ananjeva et al., 1998; Bozhansky, 2001). Nevertheless, this point of view was subjected to criticism (Bakiev et al. 1999; 2000; Joger et al., 1997).

The black viper, *Vipera nikolskii*, from southern parts of the European Russia and Ukraine currently has unclear taxonomical status and distribution. The status of this viper varied from color morph to full species during last 230 years. This work is aimed to determine the diagnostic characters and status of this species. It is based on analysis of external morphology and data on distribution.

MATERIAL AND METHODS

About 1000 specimens from Russia, Ukraine, Moldova, and Belarus' stored in the collections of Zoological Institute Russian Academy of Science, St. Petersburg (ZISP), Museum of Nature of Kharkov National University (MN KNU), National Museum of Natural History Ukrainian Academy of Sciences (NNHM NASU), Zoological Museum of Moscow State University (ZMMU) as well as alive snakes in the nature were examined in this work. We recorded 10 morphological characters traditionally used in systematic of Viperidae (Vedmederja, 1989) and some others, which are useful in *Vipera berus-nikolskii* determination. For each specimen the following characters were used in multivariate analysis: number of ventral scales (ventralia, Ventr.); number subcaudal scales (subcaudalia, S.cd.); number of scales around midbody (squamae dorsalis, Sq.) except of ventral shields; number of supralabial shields (labialia, Lab.); number of sublabial shields (sublabialia, S.lab.); number of scales around the eye (circumocularia, C.oc.); number of subocularia (subocularia, S.oc.) rows; number of the loreal scales between canthal, circumocular, nasal and supralabial shields (lorealia, Lor.); number of scales between apical, canthal and frontal shields (intercanthalia, Ic.); number of shields between supraocular, frontal and parietal shields (parafrontalia, Pf.).

The following features were checked: shape and proportions of the frontal shield (frontale), number of rows of the postocular shields (postocularia, p.o.), type of the dorsal coloration pattern in adults — totally black and black with light elements (visible zigzag, light spots on supralabials and ventrals, reddish throat), venom fluid coloration (colorless in *nikolskii* and yellow in *berus*) and albumin composition (electrophoresis data). Patterns of geographical variation were studied by means of principal component analysis (PCA) using Statistica 6.0 Software Package. Samples were united according to regional distributional principle. Females and males were studied separately because the sexual dimorphism is well expressed. The arithmetical mean of morphological characters for samples were used in analysis.

Hemipenes were everted in fresh killed snakes and preserved in formalin. Terminology on hemipenial morphology follows Keogh (1999). Coloration was determined on the basis of color standard (Bondartsev, 1954).

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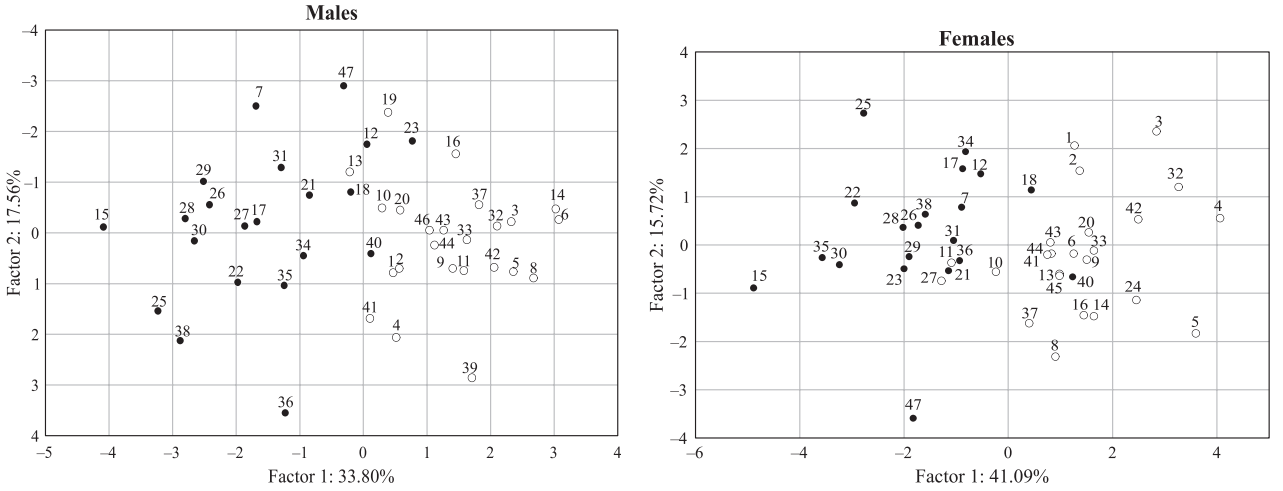

Fig. 1. Ordination of samples along the first two principal components. Numeration of samples is the same as in Table 1. Black dots are populations with predominance of black-colored snakes.

Distributional maps were completed as a result of the collection materials study. Data of geobotanical and geomorphological maps and maps of Glaciations in Europe (Atlas..., 1962, 1984; Markov et al., 1965; Paleogeography of Europe..., 1982; Markova et al., 2002) were used for interpretation and discussion of the viper's distribution.

RESULTS

In Fig. 1, the ordination of samples along the first two principal components is given, resulting from PC analysis, separately for males and females (samples list see in *Appendix*). The results were similar but not identical for males and females. The ordination plots demonstrate the existence of two not clearly distinct groups. In both sexes all populations are distributed and in the case of females are divided on two groups along the first PC axis. The first group is completed by populations from northern and north-western part of the Eastern Europe. The second group includes populations from Southern and South-Eastern part of this territory. Also we considered the third group of populations that include individuals with transitional morphological characters between the two previous groups. Groups' 95% variation interval of samples' average values of morphological characters, which were calculated for 16 samples of Nikolsky's viper, 22 samples of males and 23 samples of females of common adder and 11 samples of vipers from mixed populations, are given in Table 1.

We recorded several types of coloration patterns: total melanistic, partially melanistic and normally patterned

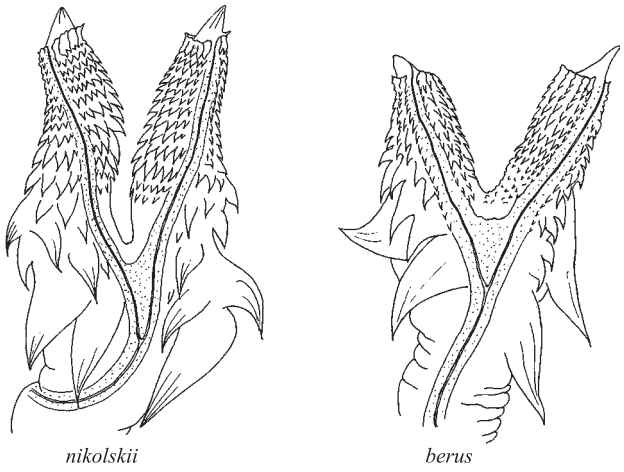

Fig. 2. Hemipenes of *V. b. nikolskii* and *V. b. berus*, sulcate view.

type. Full description of coloration places in chapter "Redescription." Comparison of hemipenial structure demonstrated good differences in size and structure: hemipenes of common adder are short and compact, while Nikolsky's viper hemipenes are elongated and deeply forked (Fig. 2). Redetermination of collection materials and analysis of literature data allow the description of the Nikolsky's viper range (Fig. 3).

DISCUSSION

Some characters that were proposed by Vedmederja et al. in 1986 as diagnostic for Nikolsky's viper, correlate very well with first principal components (Fig. 4). These

are increased number of ventral, supralabial, sublabial shields and scale rows around midbody. We support the significance of these morphological characters for distinguishing the viper's taxa. An increased number of loreal scales (between preocular, canthal, nasal and supralabial shields), high frequency of registration of two complete or almost complete subocular rows (up to 77.7% of female and 23.3% male specimens have 2 rows), increased number of loreal scales (between preocular, canthal, nasal and supralabial shields) are characters that, according to the results of our analysis, are diagnostic too.

Also shown is a high frequency of two rows of postocular shields encountered in Nikolsky's viper. The ratio of the height of second and third supralabials as 0.72 – 1.15 (0.93 ± 0.01) and ratio of height and width of rostral shield as 1.24 – 2.23 (1.65 ± 0.02) were given earlier (Vedmederja et al., 1986).

According to our results Nikolsky's viper has on average a larger full body length.

According to published data, the skull of Nikolsky's viper differs from the common adder skull by 11 measurements and 18 indexes in males and by 5 measurements and 9 indexes in females. They differ in shape of basisphenoid-basioccipital suture: it is clearly W-shaped in both forms, but suture angles are broader, less divided and less extended in *V. nikolskii* (Koldoba, 1983). The venom of Nikolsky's viper is colorless (yellowish in common adder), has less proteolysis activity (Orlov et al., 1990; Murzajeva et al., 1995) and has differences in albumen composition (Davljatov, 1985; Starkov and Utkin, 2001).

Our data on hemipenial morphology (Fig. 2) contradict those of Joger et al. (1997), which may be the consequence of imperfect methodology.

Nikolsky's viper is characterized by some peculiarities of coloration pattern in non melanistic specimens. It is worth mentioning that black coloration can appear in *V. berus berus* populations independently (Forsman, 1993; Monney et al., 1995; Völkl and Thiesmeier, 2002). Inter-

TABLE 1. Variation of Selected Morphological Characters in Populations of *Vipera berus nikolskii* (16 samples), *Vipera berus berus* (22 male and 23 female samples), and *Vipera berus* ↔ *nikolskii* (11 samples), Given as 95% Section of Mean Variability

	V. b. nikolskii		*V. berus berus*		*V. berus berus*/*V. berus nikolskii*	
Ventralia ♀♀	153 – 154.2		147.4 – 149.7		149.7 – 153.3	
Ventralia ♂♂	149.7 – 151.6		143.6 – 145.3		146.5 – 148.5	
Subcaudalia ♀♀	32.0 – 33.3		30.4 – 31.8		31.8 – 32.9	
Subcaudalia ♂♂	40.7 – 42.3		37.8 – 39.9		39.4 – 41.4	
Squamae dorsalis ♀♀	19, 0.5%; 20, 1.5%; 21, 74.0%; 22, 7.2%; 23, 16.8%	21.2–21.7	19, 11.4%; 20, 3.5%; 21, 79.0%; 22, 4.4%; 23, 1.7%	20.6–21.0	19, 4.7%; 21, 81.3%; 22, 6.3%; 23, 7.8%	21.0–21.5
Squamae dorsalis ♂♂	21, 77.3%; 22, 6.7%; 23, 16%	21.3–21.6	19, 17.5%; 20, 2.8%; 21, 71.6%; 22, 3.8%; 23, 4.3%	20.5–20.9	19, 2.2%; 20, 1.1%; 21, 82.3%; 22, 3.3%; 23, 11.1%	21.0–21.5
Labialia ♀♀	9.0 – 9.2		8.6 – 8.8		8.6 – 9.0	
Labialia ♂♂	8.8 – 9.1		8.6 – 8.8		8.7 – 8.9	
Sublabialia ♀♀	10.7 – 11.0		9.9 – 10.3		10.3 – 10.8	
Sublabialia ♂♂	10.6 – 10.8		10.1 – 10.4		10.2 – 10.6	
Circumocularia ♀♀	9.5 – 10.0		9.2 – 9.7		8.8 – 9.8	
Circumocularia ♂♂	9.5 – 10.1		9.2 – 9.6		9.0 – 9.7	
Subocularia ♀♀	1, 31.4%; 1–1.5, 14.4%; 1.5, 28.1%; 1.5–2, 11.8%; 2, 14.4%	1.3 – 1.6	1, 83.8%; 1–1.5, 8.1%; 1.5, 6.9%; 1.5–2, 0.6%; 2, 0.6%	1.0 – 1.1	1, 67.2%; 1–1.5, 11.5%; 1.5, 13.1%; 1.5–2, 1.6%; 2, 6.6%	1.1–1.3
Subocularia ♂♂	1, 62%; 1–1.5, 12%; 1.5, 17.2%; 1.5–2, 2.1%; 2, 6.8%	1.1 – 1.3	1, 97.4%; 1–1.5, 1.3%; 1.5, 1.3%	1.0	1, 88.4%; 1–1.5, 7.0%; 1.5–2, 1.2%; 2, 3.5%	1.0–1.1
Intercanthalia ♀♀	8.1 – 9.9		8.7 – 10.4		8.5 – 10.3	
Intercanthalia ♂♂	7.6 – 9.4		8.3 – 10.0		7.4 – 10.9	
Parafrontalia ♀♀	7.6 – 8.9		7.6 – 8.5		7.4 – 8.6	
Parafrontalia ♂♂	7.0 – 8.4		7.3 – 8.1		6.9 – 7.7	
Lorealia ♀♀	4.1 – 4.7		2.9 – 3.2		3.4 – 4.1	
Lorealia ♂♂	3.3 – 3.7		2.5 – 2.9		2.5 – 3.3	
Lfr/Ltfr	0.77 – 1.87		0.87 – 1.66		0.45 – 1.78	

For Sq. and S.oc. given frequencies of different states of the character have been pooled for all samples.

estingly, it is absence of typical sexual dichromatism in dorsum pattern.

An important result of the analysis is a strong heterogeny within both groups of vipers. Well distinguished populations and populations exhibiting a tendency to similarity with another taxon are represented. Some populations have intermediate positions and can not be attributed to any taxa. In our opinion, this situation results from introgressive hybridization. A successful hybridization in captivity was shown earlier (Zinenko, 2003; Kurilenko, 2003). In some cases a sharp transition between two forms was observed in the contact zone. In Cherkassy Oblast', near Kanev, a *berus*-like adder inhabits the left bank of the Dnepr River and Nikolsky's viper inhabits the right bank. In Sumy Oblast', Putivl District both forms live on the same bank of the Seym river, but in different landscapes. However, traces of introgression are present in both cases (Zinenko and Ruzhilenko, 2003; our data). The broad intergradational zone between these taxons covers territory from the middle part of Dnepr in Ukraine to the Volga basin in Russia and includes samples from a third group (see *Appendix*). The intermediate position of vipers from this area has been reported by other authors (Sokolov, 1979; Murzaeva et al., 1995; Bakiev et al., 2000; Peskov et al., 2003; Starkov and Utkin, 2001, 2003; Zinenko and Ruzhilenko, 2003).

The most morphologically specific vipers were recorded far from contact zone with *V. berus berus*. Among samples of vipers studied by us, snakes from Khopyor River in Saratov Oblast' (Russia) and Kirovograd Oblast' (Ukraine) have very well expressed morphological characters of Nikolsky's viper. In contrast, clear populations of the common adder inhabit the northwestern part of the East European Plain. The big rivers like Dnepr, Seym, and Volga crossing the Russian Plain in a direction from north to south serve as dispersal routes for vipers. Generally,

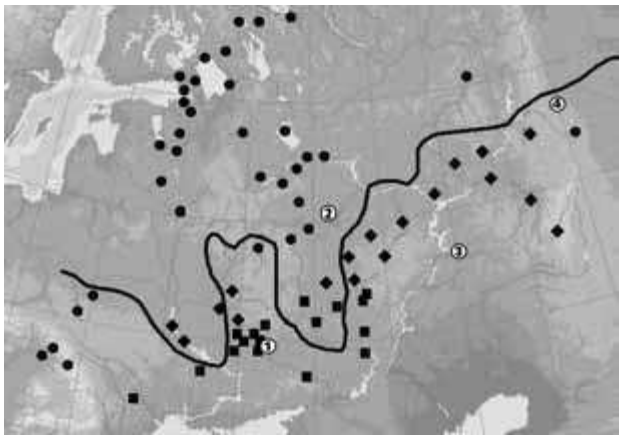

Fig. 3. Distribution *V. b. nikolskii* and *V. b. berus* in the Eastern Europe. ●, localities of *V. b. berus*; ■, *V. b. nikolskii*; ◆, populations with mixed morphological characters. Black solid line indicates southern border of the glacial landscapes (maximal distribution of the Dnepr Glaciation). *1*, Ukraine, Kharkov vicinities, between Bezludovka and Vasitschevo, Udy river, terra typica of *Vipera nikolskii* Vedmederja, Grubant et Rudaeva, 1986; *2*, Russia, Vladimir Oblast', near Gusevo, Cherseevo village, terra typica of *Vipera berus* var. *sphagnosa* Krassawzeff, 1932; *3*, Russia, Samara, terra typica of *Coluber melanis* Pallas, 1771; *4*, Russia, Sverdlovskaya Oblast', near Blagodat settl., Kushva st., terra typica of *Coluber scytha* Pallas, 1773.

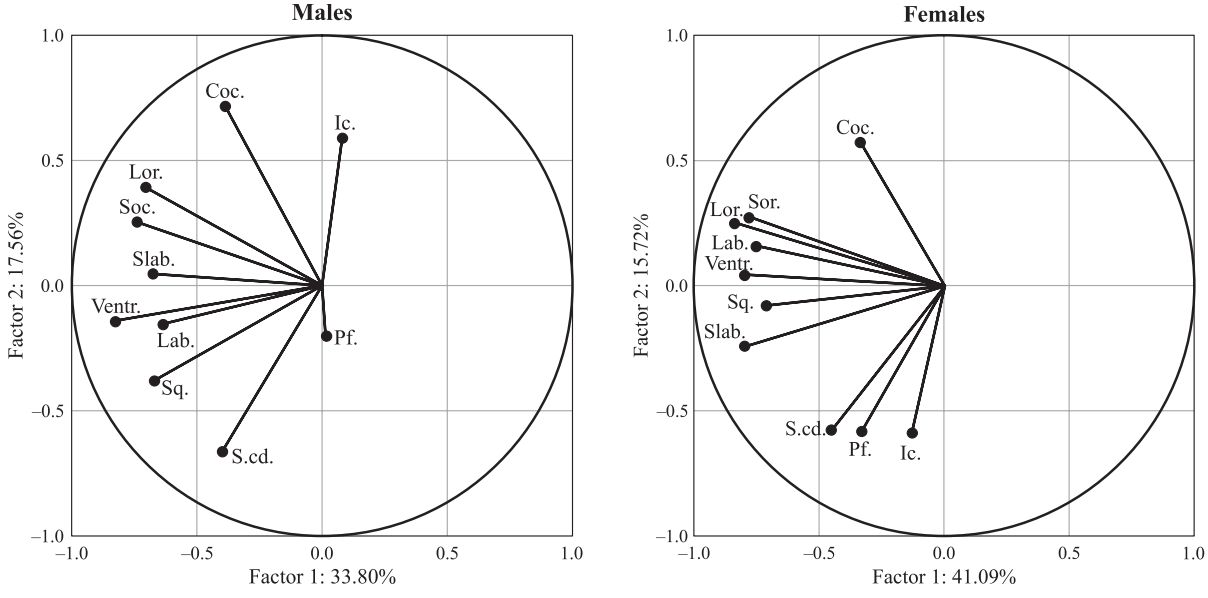

Fig. 4. Projection of characters on the first two factor's plane. Characters abbreviations are the same as in the text.

basins of these rivers are inhabited by vipers with mixed morphological characters of both forms.

A broad zone of intergradation of two vipers is evidence of unhampered interbreeding of these taxa. A genetic similarity of these vipers was confirmed by successful hybridization in captivity and mtDNA structure data (Joger et al., 1997). Morphological and genetic similarity and broad zone of intergradation allow consideration of a Nikolsky's viper only as a subspecies of *Vipera berus*.

TAXONOMICAL COMMENTS

The names proposed by Pallas cannot be applied because terra typica of *Coluber melanis* and terra typica of *Coluber scytha* are located outside the main distribution of Nikolsky's viper, in the zone inhabited by vipers with mixed morphological features. In 1870, K. Pengo used two names. He described a black-colored female (*Pelias berus* var. *nigra*) and it is normally colored new-borns (*Pelias berus* var. *varia*) and concluded that both black and typical vipers are color morphs and belong to one species. The name nigra is the primary junior homonym in the genus *Vipera* Laurenti and was preoccupied by *Vipera aspis* var. *nigra* Bonaparte, 1834 (recently, junior synonym of *Vipera aspis aspis*) (Mertens, Wermuth, 1960). An analogous situation with *varia*-name is that used in combinations for the designation of different varietes of the common adder. *Vipera berus* var. *sphagnosa* was described by B. A. Krassawzeff from territory (Cherseevo village, near Gusevo town, Ivanovo Oblast' — recent Vladimir Oblast') located far from Nikolsky's viper range. Invalidity of the name prester was shown by Vedmederja et al. in 1986. *Pelias berus* var. *ater* cited in the work of A. Andrzejowski (1832) also cannot be applied as a valid name for Nikolsky's viper. In 1820 Merrem used ater for the description of coloration of the melanistic common adder, but not as a specific name. A. Andrzejowski in his work mixed all black adders under the name *Vipera prester* (= *Pelias berus* var. *ater*). Moreover, this name is a junior synonym of *Vipera atra* Meisner, 1820 (= *Vipera aspis*) (Mertens and Wermuth, 1960). Therefore we should conserve the name proposed by Vedmederja, Grubant, and Rudaeva in 1986:

Vipera berus nikolskii VEDMEDERJA, GRUBANT ET RUDAEVA, 1986

Pelias berus — Merrem, 1820: 148 (part.); Schreiber, 1875: 202 (part.).

Vipera berus — Czernay, 1851: 279; Strauch, 1868: 287 (part.); Strauch, 1873: 206 (part.); Lindholm, 1902: 49; Schreiber, 1912: 614 (part.); Brauner, 1904: 30 (part.); Tarashchuk, 1950: 164; Pashchenko, 1955: 132 (part.); Bruno and Maugeri, 1990: 191 (part.).

Vipera prester — Eichwald, 1830: 234 (part.); Andrzejowski, 1832: 337 (part.); Krynicki, 1837: 61; Grubant et al., 1973: 71.

Pelias berus* var. *ater — Andrzejowski, 1832: 337 (part.).

Pelias prester — Dwigubsky, 1832: 29.

Viperus berus (sic!) — Czernay, 1850: 30; Kheruvimov et al., 1977: 44.

Vipera berus* var. *prester — Kessler, 1853: 92.

Pelias berus* var. *nigra — Pengo, 1870: 17.

Pelias berus* var. *varia — Pengo, 1870: 17.

Vipera praester (sic!) — Brauner, 1904: 30.

Vipera berus* var. *praester (sic!) — Brauner, 1906: 7.

Coluber berus berus — Nikolsky, 1916: 227 (part.); Ognev and Worobiev, 1923: 250; Ptushenko, 1934: 49.

Coluber berus* morpha *prester — Ognev and Worobiev, 1923: 250.

Vipera berus prester — Krassawzeff, 1932: 80; Tarashchuk, 1959: 231.

Vipera berus berus — Kren, 1939: 187; Tsemsh, 1939: 110; Mertens, Müller, 1940: 55; Terentyev and Chernov, 1949: 271 (part.); Mertens and Wermuth, 1960: 198; Bannikov et al., 1971: 294 (part.); Steward, 1971: 164 (part.); Street, 1979: 194 (part.); Welch, 1983: 86; Brodmann, 1987: 101 (part.).

Vipera nikolskii Vedmederja et al., 1986: 84; Golay, 1993: 287; Tabachishin et al., 1996: 60; Nilson and Andrén, 1997: 396; Ananjeva et al., 1998; Bakiev et al., 1999: 4; Franzen and Heckes, 2000: 63; Pavlov, 2000: 48; Bozhansky, 2001: 348.

Vipera barani — Stumpel-Rienks, 1990: 114.

Vipera berus nikolskii — Joger et al., 1997: 193.

Holotype and terra typica. MNKNU. 14703. adult female, near Bezludovka and Vasishchevo, Kharkov vicinities, Udy river, Ukraine, leg: K. Pengo, 1867.

Paratypes. MNKNU 14703.12 juv.,; ZISP 3376.2 juv. (now lost); ZISP 22012.2 juv. All from the same locality.

Diagnosis. Black colored subspecies of *Vipera berus* with increased number of loreal, ventral, and subcaudal shields. One or two rows of the shields behind eye and between supralabials and eye. Deeply forked hemipenes are elongated (Table 2).

Redescription. $L._{min\text{-}max}$ ad 440 – 760, L. ♂♂ (n = 56) 440 – 645 (512 ± 6.8) mm, L. ♀♀ (n = 72) 450 – 760 (576 ± 6.7) mm; $L.cd._{min\text{-}max}$ ad 37 – 105, L.cd. ♂♂ (n = 55) 70 – 105 (86.2 ± 1.3) mm, L.cd. ♀♀ (n = 71) 37 – 99 (74.1 ± 1.1) mm; $Sq._{min\text{-}max}$ 19 – 23, Sq. ♂♂ (n = 251) 21 – 23 (21.40 ± 0.05), Sq. ♀♀ (n = 206) 19 – 23 (21.41 ± 0.06); $Ventr._{min\text{-}max}$ 140 – 160, Ventr. ♂♂ (n = 271) 140 – 160 (150.03 ± 0.18); Ventr. ♀♀ (n = 215)

143 – 160 (153.39 ± 0.22); S.cd.$_{min\text{-}max}$ 26 – 50, S.cd. ♂♂ (n = 262) 33 – 50 (41.21 ± 0.15), S.cd. ♀♀ (n = 203) 26 – 38 (32.82 ± 0.17); Lab.$_{min\text{-}max}$ 5 – 11, Lab. ♂♂ (n = 251) 5 – 11 (8.96 ± 0.03), Lab. ♀♀ (n = 210) 8 – 11 (9.07 ± 0.03); Slab.$_{min\text{-}max}$ 7 – 13, Slab. ♂♂ (n = 199) 7 – 13 (10.67 ± 0.05), Slab. ♀♀ (n = 158) 9 – 13 (10.79 ± 0.06); C.oc.$_{min\text{-}max}$ 7 – 12, C.oc. ♂♂ (n = 187) 7 – 12 (9.73 ± 0.66), C.oc. ♀♀ (n = 147) 7 – 12 (9.61 ± 0.07); S.oc. ♂♂ (n = 188) 1 – 2 (1.21 ± 0.02); S.oc. ♀♀ (n = 151) 1 – 2 (1.39 ± 0.03); Ic.$_{min\text{-}max}$ 1 – 19, Ic. ♂♂ (n = 188) 1 – 18 (8.96 ± 0.24), Ic. ♀♀ (n = 147) 2 – 19 (8.81 ± 0.25); Pf.$_{min\text{-}max}$ 0 – 15, Pf. ♂♂ (n = 188) 0 – 15 (7.64 ± 0.17), Pf. ♀♀ (n = 147) 0 – 14 (8.27 ± 0.19); Lor.$_{min\text{-}max}$ 1 – 7, Lor. ♂♂ (n = 186) 1 – 6 (3.39 ± 0.07), Lor. ♀♀ (n = 143) 2 – 7 (4.25 ± 0.08); Lfr/Ltfr$_{min\text{-}max}$ 0.77 – 1.78, Lfr/Ltfr ♂♂ (n = 133) 0.77 – 1.78 (1.39 ± 0.01), Lfr/Ltfr ♀♀ (n = 109); 1.09 – 1.78 (1.40 ± 0.01).

One-two shield rows between supralabials and eye; one-two shield rows behind the eye; head pholidosis pattern, shape, size, number and arrangement of scales is variable. Number of the scales around the eye is increased (Fig. 5). In comparison to *V. b. berus* hemipenes are large, with elongated apical lobes, well expressed spines, spine lines and basal hooks.

Adult coloration is totally black, only the tip of tail is pigmented by yellow, orange or whitish. In some cases the adults, especially females, have light dots and spots on supralabials and ventrals and reddish-brown colored throat. Non melanistic individuals are rarely encountered. Brown-colored specimens with zigzag on the dorsum (weakly expressed sexual dichromatism), monochromatic brown-colored without zigzag and *berus*-like colored specimens are represented in some populations with a frequency of 10%. The coloration of young specimens is gravel, reddish-brown or deep-brown.

Variation. Individual variability in pholidosis characters is very high. Amongst different populations average values of characters vary significantly. Similarity between *V. b. berus* and *V. b. nikolskii* increases from southern-east to northern-west. Snakes from intermediate populations have mixed morphological characters. The venom composition is mixed in some populations (Samara Oblast', Sumy Oblast') (Mursaeva et al., 1995; Starkov and Utkin, 2003).

Differences are known between western (Ukraine) and eastern (Russia, Volga Basin) populations in pholidosis and body size. Small body size in females and a reduced number of ventral shields are typical for the eastern population. A ratio of second and third upper labial heights was used by V. N. Grubant et al. (1973) as diagnostic character. This character shows wide geographical variability. This ratio is 0.73 – 1.00 for vipers from Kharkov and 0.80 – 1.16 for individuals from Saratov Oblast' (Vedmederja et al., 1986; Tabachishin et al., 1996).

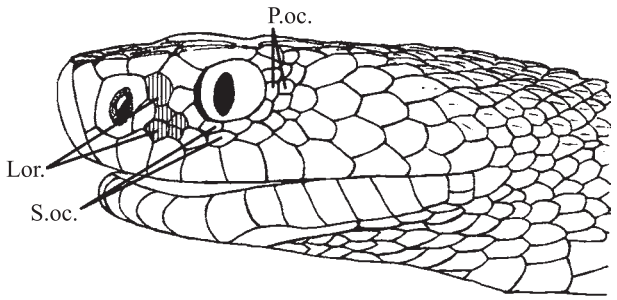

Fig. 5. Polymerized head scalation in *V. b. nikolskii*.

In the "pure" populations of *V. b. nikolskii* located far from contact zone with *V. b. berus*, all adults are totally black with exception of tail tip. In the hypothetical intergradational zone (Perm Oblast', Samara Oblast', Udmurtia, Tatarstan, northern part of Saratov Oblast', possibly Kursk Oblast'), the black-colored and light-colored individuals with zigzag live together (Ptushenko, 1934; Tarashchuk, 1950; Tabachishin et al., 1996; Al-Zavakhra, 1992; Pavlov, 2000; our data). The normally patterned snakes are not numerous. For example, in Tatarstan the non black coloration is presented in 4.5% (Al-Zavakhra, 1992). The white colored upper labials, reddish throat, light spots on the ventral and other light elements in coloration were registered in such a mixed population (Sokolov, 1979; Zinenko and Ruzhilenko, 2003). Moreover, a monochromatic grayish-beige colored specimen is known (ZISP 21295).

The coloration of young specimens varies from gravel to dark-brown with atro-olivaceus, saturate-fumosus or murinus background and atro-brunneus, atro-olivaceus or atro-cinnamomeus zigzag. Young males are brighter col-

TABLE 2. Comparison of Two Subspecies of *Vipera berus*

Vipera berus berus	*Vipera berus nikolskii*
0- – 70 % of adults are black, sexual dichromatism in the dorsal pattern is well expressed, juvenile coloration is grayish-brown	90 – 100% of adults are black, sexual dichromatism in the dorsal pattern of coloured specimens is weakly expressed, juvenile coloration is reddish-brown
1 row of scales between supralabial shields and eye	1 – 2 rows of scales between supralabial shields and eye
19 – 21 rows of scales around midbody	21 – 23 rows of scales around midbody
Average number of ventral shields is 144 – 149	Average number of ventral shields is 150 – 155
Hemipenes are relatively short, shallowely-forked	Hemipenes are large, deeply forked, with elongated apical lobes
Venom is yellowish	Venom is colorless

ored, with grayish background, females are light-brown. Iris coloration varies from reddish (rufescens), chestnut (spadiceus) and brown (rubiginosus, argillaceus, prunicolor) in the upper part to umbrius, atro-castaneus, nikotianus, bistraceus, sordide violaceus and niger in the lower part.

In the second year young snakes have cacao-fuscus color with feebly marked zigzag and light dots on the supralabials and ventrals. At the age of 3 – 4 years they get adult coloration.

Sexual dimorphism. Sexual dimorphism at *V. b. nikolskii* in coloration was reported for Tambov Oblast' (Kheruvimov et al., 1977). A chestnut-colored iris is typical in males and from ochre-yellow to reddish in females. The lower part of the tail tip is black in males and terracotta-pale or sepia with terracotta-pale dots in females. In the Kharkov Oblast' and in the vicinities of Kanev the tail tip is bright colored (yellow, orange) in females, and whitish in males. Males with completely black tail are rare. Iris in snakes from Kharkov vicinities is umber, chestnut- and deeply chestnut-colored in males and reddish-brown in females. Like in the Tambov Oblast', males from Kanev have chestnut-colored iris and females have ochre-yellow, reddish and reddish-pale-colored iris.

Non melanistic, normally colored males and females with zigzag may have no differences in dorsal coloration. Hence sexual dimorphism of the coloration pattern in *V. b. nikolskii* is weakly expressed and connected with some details of coloration. Unlike *V. b. berus* (Bruno and Maugeri, 1990; Shine and Madsen, 1994), in *V. b. nikolskii*, the phenomenon of sexual dichromatism is well visible in juveniles only.

Sexual dimorphism is present in pholidosis characters. Like in *V. b. berus*, females of *V. b. nikolskii* have an increased number of ventralia, subcaudalia, intercanthalia, parafrontalia, lorealia, squamae dorsalis, supralabialia, sublabialia, and rows of subocularia.

Range. *V. b. nikolskii* inhabits the south and south-eastern part of the East European Plain, from Podolia Hills in the west to Cis-Volga Hills. Its range includes territories of Moldova, probably Romania (Fuhn and Vancea, 1961), Central Ukraine, and southern part of European Russia. In Ukraine it occurs in Odessa Khmelnitsky, Vinnitsa, Kirovograd, Cherkassy, Kiev, Poltava, Sumy, Kharkov, Lugansk, and Donetsk Oblast's; in Russia — in Kursk, Belgorod, Voronezh, Tambov, Penza, Saratov, and Volgograd Oblast's.

The northern limit of distribution agrees with description of Vedmederja et al. in 1986. However new records of *V. b. nikolskii*, on the left bank of the Kodyma River in Balta District on the north of Odessa Oblast' (Tabachishin et al., 2003), near Shepetovka in Khmelnitsky Oblast' of Ukraine, in Orgei Oblast' of Moldova expand the border of distribution to the west.

The intergradation zone between *V. b. berus* and *V. b. nikolskii* covers the broad territory of eastern Ukraine and Central and Eastern European Russia. Vipers with intermediate morphological characters are recorded for the territory of Cherkassy, Kiev, Chernigov, and Sumy Oblast's in Ukraine and Kursk, Tambov, Samara, Perm, Penza Oblast's, Tatarstan, Chuvashia, Udmurtia, and Bashkortostan in Russia. Northern Ukraine, Belarus', Northern and North-Eastern European Russia are inhabited by *V. b. berus*.

Habitats. *V. b. nikolskii* inhabits preglacial landscapes to south from the border of maximum glaciation in the Eastern European Plain. The distributional range embraces a woodland steppe zone, sometimes *V. b. nikolskii* penetrates to steppe zone along the river valleys (Donets River, Don River) and the hills (Donetskii Kryazh).

Distribution of *V. b. nikolskii* correlates with location of forest refugia that were existing during maximum stage of Valdai Glaciation at 18 – 20 thousand years ago in the middle part of Don and Volga river basins. Some of these refugia placing on hills were reservations of genetic diversity of *Vipera berus*.

Some authors (Andrén and Nilson, 1981; Madsen and Stille, 1988) proposed a hypothesis that the black morph of *V. berus* has some preferences under cold climate conditions in comparison with the normally colored one. However there are facts contradicting this hypothesis. The warmest part of *V. berus* range is inhabited only by melanistic adders. It may be supposed that the change to black coloration took place during the Ice Age as an adaptation to rough conditions in preglacial landscapes.

Dispersal routes. Apparently, the south-eastern part of East European Plain was occupied by *V. b. nikolskii* before the Dnepr Glaciation. The territory that was created from Dnepr and subsequent Valdai Glaciation was occupied by taiga forests and recent *V. b. berus* accordingly. To the west, the fauna dispersed from Eastern refugia. The relict *V. b. nikolskii* together with other species of the East-European faunistic complex were able to survive in refugia in the Middle Volga, Middle Don and Donets rivers, Lower Dnepr river, and Prut river valley.

Remarks. Two different morphotypes in *V. berus* are known. Typical adders have a splay edge of the snout, decreased number of the scales in pileus, one row of the shields around eye. The second morphotype is characterized by flat upper surface of the snout, sometimes the snout is slightly turned up; two rows around the eye and increased number of small shields on pileus (Gasc and Gourmain, 1968). Both morphotypes are presented in *V. b. nikolskii* populations. Also this polymerized *aspis*-like type of squamation in *V. b. bosniensis* is common. A

pileus pattern with numerous small shields is rarely observed in *V. b. berus* (Benson, 1999).

Probably, *V. b. nikolskii* is closely related to Balkan subspecies *V. b. bosniensis*. These subspecies exhibit a tendency to increase of number of prefrontal, loreal and postocular shields. In contrast to *V. b. berus*, both *V. b. nikolskii* and *V. b. bosniensis* have more intense and brighter body coloration. It is important to notice that these relict subspecies survived in Ice Age refugia and retained some ancestral characters. Moreover, *V. b. bosniensis* is allied to species of *V. aspis*-complex as distinct from *V. b. nikolskii*. Separately, we should mention presumptive close affinities between *V. b. nikolskii* and *V. barani*. Good morphological differences and genetic distance between these species were shown early after molecular analysis (Joger et al., 1997) and completed analysis of morphological characters (Franzen and Heckes, 2000) of both forms.

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APPENDIX. The list of sampled localities

***Vipera berus berus*:** Ukraine — Zakarpatskaya Oblast', Berehove and Vinogradiv Distr. (sample 1); Zakarpatskaya Oblast', V. Berezan Distr., Svalyava settl. and Perechin settl. (sample 2); Zakarpatskaya Oblast', Volovets and Turka Distr., Mezhhirya (sample 3); Zakarpatskaya Oblast', Rakhiv Distr. and Ivano-Frankivska, Verhovyna Distr. (sample 4); Volyn Oblast' (sample 5); Sumy Oblast', S. Buda Distr. (sample 16); Russia — Karelia, Segozero, Suojarvi Distr., Toyvola vill., Tolvojarvi vill., Sortavala, Risklan-sari is., Vygozero (sample 20); Leningradskaya Oblast', near Vyborg, near Zelenogorsk, Priozerskii Distr., near Vuoksa lake, near Petergof, Gatchina Distr., Siverskaya settl., Luga Distr., Lodeinoe Pole Distr., Gumbaritsy vill. (sample 9); Novgorod Oblast', Mosheno Distr., Kocherovo vill., Opochetskii Posad settl. (sample 14); Pskov Oblast', Porkhov Distr., Gvozdno vill., near Sebezh town, near Plussa st., Pechery Distr., near malye Kalki vill. (sample 6); Vologda Oblast', Darvinovsky Resrve; Yaroslavl Oblast', Pereyaslavsky Distr., Pletschevo Lake, Rostov Distr.; Tver Oblast', Beloye Lake (sample 24); Moscow Oblast' (sample 33); Kostroma Oblast' (sample 37); Arkhangelsk Oblast', Onega Distr.; Komi, southern part; Tula Oblast', Venev Distr. and Zaokskii Distr. (sample 32); Ryazan Oblast'; Sverdlovskaya Oblast'; Tomsk Oblast' (sample 44); Belarus', Vitebsk Oblast' (sample 8); East Kazakhstan (sample 43); East Siberia (sample 45); Yakutia (sample 46);

Vipera berus nikolskii: Moldova, Strashensky Distr. (sample 7); Ukraine — near Kharkov, between Vasishchevo and Bezludovka (sample 25); Kharkov (sample 26); Kharkiv, northern vicinities (sample 27); Kharkov Oblast', Krasnokutsk Distr. (sample 21); Kharkov Oblast', Dergachi Distr. (sample 28); Kharkov Oblast', Chuguev Distr. and Pechenegi Distr. (sample 29); Kharkov Oblast', Zmiyev Distr. (sample 30); Kirovograd Oblast', Znamenka settl. (sample 15); Poltava Oblast' (sample 17); Sumy Oblast', Akhtyrka Distr. (sample 22); Lugansk Oblast' (sample 34); Russia — Kursk Oblast', Dmitriev Distr.; Belgorod Oblast' (sample 31); Voronezh Oblast', Khoper Reseve (sample 35); Saratov Oblast', near Alekseevka, Arkadak Distr., near Semenovka vill. (sample 38); Volgograd Oblast', Don River, Log st., Mikhaylovka Distr., Medveditsa Riv.;

V. b. berus*/*V. b. nikolskii: Ukraine — Kiev Oblast', right bank of the Dnepr riv. (sample 10); Kiev Oblast', left bank of the Dnepr River (sample 11); Cherkassy Oblast', near Kanev, right bank of the Dnepr River (sample 12); Cherkassy Oblast', near Kanev, left bank of the Dnepr River (sample 13); Sumy Oblast', Putivl Distr., N. Sloboda settl. (sample 18); Sumy Oblast', Putivl Distr., Spadschina settl. (sample 19); Sumy Oblast', Sumy Distr. (sample 23); Russia — Tambov Oblast', near Kirsanov and Vorona River (sample 36); Chuvashia, Alatyr Distr., "Prisurskii" Reserve (sample 39); Udmurtia, Sumsi Distr., Kilmez vill., near Karakulino, Yashkur-Bodya Distr. (sample 41); Perm Oblast', Uktu st. and Kungur Distr., near Kishert settl. (sample 42); Penza Oblast', Lashma; Zemetchino Distr., Dolgovo settl.; near Samara (sample 40); Bashkortostan, Belaya River; Bashkortostan, Bashkirskii Reserve; Hybrids (sample 47).