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Systematics of the Vipers of the Caucasus: Polymorphism or Sibling Species?

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Abstract. -Inter- and intramorphological variation were examined in sympatric and allopatric polymorphic and monomorphic populations of the *Vipera ursinii* and *Vipera kaznakovi* complexes. The alpine *Vipera dinniki* populations in upper Great Caucasus show a pronounced, and to a certain extent geographical, polymorphism. Color patterns include among others 'kaznakovi', 'tigrina', 'berus', 'bronze', and 'ursinii' types. Several of these patterns can be represented within the same litter in certain populations. *Vipera dinniki* is sympatric with the Caucasian representative of the *Vipera ursinii* complex in some areas. This last taxon shows a similar degree of polymorphism, which is unique for this complex, and due to morphological and molecular distinction, we consider it to be a Caucasian evolutionary species within the *ursinii* complex - *Vipera lotievi* sp.n.

Key Words: Reptilia, Squamata, Viperidae, *Vipera dinniki, V. kaznakovi, V. ursinii, V. renardi, V. lotievi* sp.n., Caucasus, Russia, Georgia, taxonomy, morphology, polymorphism.

Introduction

The taxonomy of the vipers of Caucasus has for a long time been confusing and contradictory. According to the traditional view a single species, *Vipera kaznakovi*, is distributed in the moist and warm lowlands of the western Caucasus as well as in the mountain valleys towards the east. In the east the habitat is drier and along the range the vipers gradually change toward *Vipera ursinii* in appearance. In the east Caucasus only this last viper was supposed to occur. Thus there seemed to be a somewhat clinal transformation from "pure" *V. kaznakovi* in the west to "pure" *V. ursinii* in the east. Vipers from the intermediate region could be difficult to determine. Within the same locality some specimens look like *V. kaznakovi*, other ones are more like *V. ursinii*, while still some can be intermediate.

Nikolsky (1913) separated the alpine populations into the taxon *Vipera berus dinniki*, which was based on alpine specimens of the conventional *V. kaznakovi* from high altitudes in the western Caucasus (Malaya Laba River- terra typica restricta and Svanetia) as well as from other places. The name *dinniki* was long considered as a synonym of *V. kaznakovi* until Vedmederja et al (1986) recognized it as a separate species inhabiting alpine and subalpine meadows in the Caucasus, and thus restricting *V. kaznakovi* to lower altitudes in western Caucasus and adjacent moist lowland habitats along the eastern Black Sea coast. Thereby the problem of the gradual transformation from *V. kaznakovi* in the west of the Caucasus to *V. ursinii* in the east is restricted to the high Caucasus populations, now including *V. dinniki* and *V. ursinii*. *Vipera kaznakovi* is well defined and restricted in distribution, and geographically separated from all the other viper species in the region.

The complex history of nomenclature and taxonomy has been clarified to a great part in some recent publications (see Orlov & Tuniyev, 1986; 1990), together with hypotheses about the phylogeny of this group. Concurrently the need of genetic studies was stressed, and this has led to the present work where we in a series of papers intend to clarify the taxonomy and evolution of the vipers of this region. The work is planned to have a broad perspective including phenetic and phylogenetic analyses, habitat choice, niche-breadth, and reproduction. Different methods take different time and in this first paper the morphology is reexamined, based on available material in Museum collections and freshly collected material from a number of new places, as well as on inheritance of color pattern. Genetic structures based on phenetic analyses of allozyme data are also presented.

The morphological distinction between *Vipera dinniki* and *V. kaznakovi* has been presented elsewhere (Orlov and Tuniyev, 1986; 1990) and will not be repeated in this study. In the present paper we are focusing on patterns of morphological and molecular variation within and between the different populations in the Caucasus, and the taxonomy of these populations.

Material and Methods

The work has mainly been a study of variation in external morphology, allozymes and reproduction in order to reveal patterns of sympatry and sibling species. Additional genetic studies will follow when material becomes available in suitable samples (presently delayed due to political reasons). Thus live and preserved museum material has been examined concordantly with studies of reproduction in the laboratory.

Additional preserved material used in this study originates from the Natural History Museum in Göteborg (GNM); Dipl.-Biol. F. J. Obst, Staatliches Museum für Naturkunde, Dresden (MTKD D); Aram Agasian, Zoological Institute, Academy of Sciences, Eriwan, Armenia. Abbreviations for museums as used in the text are: CNR- Caucasian State Biosphere Reserve, Collection of Boris Tuniyev at Yew-box Groove, Sochi; GNM- Göteborg Natural History Museum, Göteborg; MTKD- Staatliches Museum för Naturkunde, Dresden; ZIEr- Zoological Institute, Academy of Sciences, Eriwan; ZIG- Department of Zoology, University of Göteborg; Göteborg- (authors' collection, which later will be incorporated in GNM); ZIN- Zoological Institute, Academy of Sciences, St. Petersburg.

Altogether about 300 preserved or live specimens of vipers from the Caucasus and adjacent regions have been seen during the study. Joint field trips were made in different parts of the Caucasus in 1990 and 1992, but two of us (Tuniyev and Orlov) have performed extensive research in the region prior to that. For morphometric studies 183 preserved snakes within the *ursinii* and *kaznakovi* complexes have been examined more carefully, and for most of these specimens 30 different items of data have been collected. This information was used, down to population level, in morphological descriptions, taxonomical analyses and conclusions about zoogeography and range overlap. Inheritance of color pattern was studied based on 23 pregnant females and their offspring.

Data collected were: total length and tail length; number of preventrals, ventrals, subcaudals, anterior and mid-body dorsal scale rows, apical plates, supralabials, sublabials, circumocular scales, loreals, second chinshields, mentals, crown scales (=intercanthals + intersupraoculars), and zig-zag windings in dorsal band. Further rostral index (height/breadth) and head index (breadth/length) were calculated. Division of parietals, frontal, and nasalia was noted, as was the color of dorsal and ventral sides, and iris (in live specimens). Further, upper preocular size; and head, labial and lateral body patterns, as well as distinctiveness of canthus rostralis were examined. Details about these methods are found in Nilson and Andrén (1986).

Morphology/phenetics

Standard errors accompanying mean character ratios were used as relative measurement of dispersion. For the analysis of intra- and interpopulational morphological variation (phenetic analysis) the samples were divided into subsamples depending on questions raised. Thus besides an analysis of morphological variation also a pattern confirming or rejecting the present taxonomic pattern could be achieved. This pattern could also be

TABLE 1. Number of specimens used in the genetic analyses and localities (Russia if nothing else is stated) for the examined taxa.

kaznakovi:
1. Dagomys, north of Sochi. Six specimens.
2. Rudorova, inland locality, 900 m alt. Four specimens.

dinniki:
3. Fisht/Oshten, the westernmost locality of the main Caucasus range. Seven specimens.
4. Lake Impsi, 1,980 m. alt., at a tributary to the Little Laba River on the northern slope of the main range. Seven specimens.
5. Aishkha-II on the southern slope of the main range. Three specimens.
6. Lake Kardyvach at upper Mzymta River on the southern slope of the main range Seventeen specimens.

lotievii:
7. Armkhi, Checheno-Ingushetia. 2,000 m altitude. Seven specimens.

berus:
8. Uppsala (terra typica), Sweden. Eleven specimens.

eriwanensis:
9. pooled sample from Asbua and Cildir, Kars, east Turkey; and Sevan, Armenia. Six specimens.

supported or rejected by the parallel biochemical studies. Thereby it is possible to state or reject the occurrence of convergent or parallel evolution, i.e. sibling species.

Estimation of the different color pattern frequencies in local populations was based on observations during the field work. Small museum samples collected by others were not included in this analysis due to uncertainty of randomness in sampling (unusual morphs might have been collected and preserved at a higher degree).

Biochemical data

Enzyme electrophoresis.— Sixty-eight specimens representing different taxa of Caucasus vipers, and *Vipera berus* from Sweden were examined. The samples were treated as nine independent operational taxonomic units (OTUs) in the genetic analysis, in order to avoid a priori assumptions of taxonomic relationships among the eight Caucasus populations studied (see Table 1, for locality data and sample sizes). A potential risk of sampling error due to syntopic occurrence of two taxa may be avoided by testing observed genotype distribution within a locality against Hardy-Weinberg expectations (see results). Fresh or frozen tissues (-75°C) from liver and skeletal muscle were homogenized in distilled water. The extracts were centrifuged for 10 min at 10,000 rpm and 4°C and the supernatants were then stored at -75°C until used. Standard horizontal starch gel electrophoresis was carried out, as described by Harris and Hopkinson (1976) and Murphy et al. (1990). Gels (11% w/v) were prepared from Sigma starch (Sigma Chemical Co., St. Louis, Mo). Two buffer systems were used: (A) Gel: 0.03 M tris-0.005 M citric acid; Electrode: 0.06 M lithium hydroxide-0.03 M boric acid, pH 8.0 (Ridgway et al., 1970). (B) Gel: 0.002 M citric acid, pH 6.1; Electrode: 0.04 M citric acid, pH adjusted with N-(3-amino-propyl)morpholin

TABLE 2. Enzymes and electrophoretic conditions of the polymorphic loci scored in this study. Nomenclature and commission numbers following the International Union of Biochemistry, Nomenclature Committee (1984). Abbreviations for tissue sources are: L=liver and M= skeletal muscle.

Enzyme	Commission no.	Locus	Tissue	Buffer system	Reference
Alcohol dehydrogenase	1.1.1.1	Adh-1	L	B	1
Glucose-6-phosphate isomerase	5.3.1.9	Gpi-1	M, L	B	5
Hexokinase	2.7.1.1	Hk-1	L	B	1, 3, 4
Isocitrate dehydrogenase	1.1.1.42	Idh-1	L	B	1
		Idh-2	L		
L-Lactate dehydrogenase	1.1.1.27	Ldh-2	M, L	B	3
Phosphoglucomutase	5.4.2.2	Pgm-2	L	B	1
Superoxide dismutase	1.15.1.1	Sod-1	L	A	1, 2

1) Harris and Hopkinson (1976)
2) Johnson et al. (1970)
3) Shaw and Prasad (1970)
4) Murphy et al. (1990)
5) De Lorenzo and Ruddle (1969)

A) Tris-citrate/lithium hydroxide, boric acid, pH 8.0, 10V/cm, 4h (Ridgway et al., 1970)
B) N-(3-amino-propyl)morpholine/citrate, pH 6.1, 10V/cm, 6h (Clayton and Tretiak, 1972)

(Clayton and Tretiak, 1972). Enzymes assayed, tissues, modified electrophoretic conditions and staining references (Table 2) follow Nilson et al. (1994).

Reproduction

Inheritance of color morphs within broods was studied by keeping pregnant females in the laboratory until giving birth. By this, various hypotheses of polymorphism and its inheritance patterns could be evaluated.

Fieldwork

Substantial information has been gathered during several years in the field in Russia, Georgia, Armenia and Turkey. A more intensive field survey was performed in the western Caucasus in July, 1990, in order to obtain information of color morphs in natural populations. Together with preserved material, this information was the base for the study of morphological intrapopulational variation in *V. dinniki*. Material was also used for reproductive studies (see above).

The *V. dinniki* localities, situated in the Caucasian State Biosphere Reserve and in the Sochi Nature State National Park and listed below were included in this study:

Fisht/Oshten— The westernmost high mountain area of the main Caucasus range, and of the Reserve, characterized by the peaks Mt. Fisht (2868 m. alt.) and Mt. Oshten (2804 m. alt.). This region is separated and isolated from the main range (with Mt. Chugush 3237 m. alt.) by the forested, moist and warm "Colchis Gate" at low altitude (not more than 1500 m).

Loyub— Mt. Loyub (2990 m. alt) at the uppermost part of the Mzymta River in the eastern part of the Reserve, situated on the southern slope of the main range.

Aishkha-II (2858 m. alt)— in the same mountain massif, a little bit further to the west, and situated on the southern slope of the main range.

Lake Kardyvach (1850 m. alt)— the eastern border of the Park, close to Mt. Loyub but a little further down the Mzymta

FIG.. 1. The typical "dinniki" pattern type of *Vipera dinniki*, with unicolored lateral sides typical for Fisht/Oshten (ZIG).

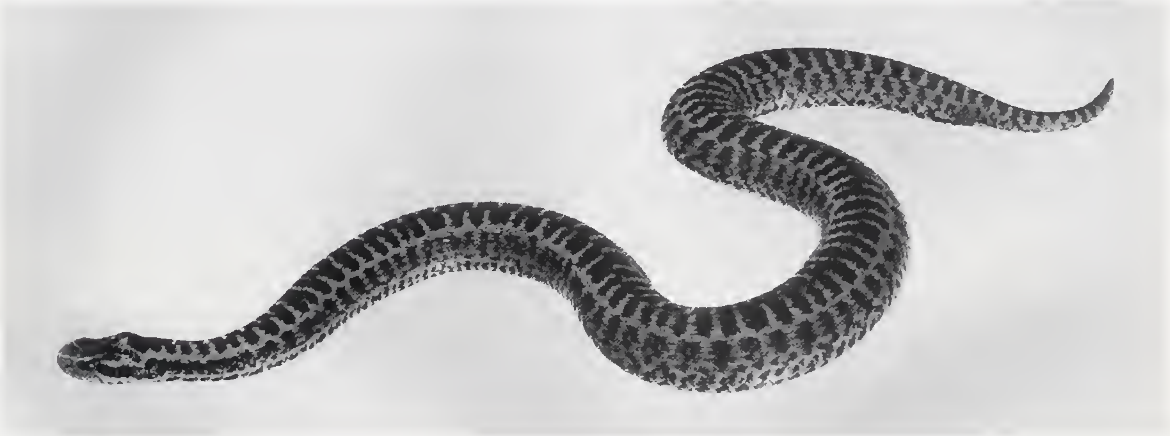

FIG. 2. The "dinniki" pattern type of *Vipera dinniki*, with a tendency towards the "tigrina" morph. From Kardyvach (ZIG).

River. Also situated on the southern slope of the main range.

Lake Impsi— at 1980 m. alt., situated at the Tsahvoa River, a tributary of the Little (Malaya) Laba River. The locality is mainly on the slopes of the Damhorts Range at the northern part of the Reserve, and partly on Akaragvarta Mountain situated on the northern slope of the main range.

In addition much information on *Vipera kaznakovi* was gathered at the lowland Black Sea coast localities of Dagomys, north of Sochi (Russia) and Hopa, Artvin Province (Turkey).

Results

The results of the analyses of morphometrics and enzyme electrophoresis are presented separately.

Intra- and interpopulational variation in morphology

A great number of different color morphs are expressed in the Caucasian vipers. Although several stages of overlapping and intermediate forms could be seen, we define the following major pattern types:

a. The "ursinii" pattern type of *Vipera dinniki*, from Kardyvach (ZIG).

b. The "tigrina" morph of *Vipera dinniki*, from Impsi with partly divided transverse bars (ZIG).

c. The "bronze" morph of *Vipera dinniki*, from Impsi (ZIG).

d. The "bronze" morph of *Vipera lotievi* from Itum Kali, Checheno-Ingushetia.

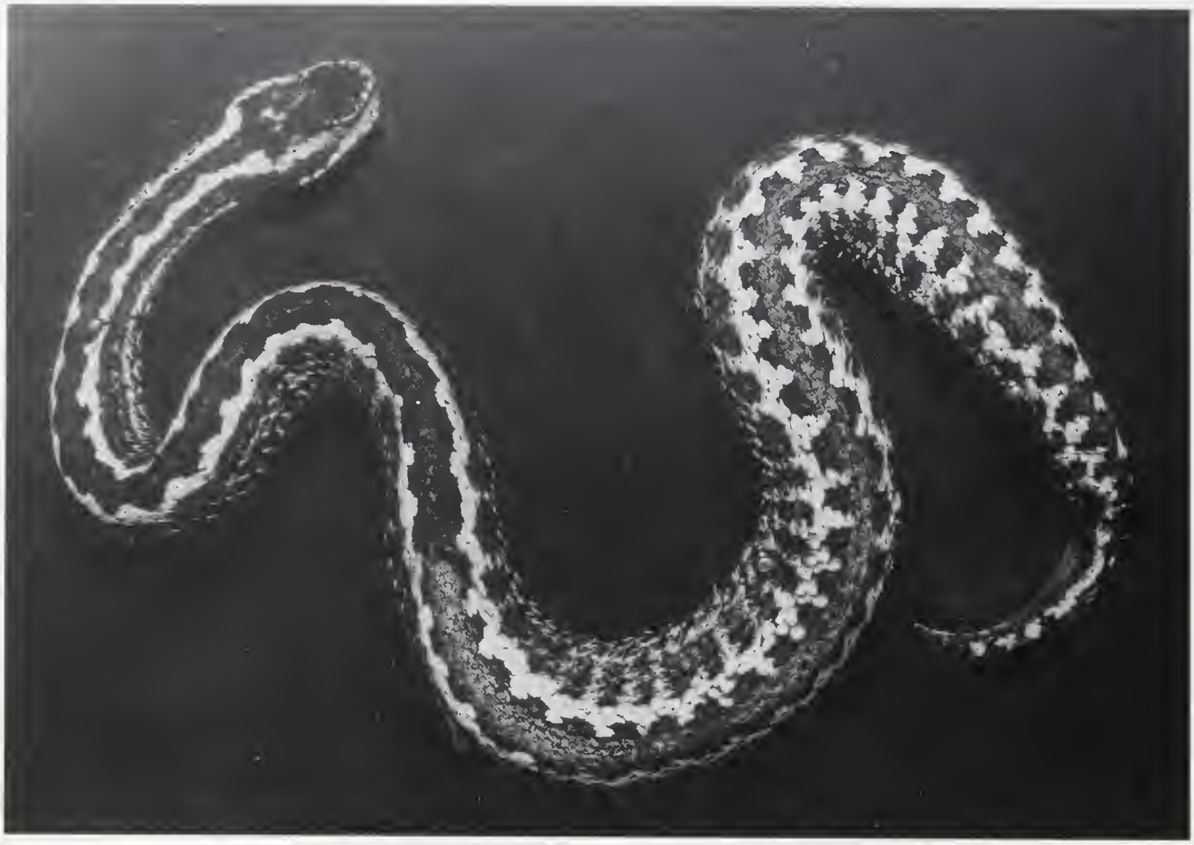

FIG. 3. The "kaznakovi" morph of *Vipera dinniki*, from Fisht/Oshten (Mt.Oshten - Armenian pass).

A. "dinniki": a more or less continuous zig-zag band, and pronounced lateral blotches. Sometimes nebulous in pattern. Sometimes rather *Vipera berus* like (Figs. 1, 2).

B. "kaznakovi": pronounced black lateral and dorsal longitudinal bands, and yellow or orange ground color. The dorsal band is waving or expressed as a straight band resulting in a contrasting more or less bilineated pattern. Besides these we could define a "bilineated" morph which is similar to the "kaznakovi" type of pattern but much lighter. In the analysis below it is included in the "kaznakovi" type (Fig. 3, compare Fig. 4).

C. "ursinii": a black-edged continuous dark brown zig-zag band on a paler ground color and lighter sides of body (Fig. 5, Plate 1a).

D. "tigrina": dorsal pattern fragmented into broad or narrow transverse bands. Also spotted pattern could be seen in some populations. This pattern type is most close to "tigrina", but differ by being divided along the vertebral line thus resulting in two rows of dark spots along the dorsal side of the body (Fig. 6, Plate 1b).

E. "bronze": a uniform greyish to brownish or blackish ground color covering all parts of body except the head. Sometimes with a darker narrow or broad vertebral stripe (Figs. 7, 8, Plate 1c).

F. "melanism": black, with a high production of melanin covering all other color patterns.

The different morphs were represented in different frequencies at the different localities examined, and some morphs seemed to be restricted to one or a few

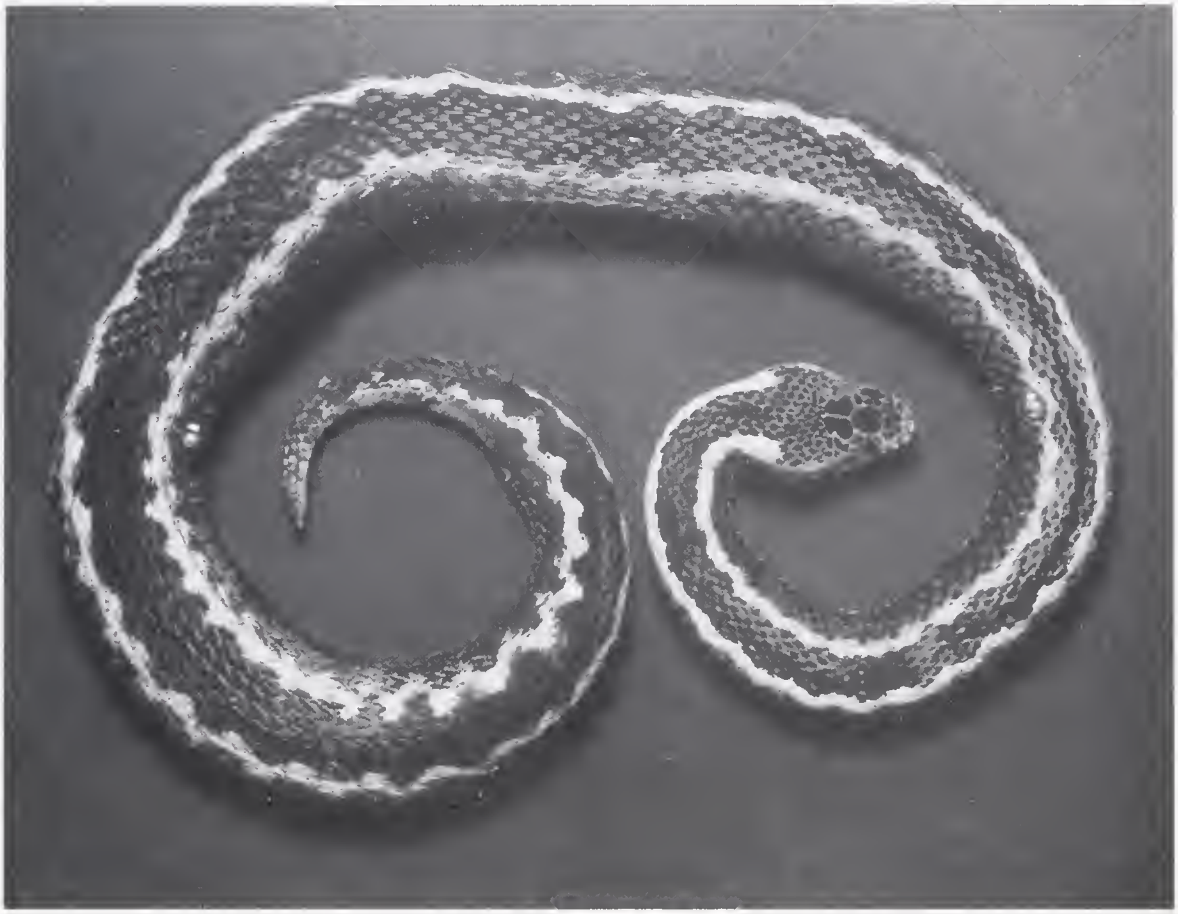

FIG. 4. A typical *Vipera kaznakovi* from the inland locality cordon Babuk-Aul at the foothills of Mt. Fisht (ZIG).

FIG. 5. The "ursinii" pattern type of *Vipera dinniki*, with more unicolored lateral sides from Mt. Fisht (ZIG).

localities (Table 3). Also variation in other color characteristics was obvious when comparing populations. The number of windings in the dorsal zig-zag band varied markedly with low number in the western isolated Fisht population and high in the more eastern populations (Fig. 9). This was especially pronounced when comparing Fisht with Kardyvach, characterized by a high frequency of "tigrina" morphs (Table 3). Almost no overlap was detected as in Kardyvach the vipers have 68 or more windings while in the Fisht population the corresponding figures are 69 or less (Table 4). In general the west Caucasian samples (except Fisht) have higher number of dorsal windings or transverse bars than central and east Caucasian *dinniki* vipers. Also *V. kaznakovi* has fewer windings.

FIG. 7. The "bronze" morph of *Vipera dinniki*, from Mt. Loyub (ZIG).

TABLE 3. Distribution of color morphs in samples of *V. dinniki* and *V. kaznakovi* (Dagomys) in absolute numbers and in percentage (in some cases) in 1991. Sample size in parenthesis.

	Impsi (16)	Kardyvach (33)	Aiskha-II (6)	Fisht (11)	Dagomys (8)
"dinniki"	9 (56%)	4	3	2	0
"tigrina"	3	11 (33%)	1	3	0
"ursinii"	2	9 (27%)	0	2	0
"kaznakovi"	1	1	2	2	7
"bronze"	1	8 (24%)	0	0	0
"melanistic"	0	0	0	2	1

Inheritance of color morphs

The different color morphs can be seen in broods from different types of females (Table 5), verifying that at these localities a single polymorphic species is involved. The sample is not big enough for allowing definite conclusions about inheritance, but some indications can be obtained. The three "bronze" females only gave birth to "bronze" juveniles (one brood) or mixture of "bronze" and narrow banded "tigrina" juveniles (two broods). No other female than these three (in the total sample of 23 pregnant females) gave birth to "bronze" juveniles. Further, the "tigrina" pattern seems dominant as it shows up in several broods, and is always expressed when the female has a pattern towards "tigrina". In the three pure "tigrina" females that gave birth all juveniles were of "tigrina" type (N=8). Further (although not seen from the table) eleven females with other pattern types than "tigrina" also produced "tigrina" juveniles together with other morphs. Thus "tigrina" and "bronze" were the most frequent juvenile morphs in the *dinniki* material.

FIG. 6. The narrow-banded "tigrina" morph of *Vipera dinniki*, from Kardyvach (ZIG).

FIG. 8. The "bronze" morph of *Vipera dinniki*, from Mt. Loyub (ZIG).

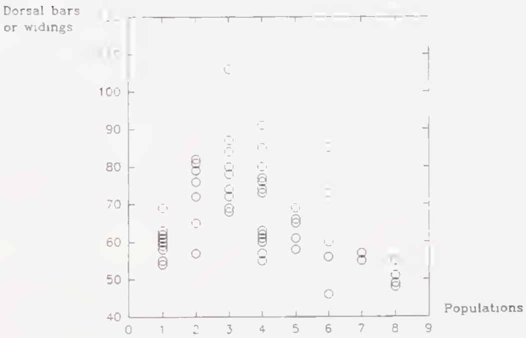

FIG. 9. Distribution of number of bars and/or windings in the dorsal zig-zag band in the different *Vipera dinniki* populations, running from west towards east in high Caucasus (I: Fisht, 2: Loyub, 3: Kardyvach, 4: Impsi, 5: "central Caucasus" (=Elbrus and surroundings), 6: "east Caucasus" (=mountains above Lagodechi, Georgia), and *V. kaznakovi* populations (7: Sochi-Adler, 8: Hopa, Artwin).

Of the juveniles taken together half (50%) were "tigrina". When considering the Kardyvach material alone (10 broods with 29 juveniles) 52% were "tigrina" while 24% were "bronze". Of 47 adults observed in the field in July 1991 at this locality 24% were "bronze". The number of adult "tigrina" observed (33%) was lower than the frequency of juvenile "tigrina" produced while the number of adult "ursinii" was rather high (27%). This slight reduction of the "tigrina" pattern between juveniles and adults can have an ontogenetic explanation as pattern often fades with age.

In other populations examined the combinations of morphs were different, with other patterns dominating. The number of windings is much lower in Fisht compared to the Kardyvach sample (with "tigrina" predominating). "Melanism" was only observed at Fisht, but it is known also from Aishkha-II and the Bezymyanka River. "Bronze" was only observed at Kardyvach and Impsi. When comparing field observations and all available specimens in collections, this morph was not documented from any other locality along the entire area. At Impsi the typical "dinniki" pattern was dominating (56%).

Analysis of scalation characters in the different dinniki *populations*

Geographic variation in color morph frequencies is also reflected in scalation characters (Table 4). Going from the west Caucasus towards east, certain changes could be observed. The central and east Caucasus samples of *dinniki* have higher mean number of preventral plates, lower

TABLE 4. Variation in scalation and color pattern characters between different isolated populations of *Vipera dinniki* The localities include a series of isolates at close distance in the Caucasus State Biosphere Reserve (1: Mt Fisht/Oshten; 2: Mt. Loyub; 3: Lake Kardyvach; 4: Lake Impsi), and 5: central Caucasian population (Mt Elbrus region) and 6: east Caucasian population (the mountain region of Lagodekhi) sample. Given as Mean value, S.E. and range (except for preventrals and apicals). Number of specimens in parentheses.

	1 (13)	2 (9)	3 (16)	4 (16)	5 (7)	6 (6)
Pre-ventrals	1.4±0.2	1.7±0.3	1.9±0.2	1.7±0.2	2.0±0.2	2.2±0.5
Ventrals	135.3 ±1.05 129-141	135.3 ±1.0 131-140	132.8 ±1.1 126-141	134.4 ±0.7 129-139	133.3 ±0.9 130-136	131.2 ±1.2 127-134
Rostral index	1.1±0.1 1.0-1.4	1.1±0.0 1.0-1.3	1.1±0.0 0.9-1.3	1.1±0.1 0.9-1.1	1.0±0.0 0.9-1.3	1.1±0.1 1.0-1.3
Apicals	1.46 ±0.14	1.33 ±0.17	1.47 ±0.13	1.50 ±0.13	1.00 ±0.00	1.17 ±0.17
Circum-oculars*	18.3 ±0.5 15-21	19.1 ±1.0 14-23	18.4 ±0.5 14-22	17.8 ±0.6 13-22	17.3 ±0.9 12-19	19.2 ±0.8 18-23
Loreals*	8.23 ±0.6 5-12	8.44 ±0.8 5-12	9.0 ±0.6 6-12	8.13 ±0.4 6-11	6.86 ±0.6 5-9	7.17 ±0.9 3-9
Crown scales	12.46 ±0.8 9-19	14.78 ±1.6 9-23	14.33 ±0.7 10-18	15.19 ±0.9 10-22	12.43 ±0.5 10-14	16.67 ±1.3 12-21
Zig-zag wind-ings **	60.8 ±1.3 54-69	73.14 ±3.5 57-82	79.78 ±3.9 68-106	70.07 ±2.8 55-91	63.57 ±1.4 58-69	64.0 ±6.8 46-85

* Counted as sum of both sides.
** Unicolored "bronze" specimens as well as completely bilineate and melanistic specimens excluded.

TABLE 5. Phenotypic expression of inheritance of color patterns in 23 clutches of *Vipera dinniki*. Given as taxa, female morph, number of clutches, numeric distribution of morphs in group of juveniles of each female morph.

Taxa (LOCALITY)	Female morph	No. of clutches	No. of juvenile morphs
kaznakovi (DAGOMYS)	"kaznakovi"	3	8 "kaznakovi"
dinniki (FISHT)	"melanism"	1	6 "dinniki"
			1 "ursinii"
dinniki (KARKYVACH)	"dinniki"	3	4 "dinniki"
			2 "tigrina"
	"bronze"	3	7 "bronze"
			4 "tigrina" (narrow-banded)
	"tigrina"	2	4 "tigrina"
	"dinniki/ursinii"	1	2 "tigrina"
			2 "ursinii"
	"tigrina/ursinii"	1	2 "tigrina"
			1 "tigrina/ursinii"
			1"dinniki/bilineate"
dinniki (IMPSI)	"dinniki"	6	7 "dinniki"
			4 "spotted-divided"
			4 "tigrina
			2 "bilineate"
	"ursinii"	1	2"bilineate/tigrina 1 "bilineate"
	"ursinii/tigrina"	1	1"bilineate/tigrina"
			1 "tigrina/ursinii"
	"tigrina"	1	4 "tigrina"

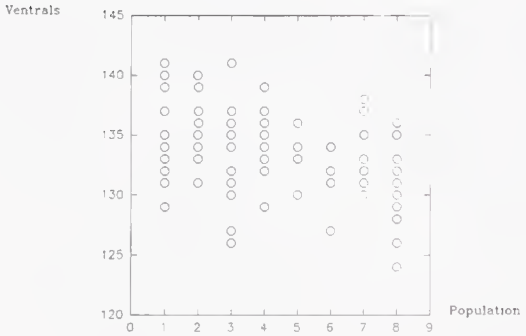

FIG. 10. Distribution of ventral numbers in the different *Vipera dinniki* populations, running from west towards east in high Caucasus (1: Fisht, 2: Loyub, 3: Kardyvach, 4: Impsi, 5: "central Caucasus" (=Elbrus and surroundings), 6: "east Caucasus" (=mountains above Lagodechi, Georgia), and *V. kaznakovi* populations (7: Sochi-Adler, 8: Hopa, Artwin).

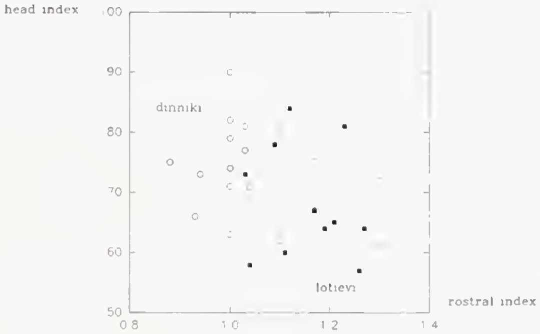

FIG. 12. Head index (breadth/length) and rostral index (height/ breadth) in sympatric sibling species of east Caucasus. White circles= *V. dinniki* ("east-dinniki"); black squares= *V. lotievi*.

mean number of apical scales, and lower number of loreal scales. Also the number of ventrals showed a slight decrease towards the east, a pattern also observed between northwestern and southern populations of *Vipera kaznakovi* (Fig. 10).

Analysis of scalation characters in the different *dinniki* morphs

In subalpine and alpine mountain belts of the west Caucasus (eastward to the basin of the Big Laba River) the "ursinii" morph belongs to the same species as the rest of the mountain vipers: *Vipera dinniki*. But in the extreme eastern part of the west Caucasus, and the central and east parts of the high Caucasus, the "ursinii" and "bronze" morphs belong to a different species. An examination of the morphology of the different morphs clearly indicate that in the eastern half of high Caucasus there are two sympatric species (Figs. 11 and 12).

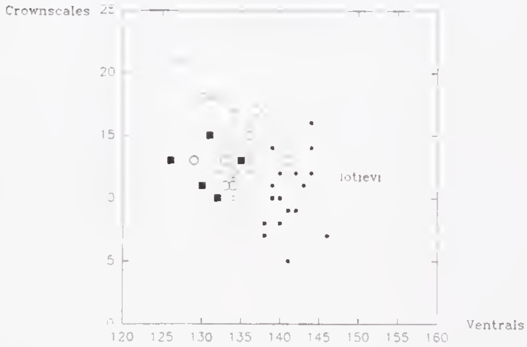

FIG. 11. Numbers of crown scales and ventral plates in "ursinii/ bronze" and "dinniki" morphs and sympatric sibling species of west and east Caucasus. The dotted line indicate the main separation between *V. lotievi* and the *V. dinniki* from different regions. Big white circles= the "dinniki" morph of western Caucasus (*V. dinniki*); big black squares= the "ursinii/bronze" morphs of western Caucasus (*V. dinniki*); small white circles= the "dinniki" morph of eastern Caucasus (*V. dinniki*="east-dinniki"); small black squares= the "ursinii/bronze" morphs of eastern Caucasus (*V. lotievi*)

Vipera kaznakovi (Fig. 4).

This species also shows some regional variation, although not so pronounced as in *V. dinniki*. When comparing the southern (Turkish) populations with the northern (Russian) ones, differences in color pattern as well as in scalation could be detected. Specimens from the southernmost population in Hopa (Turkey) are more yellowish in ground color compared to the snakes in the northern parts (Dagomys). To the contrary, specimens in the north often have more black areas on the body and often the orange or reddish ground color is expressed only as two dorsolateral rows of spots. Melanism is frequent in this northern

TABLE 6. Variation in scalation and color pattern characters between the northern and southern *Vipera kaznakovi* populations. The samples are from northeastern Black Sea regions in Russia (Sochi-Adler); and from northeastern Turkish Anatolia (Hopa, Artvin province). Given as Mean value, S.E. and range (except for preventrals and apicals). Number of specimens in parentheses.

	Sochi - Adler (17)	Hopa (13)
Preventrals	1.41±0.19	1.54±0.18
Ventrals	133.8±0.6, 130-138	130.4±0.9, 124-136
Rostral index	1.1±0.02, 1.0-1.27	1.1±0.06, 0.87-1.5
Apicals	1.50±0.13	1.64±0.14
Circumoculars*	20.0±0.48, 16-23	19.31±0.43, 15-21
Loreals*	11.06±0.76, 7-16	8.69±0.60, 5-12
Crown scales	14.94±0.92, 10-23	17.33±1.08, 11-22
Zig-zag windings**	56.33±0.67, 55-57	50.75±1.55, 48-55

* Counted as sum of both sides.
** Four completely bilineate and melanistic specimens are excluded.

TABLE 7. Allele frequencies of polymorphic loci (see Table 2 for locus abbreviations). For taxon abbreviations, sample sizes and localities, see Table 1.

Locus	Allele	KA 1	KA 2	DI 1	DI 2	DI 3	DI 4	LOT	ERI	BER
Adh-1	-100	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	
	-110									1.00
Gpi-1	-100	0.75	1.00	1.00	1.00	1.00	1.00			
	-50	0.25						1.00	1.00	
	-75									1.00
Hk-1	-100	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	
	-120									1.00
Idh-1	-100	1.00	1.00	0.93	0.86	0.83	0.97	1.00	1.00	
	-10			0.07	0.14	0.17	0.03			
	-130									1.00
Idh-2	100	1.00	1.00	1.00	1.00	1.00	1.00	1.00		1.00
	130								0.10	
	180								0.90	
Ldh-2	100	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.77
	120									0.23
Pgm-2	100	1.00	1.00	0.71	1.00	1.00	0.88	1.00	1.00	
	103									1.00
	105			0.29			0.12			
Sod-1	100			0.71	0.21	1.00	0.71			
	33	0.50	0.12	0.29	0.79		0.29	1.00	1.00	
	95	0.50	0.88							
	103									1.00

population, a phenomenon never observed in the southern one. It can be added that melanistic specimens have been found in more or less all Russian populations. During a stay 1992 at an inland locality along the Psou River we observed ten adult specimens of which all but three were melanistic.

In scalation characters there are some minor differences: e.g. the Hopa population has a lower mean value in number of ventrals and crown scales (Table 6).

TABLE 8. Genetic distances (above diagonal) and genetic identities (below diagonal) of eight OTUs of Caucasus vipers and *Vipera berus*. 1- *kaznakovi*, Dagomys; 2- *kaznakovi*, Rudorova; 3- *dinniki*, Fisht; 4- *dinniki*, Impsi; 5- *dinniki*, Aishka; 6- *dinniki*, Kardyvach; 7- *lotievii;* 8- *berus;* 9- *eriwanensis*.

OTU	1	2	3	4	5	6	7	8	9
1		0.01356	0.03323	0.01501	0.04121	0.02912	0.03759	0.25418	0.07680
2	0.98653		0.04061	0.03826	0.03849	0.03810	0.07696	0.25325	0.11778
3	0.96731	0.96020		0.01767	0.00558	0.00125	0.06515	0.25325	0.10549
4	0.98511	0.96246	0.98249		0.02769	0.01358	0.03962	0.25325	0.07892
5	0.95962	0.96224	0.99443	0.97269		0.00448	0.07774	0.25325	0.11859
6	0.97130	0.96262	0.99875	0.98651	0.99553		0.06021	0.25325	0.10034
7	0.96311	0.92593	0.93692	0.96115	0.92521	0.94156		0.25325	0.03774
8	0.77555	0.77627	0.77627	0.77627	0.77627	0.77627	0.77627		0.30214
9	0.92607	0.88889	0.89989	0.92412	0.88817	0.90453	0.96296	0.73924	

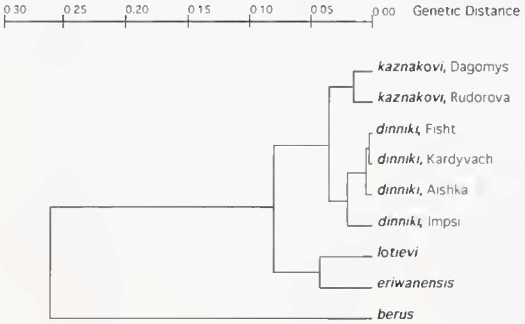

FIG. 13. UPGMA phenogram clustering modified Nei genetic distances (Hillis 1984) among eight OTUs of Caucasus vipers and *Vipera berus*.

Phenetic analysis of electrophoretic data

Of twenty-seven presumptive gene loci scored, from 14 enzyme systems and one general protein, only eight were polymorphic. Allelic products (allozymes) for each locus were designated numerically in order of increasing anodal mobility to identify genotypes (Table 7), with the relative mobility of the most common allele in each locus as a standard of reference ("100"). Despite the fact that average sample sizes were rather small for obtaining significant results of frequency analysis we elected not to pool different localities (except for *eriwanensis),* for reasons of objectivity discussed above, although we recognize the obvious risks of missing rare alleles through this procedure.

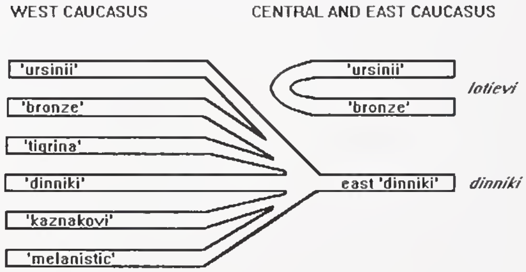

FIG. 14. The different types of morphs and species found in west and east high Caucasus.

Modified Nei genetic distances (Nei, 1978; Hillis, 1984) between OTUs were computed from allele frequencies (Table 8). A UPGMA phenogram (Sneath and Sokal, 1973) was constructed from the distance data (Fig. 13). This phenogram illustrates only the relative degree of genetic differentiation among OTUs and should not be considered as a phylogenetic tree. Observed genotype distribution of the most polymorphic locus (Sod-1) in the largest individual sample (Kardyvach; N=17) was tested against Hardy-Weinberg expectations to investigate homogeneity and possible biased sampling due to potential within-locality sympatry of taxa (i.e. Wahlund effect). A chi-square test performed to obtain the goodness-of-fit between observed and expected distributions ($X^2=0.060$, 1 df, P=0.90) strongly support unbiased sampling. The genetic analysis confirms that the four populations from the western Main Caucasus (Fisht, Kardyvach, Aishka-

II and Impsi) belong to one polymorphic taxonomic unit *(V. dinniki)*.

Discussion

The original question, whether polymorphism or sibling species are the prevailing phenomenon in the Caucasian populations of vipers, must be answered with yes in both cases. In the western Caucasus a large number of morphs can be recognized. We separate six different ones in that region while the number is restricted to three in the eastern and central parts of the mountain range (Fig. 14). As seen in the reproductive studies all six morphs ("melanism", "bilineat-kaznakovi", typical "dinniki" (including "nebulosa"), "tigrina", "bronze", and "ursinii") in the mountain habitats in the western Caucasus belong to a single species. This is also verified by cladistic analyses of biochemical and morphological data (Nilson et al., 1994). The different morphs can be seen sympatric and syntopic in suitable rocky, vegetation-rich, and moist habitats. There seems to be a certain inheritance pattern, but in principle most morphs can occur in the same brood (Table 5). Certain areas seem to have a certain range of frequency of the various morphs, which might be unique for that particular area. It must be kept in mind that only a random number of populations have been investigated, and it is likely that additional morphs will be described from other isolated localities. The isolation of the different mountains in the Caucasus is much comparable with e.g. the Andes of Ecuador, or the Galapagos islands, and a high degree of isolation has obviously taken place between the different mountain peaks.

How could this particular polymorphic pattern in the subalpine *Vipera dinniki* populations have evolved? The present warm and wet subtropical Colchis area of western Transcaucasia at the Black Sea coast has, as indicated by botanical evidence, served as a refuge for animals and plants during the whole of Pliocene and Pleistocene (Tuniyev, 1990). The total region has varied much in size during the Pleistocene glacial and interglacial periods but remained a permanent relict key area. The warm and wet adapted *Vipera kaznakovi* is distributed in this area today, and it has been considered that this species has had an occurrence in this region for a long time (Orlov and Tuniyev, 1990; Tuniyev, 1990) due to the climatic stability.

A scenario for the arise of various polymorphic *V. dinniki* populations could have taken place in two steps and been like this:

1. First, the evolution of *Vipera dinniki*. If the Pliocene Colchis region decreased in range during a Pleistocene glacial period there are two alternatives for the species in that part of the old range that have turned cold: the viper could disappear or it could adapt. If it disappears it can be done in two ways: the snake becomes extinct or it is forced down to the remaining warm zone. In both these two cases the net result will be a reduced range for the single species (*kaznakovi*) in the remaining warm and wet Colchis refuge. In the second case, if the viper is adapted to the new climate, "the cold zone", it would be a new, physiologically different race.

In an interglacial period when the climate becomes warmer again the warm and wet Colchis zone expands and "the cold zone" is forced upwards to higher altitudes in the mountains. Now, if there is a cold-adapted physiological race, again two alternatives are open: first, it could adapt, or second, it could disappear. If it is adapted back to the new warm environment, it can either go back into and unite with the old species (*kaznakovi*) which under the new climatic conditions can expand its range, or it could form a sympatric but physiological distinct taxon. In the case of sympatry there is a good possibility that it would disappear due to competition (if not ecological distinct). In both these last situations there is a great probability that the original species (*kaznakovi*) would return and again cover its original range.

If the new physiological race disappears from the region it could again be done in two ways: it simply becomes extinct due to the new "severe" climatic conditions, or it migrates upwards following the pushed up "cold zone". In the first case again only the original species (*kaznakovi*) will remain in its new expanded (=original) warm and wet range. In the second case there will be a number of cold-adapted populations at higher altitudes (the present different *dinniki*, "east-dinniki", *darevskii* populations). This would mean a number of isolated populations as the mountains of the Caucasus are rather steep and subalpine/alpine habitats are in many cases climatologically isolated. Further the geology is very complex reflecting a high degree of local endemism among plants and animals. One can postulate that the different populations, or groups of populations, must have become adapted to local conditions.

2. This may have been the prerequisite for an evolution of a polymorphic *Vipera dinniki*. During Pleistocene there were several glacial and interglacial periods, and the scenario postulated above would have been repeated several times, and during each interglacial the "cold zone" and its cold adapted viper were forced downwards with the result of a secondary contact with neighboring populations. Unique morphs could by this be spread to adjacent populations etc.

Today we can see a polymorphic color-pattern in the cold adapted *Vipera dinniki* that to a high degree is unique for one or a small number of populations in close connection, e.g. the "bronze" and "tigrina" morphs, but not seen in all populations. *Vipera dinniki* could be a polymorphic species, constituent of a number of populations that during periods are isolated from each other, but irregularly have secondary contact. In some cases the isolation could also have been more permanent resulting in a number of sister species along the range, a possible phylogenetic pattern we currently are trying to solve with genetic studies. But overall, the relative genetic differentiation between examined taxa and degree of genetic polymorphism were low, indicating a rather recent divergence.

The present geographical distribution and morphological pattern of *Vipera dinniki*, as well as the fact that in all subalpine mountain regions where *V. dinniki* is located today, there also are fragmented more or less subtropical Colchian refugia at lower altitudes, inhabited by *V. kaznakovi* (Tuniyev, 1990). This supports the evolutionary pattern postulated above.

Further east in the mountains, the habitats get drier with moist areas restricted to stream surroundings and lake shores. In central Caucasus (Mt. Elbrus) the number of morphs decreases to two ("ursinii" and "dinniki") or three in the eastern Caucasus (where again a form of "bronze" morph appears) (Fig. 14).

Now, in the region of the central and eastern Caucasus two different sympatric species are involved. As shown in the results section above, at several localities the two morphs "dinniki" and "ursinii" actually represents two sympatric species from the *kaznakovi* line and the *ursinii* line respectively. It is obvious that these two species are sympatric (but not necessarily syntopic) in a large number of places in these eastern and central parts of the main range of the Caucasus. We have in our material such records of sympatry from Mt. Elbrus in the central Caucasus (Figs. 15-18); mountains north of Lagodechi in the eastern Caucasus; at Itum- Kali, Checheno-Ingushetia (Fig. 19); and various records from Dagestan, besides several isolated records of both species from the entire eastern and central Caucasus range.

Vipers of the *kaznakovi* group are known from subalpine meadows, and snakes of the *ursinii* group have been found in the semiarid hollows between the main range and the Skalisty (Rocky) range. At several places with connection of subalpine meadows and semiarid hollows the two species have a sympatric occurrence (and syntopic along the ecotones of both types of landscapes). The *ursinii* line has probably never been widely represented in the perpetually humid western Caucasus, as this taxon is adapted to dry environments, but as stated earlier, in the extreme eastern part of

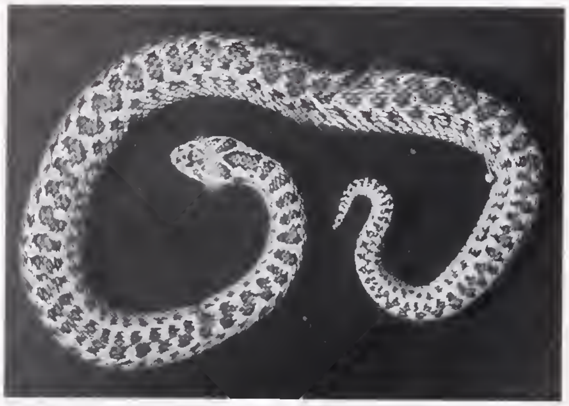

FIG. 15. Male of the east *Vipera dinniki* ("east-dinniki") at the sympatric locality, Mt Elbrus, central Caucasus. This specimen was found together with the *Vipera lotievi* on figures 17 and 18 (ZIG).

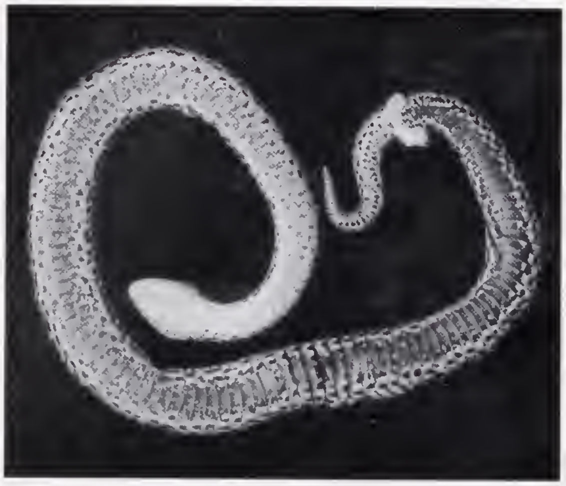

FIG. 16. Ventral side of the male of the east *Vipera dinniki* ("east-dinniki") at the sympatric locality, Mt Elbrus, central Caucasus from figure 15 (ZIG).

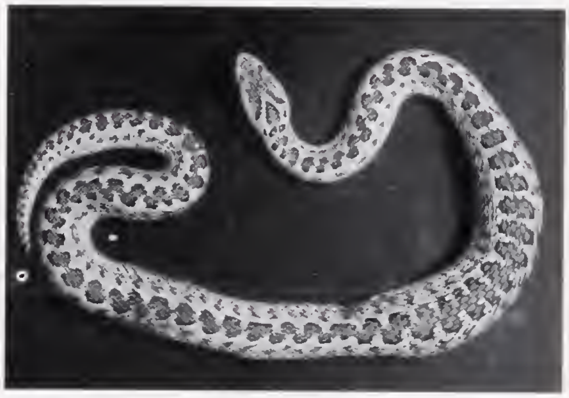

FIG. 17. Female of the *Vipera lotievi* at the sympatric locality, Mt Elbrus, central Caucasus. This specimen was sympatric with the *Vipera dinniki* ("east-dinniki") on photo 15 and 16 (ZIG).

FIG. 18. Ventral side of the female of the *Vipera lotievi* at the sympatric locality, Mt Elbrus, central Caucasus from photo 17 (ZIG).

the west Caucasus there are some isolated populations of the *ursinii* complex (from the Abishiz-Akhuba Range to Mt. Elburs).

The eastern form of *dinniki* is not polymorphic in the same way as the western populations. Rather the main color pattern is the typical "nebulosa-dinniki" kind of pattern. In sympatric areas the *ursinii* taxon is more or less typical "mountain ursinii" in color pattern although with a certain similarity to the type of bilineate pattern seen in the southwest European *V. seoanei* (Fig. 20). In some populations of this taxon in Checheno-Ingushetia, a certain fraction of the snakes are also "bronze" colored (Plate 1d). This pattern type has not been observed in the sympatric populations. The "nebulosa-dinniki" pattern of eastern *dinniki* and the "seoanei-ursinii" pattern of Caucasian *ursinii* taxon shows great similarities, and can in some specimens be difficult to separate. This is certainly the reason for much of the confusion in earlier studies of these vipers.

However, at a closer examination, the two taxa are possible to identify (Table 9). In *ursinii* the belly is lighter and the snout more concave with raised canthus. The preocular is large and in contact with the nasal, and the apical is always single. Also the crownscales are less fragmented. There

TABLE 9. Main morphological characteristics separating the sympatric *Vipera lotievi* and "east-dinniki".

	lotievi	"east-dinniki"
White belly	+	-
Preocular in contact with nasal	+	-
Snout concave	+	-
Mean no. of ventrals	>140	<136
Always a single apical	+	+/-
Mean no. of crown scales	<11	>12
Parietal ocellated spot	+	-
Iris gold-edged in life	-	+

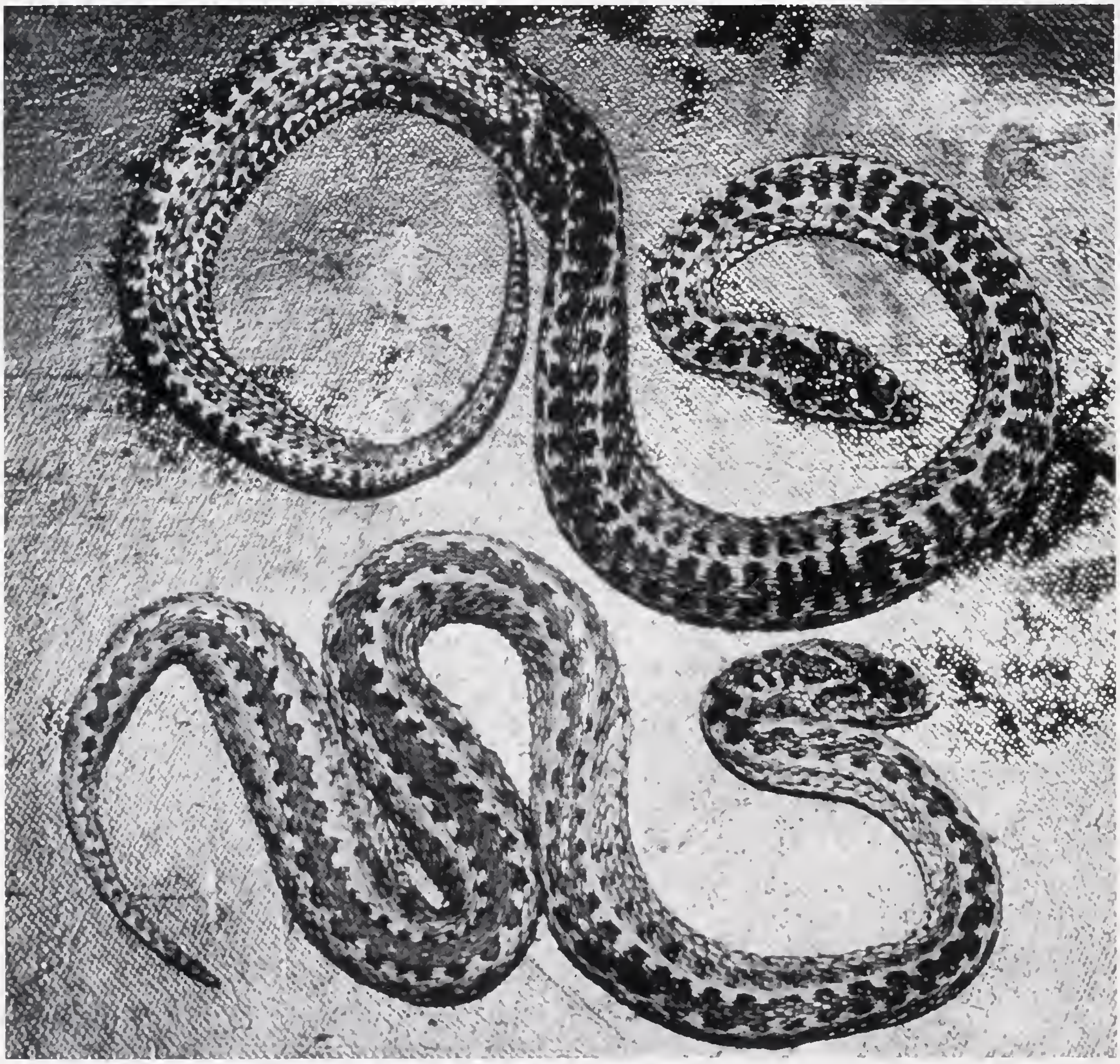

FIG. 19. *Vipera dinniki* ("east-dinniki")(upper) and *Vipera lotievi* (lower) from Itum Kali, Checheno-Ingushetia. These specimens were found together at the same time (ZIEr).

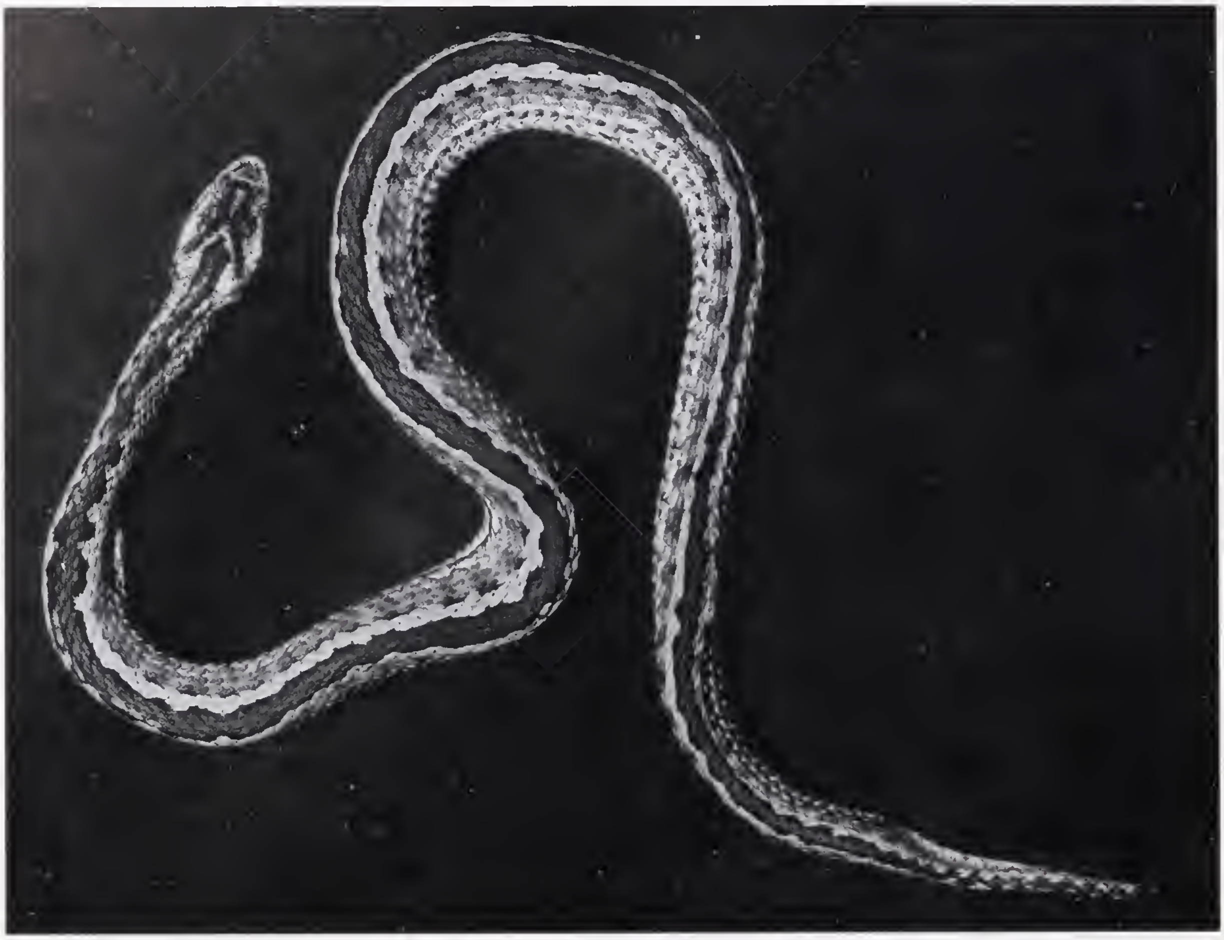

FIG. 20. Female of *Vipera lotievi* sp.n. from the type locality, the surroundings of Armkhi Village, Checheno-Ingushetia, Nazranovskiy District.

always seems to be an ocellated spot present on the parietal plate, and the ventral number is high. In the "east dinniki" taxon the belly is blackish and the snout more flat, the preocular is always separated from the nasal, and there is a higher fragmentation of the crown scales. The iris always seems to be gold-edged in live specimens (as is the case for the entire *V. kaznakovi* complex), and this is specially distinct in younger specimens. The ventral number is lower.

Although in many ways similar in pholidosis the *kaznakovi* lineage and the *ursinii* lineage are genetically well separated and paraphyletic. Immunological comparisons of blood serum albumins indicate that *Vipera kaznakovi* and related taxa belongs to the *berus-aspis* branch while *ursinii* constitute a distinct evolutionary lineage (Herrmann et al., 1987; 1992). The genetic comparisons of the west Caucasian *dinniki* and the *ursinii* taxon from Checheno-Ingushetia point in the same direction (this study; Nilson et al., 1994) except that the closer relation between *kaznakovi* and *aspis* was not supported. Thus this morphological similarity between the two lineages in Caucasus might be a case of convergent adaptation towards a similar habitat, although Muellerian mimicry might be involved.

A number of nominal taxa related to these populations are recognized from this geographical region (Russian Republic, Georgia, Azarbaidjan and Armenia): *renardi*,

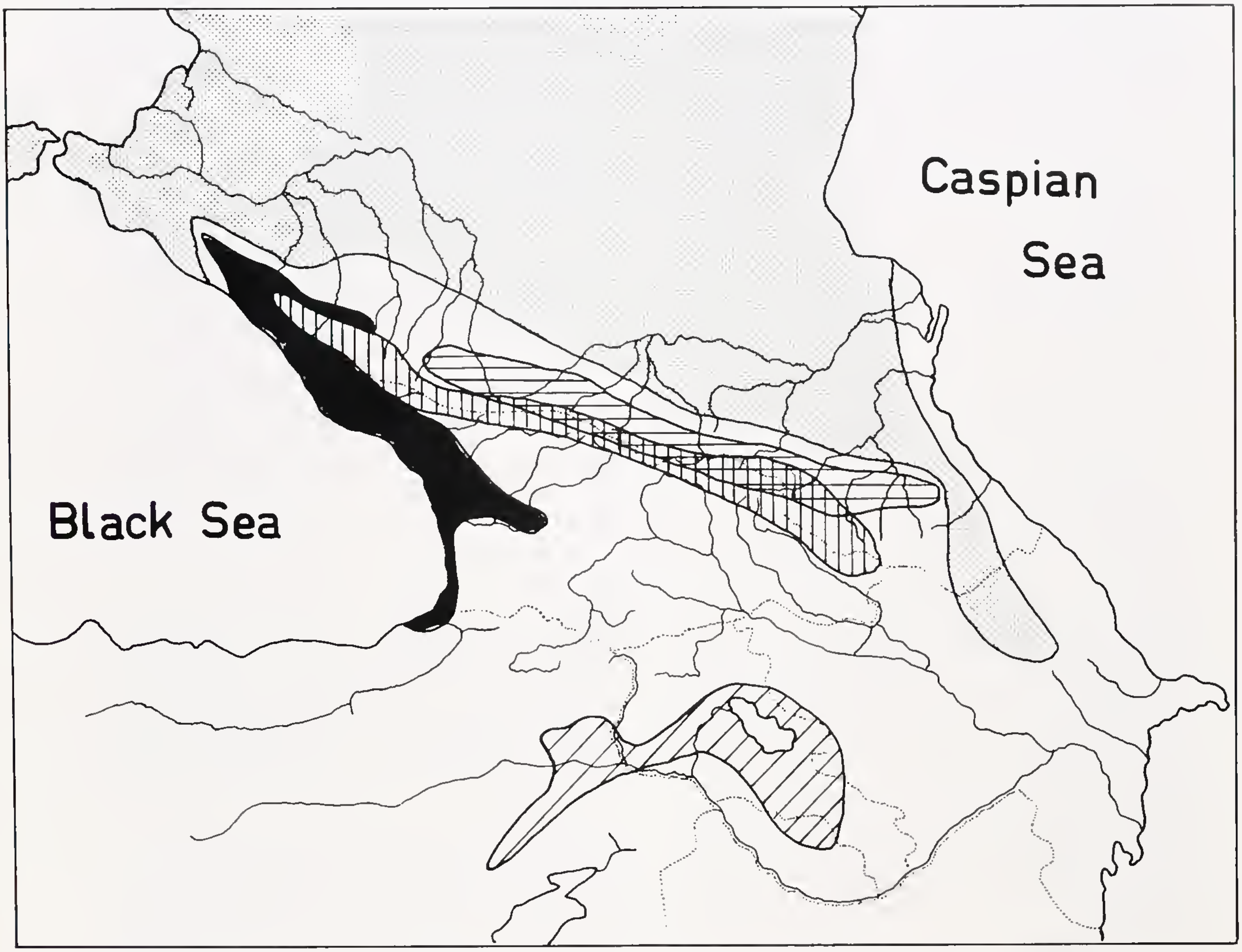

FIG. 21. Distribution of the vipers of the Caucasus and adjacent areas discussed in this paper. Light stippled= *Vipera renardi;* dark stippled= *Vipera kaznakovi;* cross-hatching= *Vipera (u.) eriwanensis;* horizontal hatching= *Vipera lotievi;* vertical hatching= *Vipera dinniki.* Due to environmental reasons the distribution of all taxa are only fragmented within the depictured ranges, a situation especially pronounced in *renardi.* Also occurring in the region and related to the vipers discussed are the north Iranian populations of the *ursinii* complex *('ebneri')* that penetrates into southeastern Azarbaidjan in the Talysh mountains, *Vipera darevskii* (of the *kaznakovi* complex) which has its known distribution restricted to northwestern Armenia (Mt. Legli), and *V. pontica* from the Artwin province in Turkey. Other species of vipers not discussed here occur sympatrically in the region.

kaznakovi, *darevskii*, *eriwanensis*, *dinniki* (Fig. 21).

What names are then available for these two different sympatric central and east Caucasian taxa? *Vipera dinniki* was originally described from Malaya Laba and Svanetia, localities situated on the western side of the upper parts of Little Laba River and the high-mountain basin of the Inguri River, respectively (Orlov and Tuniyev, 1986). The type locality has been restricted to Malaya Laba (by selection of 'The Museum of Natural History of Kharkov State University specimen no. 26044' as lectotype; Vedmederja et al., 1986). The type locality is situated in the western Caucasus and the polymorphic western

TABLE 10. Variation, given as Mean ±S.E. and range (for apicals in % of specimens with two plates) of selected morphological characters in *Vipera eriwanensis* (N=44), *Vipera lotievi* (N=14, if not otherwise stated), and *Vipera renardi* (N=42).

	eriwanensis	*lotievi*	*renardi*
Ventrals	137.66±0.34, 133-143	141.29±0.54, 138-144	142.67±0.54, 135-150
Subcaudals - males	35.0±0.4, 32-39 (N=25)	35.5±0.7, 33-38 (N=6)	34.7±0.4, 31-38 (N=25)
Subcaudals - females	26.6±0.4, 23-30 (N=19)	25.3±0.6, 23-27 (N=8)	26.8±0.4, 24-29 (N=17)
Preventrals	2.00±0.10, 1-3	2.43±0.14, 2-3	2.27±0.10, 1-3
Scale rows on neck	21.07±0.05 21-23	21.00±0.00, 21	21.24±0.095, 21-23
Midbody scale rows	21.02±0.02, 21-22	20.64±0.20, 19-21	20.98±0.02, 20-21
Ventral level of scale row reduction****	94.70±0.94, 82-109	87.50±6.49, 17-106	96.38±1.50, 71-127
Supralabials*	18.02±0.08, 17-20	17.36±0.29, 16-20	17.81±0.11, 14-19
Sublabials*	19.93±0.22, 17-25	19.64±0.49, 15-22	20.26±0.18, 18-24
Circumoculars*	18.61±0.35 (6-),15-22	18.50±0.56, 14-22	18.57±0.23, 16-21
Loreals*	10.18±0.42, 5-18	7.93±0.52, 5-12	8.76±0.32 , 4-12
Crown scales	13.07±0.36, 9-19	10.93±0.68, 7-16	10.43±0.40, 6-16
Chinshields	4.07±0.05, 4-6	4.64±0.25, 4-6	4.21±0.11, 4-8
Gulars	4.50±0.11, 3-6	3.71±0.13, 3-4	4.31±0.10, 3-6
Zig-Zag windings	65.77±0.80, 56-79	65.50±2.88, 50-81 ***	59.31±0.70, 51-72
rostral index (height/width)	1.23±0.02, 0.79-1.67	1.11±0.03, 0.92-1.27	1 04±0.01, 0.91-1.20
Apicals	1.00±0.00	1.27±0.07	1.07±0.04
CV?	0**	27.3	7.1

* Counted as sum of both sides. ** No specimen with two apicals, but one with three. Also two specimens with no apical; thus 6.8% total with more than one or without apical. *** N=16. Four unicolored "bronze" specimens not included. **** reduction from 21 to 19 dorsal scale rows (at ventral number)

dinniki populations must be referred to this name. The complex picture of separation and similarities between all the different isolated mountain populations in the western Caucasus demands parallel genetic studies. The name *Vipera kaznakowi orientalis* (Vedmederja, 1984; non *Vipera orientalis* Seba, 1734-1735; Daudin, 1801-1803; Shaw, 1802) was given by Vedmederja (1984) for eastern vipers at Lagodechi. As stated above at this locality the two species are sympatric, but the name *orientalis* is not available (nomen nudum - Orlov and Tuniyev, 1986). Besides the color pattern, the eastern *dinniki* is as well somewhat morphologically distinguished compared to western *dinniki* (Table 4). It is geographically separated from the western *dinniki* and it might be justified to treat it as a taxon of its own. The genetic distance has

TABLE 11. Frequency of certain characteristics in the populations (in percentage of investigated specimens)

	eriwanensis N=44	*lotievi* N=14	*renardi* N=42
Divided parietals	20.5	14.3	45.2
Divided frontal	4.5	14.3	14.3
Preocular(s) in contact with nasal	22.7	78.6	81.0
Without upper nasal split	71.4	43.8	61.5
Supralabial dark sutures absent	46.5	71.4	0.0
Lateral body blotches absent	38.6	28.6	0.0
Snout concave on dorsal side	51.2	78.6	78.6
Belly whitish (not dark)	71.8	78.6	17.5

however not yet been calculated as fundamental material still is lacking. Thereby we prefer not to draw any taxonomic conclusion about the "east-dinniki" populations. We preserve the terra typica restricta for *Vipera dinniki* to Malaya Laba.

The other question is to what taxon does the viper of the *ursinii* complex belong. In principle north of the Caucasus on the dry steppes *renardi* occurs while in the Armenian highlands south of the Caucasus *eriwanensis* is found (the species status of *renardi* is analyzed and discussed in Joger et al., 1992). We consider also *eriwanensis* as an evolutionary species (Höggren et al., 1993; Nilson et al., 1994). The Caucasian form is geographically separated from these two taxa, and morphologically distinguished (Tables 10 and 11, Figs. 17, 19-20, Plate 1d), also supported by genetic distinction (Tables 7, 8; Nilson et al., 1994). Taxonomically it does not fit in with these two allopatric *ursinii* s.l. taxa, although morphological similarity with *eriwanensis* can be noted. As there is no reason to believe reduced reproductive cohesion- all populations traditionally referred to *ursinii* would belong to a single species (albeit divided in several subspecies) according to the biological species concept (BSC). However, all here (and elsewhere- Nilson & Andrén, 1994) recognized taxa in this complex are allopatric and apomorphic in characters (morphological and/or genetic), and as we are interested in a taxonomy that reflects the phylogeny, we find the evolutionary and phylogenetic species concepts preferable (Frost and Hillis, 1990; Frost et al., 1992; see Nilson, 1993, for application on vipers). We therefore recognize it as a separate taxon in this group of vipers.

Taxonomic Account

Vipera lotievi sp.n. (Fig. 22)

Holotype and Terra typica: ZIN 20309, Fig. 22, female, Armkhi, Checheno-Ingushetia, Russia, below Mt. Stolovaya, 2000 m. altitude, 1986-07-20-23. leg. K. Lotiev.

Paratypes: ZIN 20305, Itum-Kali, Checheno-Ingushetia, 1990-08, leg. K. Lotiev; ZIN 20310, Armkhi, Checheno-Ingushetia, below Mt. Stolovaya, 2000 altitude, 1986-07-20-23, leg. K. Lotiev; ZIN 20304, vicinity of village Armkhi, Checheno-Ingushetia, 1988-07, leg. Gizatulin; ZIG 298-306, river Chanty-Argun w. Itum-Kali, Checheno-Ingushetia,

FIG. 22. The female holotype of *Vipera lotievi* (ZIN 20309), Armkhi, Checheno-Ingushetia, below Mt. Stolovaya, 2000 m altitude.

1986-05-28, leg. B.Tuniyev; ZIN 20307, Itum-Kali, Checheno-Ingushetia, 1987-08, leg. Lotiev; ZIN 20312, Armkhi, Checheno-Ingushetia, 1987-09, leg. Lotiev; ZIN 20313, Armkhi and Mt. Stolovaya, Checheno-Ingushetia, 1986-07-20, leg. Gizatulin; ZIG 297, Mt. Elbrus, 1986, leg Filippov, coll. Tuniyev; ZIN 18203, Teberda, State Reserve, Mt. Bolshaya Hatipara, 1969, leg. Zalslavsky; ZIN 18226, Kabardino-Balkaria, vicinity of village Terskol, 1970-08-19, leg. Kireev; ZIN 11996, Caucasus, Gunib, Dagestan, 1909-05-29, leg. Berg; ZIN 20303, Lagodechi, 1988-07, leg. Bakradze.

Diagnosis and definition: A species of the *Vipera ursinii* complex characterized by polymorphism in color-pattern, including "bilineate pattern" of the same kind as in *V. seoanei*, and "bronze" unimorphs. External morphology evolved as typical for mountain taxa of the *ursinii* complex but not similar to any of the other in color pattern.

From the sympatric "east-dinniki" it differs in several scalation characters and in color of the belly (Table 9, Fig. 11). In *lotievi* the belly is generally white, preocular in contact with nasal, snout concave, 138 or more ventrals, always a single apical, less fragmentized crown scales (7-16), parietal ocellated spot present, iris not gold-edged in life. In "east-dinniki" the belly is black, preocular separated from nasal, snout not concave, 136 or less ventrals, apical single or divided, more fragmentized crown scales (10-21), no parietal ocellated spot, iris gold-edged in life.

From the allopatric *renardi* it differs besides color pattern in morphology by having light supralabials (sutures heavily colored in black in *renardi*), a higher rostral index, smaller size, white belly (dark in *renardi*), and a different niche by being alpine (*renardi* is a lowland steppe inhabitant). No future reproductive cohesion can be postulated.

It is separated from the likewise allopatric *eriwanensis* in the Armenian highlands by the semidesert lowland of the Kura River Valley, that separates the Big Caucasus from the Small Caucasus. No connection can be postulated in an evolutionary time frame. Besides color pattern there is a differentiation in morphology by *eriwanensis* having a higher number of crown scales and a somewhat lower ventral count, and preocular separated from nasal to a higher degree (Tables 10 and 11).

Description of holotype (Fig. 22): An adult female, total length 422 mm, tail 41 mm, latter equal to 10.8 % of total length. Length of head, from posterior border last supralabial to tip of snout 16.8 mm, from posterior border of parietals to tip of snout 12.2 mm, breadth of head at broadest part of head 9.5 mm, at level of the eyes 8.0 mm, size of eye horizontally 2.5 mm and vertically 2.0 mm, distance between eye and lip 2.6 mm. Head covered with rather large scales or plates. Two large supraoculars and 1 large frontal plate on top of head, parietals large, frontal separated from supraoculars by 3 and 2 smaller scales on right and left side respectively, 1 canthal and 1 supranasal scale on each canthus rostralis, but the two supranasals are partly united with the apical; 3 intercanthals and 6 intersupraoculars. Height/depth of rostral 3.4/2.7 mm (=1.26), it is bordered by 2 supralabials, 2 internasals and the broad "apical"; eye surrounded by 8 circumoculars on each side, 5 loreals on each side, upper preocular in contact with nasal on both sides, nasal partly divided at upper edge, 8 supralabials, with forth below eye, and 9 sublabials on each side, anterior supralabials not much enlarged compared to posterior ones, 6 second chinshields bordering the anterior ones and 4 scales in the gular row. Dorsal side of snout concave resulting in a pronounced and raised canthus rostralis. Two preventrals and 141 ventrals, 24+1 subcaudals, 21 dorsal scale rows at midbody and on neck one head-length behind the head, 17 dorsal scalerows one head-length anterior to anal. Reduction from 21 to 19 dorsal scale rows at level of ventral number 89. Dorsal pattern consisting of a weakly winding zig-zag band with 48 windings, lateral body pattern dark weakly contrasting towards the lighter dorsal groundcolor. Head pattern consists of 2 dark oblique bands which do not unite, and a posterior band from eye to corner of mouth and somewhat further back along the lateral sides of neck, no dark pattern on chin or in labial region although a very weak dotted pattern at the supralabial sutures can be imagined, ground color light brown with dorsal pattern dark brown and black edged, ventral side light, throat light. Ocellated spot on frontalia.

Variation: See Tables 5 and 6. Besides the variation in scalation a pronounced variation in color and pattern is expressed. Most striking, and unique for the entire *ursinii* complex, is the bronze morph, which is found in 25 % of the investigated specimens (N=40) (Plate 1d).

Distribution: *Vipera lotievi* is distributed in the semiarid 'hollows' between the northern slope of the main Caucasian range and Skalisty range from the upper part of the Kyafar River (range Abishir-Akhuba) eastward to the interior of

Daghestan (see map). Altitudinal span in this region goes from 1200 m up to 1600 m (1800m). Further it is recorded from Mt. Elbrus in the central Caucasus, and mountains north of Lagodechi in the eastern Caucasus, besides several isolated records from the eastern and central Caucasus range.

Habitats: Typical habitats are oreoxerophytes landscapes with semiarid light-forests (like Shibliak), phrygana (with 'tragakant' astragalus) which are very similar to east-Mediterranean types of vegetation. On the upper elevation of the distribution *V. lotievi* reaches the subalpine mountain belt.

"Refuge History": The development of the xerophilous vegetation has taken place since Pliocene in the eastern part of the Caucasian Isthmus. Four main refuges are known: two humid (Colchis and Talysh-Hyrkanian) and two arid-xerophilous (Armenian and Dagestanian). The north Caucasian refuge of oreoxerophits, including shibliak and phryganas are situated along the shale-depression between the main Caucasian Range and the Skalistiy (Rocky) Range. There are several semiarid hollows from central Dagestan (Gunibskoe Plateau) and westward to the beginning of the Kuban River (at the Mt. Elbrus region). The vegetation is composed of *Juniperus oblonga*, *Paliurus spina-christi*, *Cerasus incana*, *Colutea orientalis*, *Berberis vulgaris*, *Astragalus denudatus*, *Celtis glabrata*, *Ephedra procera* and others. This vegetation superficially is very close to the vegetation of the Armenian highland and the mountains of the Near East, but the regions share relatively few species (3-5%). The major part of the plants of these hollows has an east Caucasian origin. For example, 25% of the flora of the Itum-Kali hollow (Checheno-Ingushetia) has east Caucasian origin. Altogether, more than 200 species of plants are endemic to these hollows (Galushko, 1974).

There have been different interpretations about the age of the vegetation in these hollows. Most botanists have been of the opinion that this vegetation has a Pliocene origin (Grossgeim, 1948; Krasnov, 1894; Kuznetsov, 1890), while Galushko (1974) has the opinion that the semiarid hollows of Checheno-Ingushetia are younger than the hollows of Kardino-Balkaria and Osetia in the west and Dagestan in the east, and perhaps not older than Holocene. But the remains of xerophilous flora on the crests between the semiarid hollows are the witness of the existence of a united enormous xerophilous (Mediterranean) refuge, running from Dagestan to the region of Mt. Elbrus. Later, in Pleistocene, this refuge disintegrated to several micro-refuges which have persisted to different extent until present. However, it must be pointed out that although the xerophilous vegetation (including mountain-steppe) had a wide distribution along the shale-depression, it also had the possibility to disperse up to the mountains along the river valleys. Both ways could be used by representatives of the "*ursinii*-species group" of vipers. Besides the "*ursinii*-group" also thermophilous species like *Lacerta strigata*, *Coluber najadum*, and *Elaphe hohenackeri* are present as isolates in these hollows. One should also pay attention to the occurrence of relicts of the xerothermal epoch in the western Caucasus near the mountains Jatyrgvarta and Magisko (Altukhov, 1966), but the xerophilous vegetation did never have any wide development in that area.

Literature Cited

ALTUKHOV, U. D. 1966. [About the high mountain flora of the limestone of Tryu-Yakirgvart]. Problems of botanik, vol. 8, Leningrad. (In Russian).

CLAYTON, J. W. AND D. N. TRETIAK. 1972. Amine-citrate buffers for pH control in starch gel electrophoresis. Journal of the Fisheries Research Board of Canada 29:1169-1172.

DE LORENZO, R. J. AND F. H. RUDDLE. 1969. Genetic control of two electrophoretic variants of glucosephosphate isomerase in the mouse. Biochemical Genetics 3:151-162.

FROST, D. R. AND D. M. HILLIS. 1990. Species in concept and practice: Herpetological applications. Herpetologica 46(1):87-104.

FROST, D. R., A. G. KLUGE AND D. M. HILLIS. 1992. Species in contemporary herpetology: Comments on phylogenetic inference and taxonomy. Herpetological Review 23(2):46-54.

GALUSHKO, A. I. 1974. [On the flora to arid slopes of vicinity of Itumkale (Checheno-Ingushetia)]. Pp. 5-22. *In* Flora and vegetation of the Eastern Caucasus. Ordjonikidze. (In Russian).

GROSSGEIM, A. A. 1948. [Vegetation of the Caucasus]. Publishing House of the Moscow Society of Researcher of Nature. (In Russian).

HARRIS, H. AND D. A. HOPKINSON. 1976. Handbook of Enzyme Electrophoresis in Human Genetics. North-Holland, Amsterdam.

HERRMANN, H.-W., U. JOGER, G. NILSON AND C. G. SIBLEY. 1987. First steps towards a biochemically based reconstruction of the phylogeny of the genus *Vipera*.. Pp. 195-200. *In* J.J. van Gelder, H. Strijbosch and P.J.M. Bergers (eds.), Proceedings of the Fourth Ordinary General Meeting of the Societas Europaea Herpetologica, Nijmegen 1987.

HERRMANN, H.-W., U. JOGER AND G. NILSON. 1992. Molecular phylogeny and systematics of viperine snakes I. General phylogeny of European vipers (*Vipera* sensu strictu). Pp. 219-224. *In* Z. Korsós and I. Kiss (eds.), Proceedings of the Fifth Ordinary General Meeting of the Societas Europaea Herpetologica, Budapest 1991.

HILLIS, D. M. 1984. Misuse and modification of Nei's genetic distance. Systematic Zoology 33:238-240.

HÖGGREN, M., G. NILSON, C. ANDRÉN, N. L. ORLOV AND B. S. TUNIYEV. 1993: Vipers of the Caucasus: Natural History and Systematic Review. Herpetological Natural History 1(2):11-19.

JOGER, U., H.-W. HERRMANN AND G. NILSON. 1992. Molecular phylogeny and systematics of viperine snakes II. A revision of the *Vipera ursinii* complex. Pp. 239-244. *In* Z. Korsós and I. Kiss (eds.), Proceedings of the Fifth Ordinary General Meeting of the Societas Europaea Herpetologica, Budapest 1991.

JOHNSON, A. G., F. M. UTTER AND H. O. HODGINS. 1970. Interspecific variation of tetrazolium oxidase in *Sebastodes* (rockfish). Comparative Biochemistry and Physiology 37:281-285.

KRASNOV, A. N. 1894. [Caucasian chains of mountains, paralleled to Main Ridge, and its role in formation of forest and steppe flora of the western Caucasus]. Transactions of Naturalist Society of the Kharkov University. (In Russian).

KUZNETSOV, N. I. 1890. [Geobotanical investigation of the northern slope of the Caucasus]. Reports of the Russian Geographical Society. Vol. 26. (In Russian)

MURPHY, R. W., J. W. SITES, D. G. BUTH AND C. H. HAUFLER. 1990. Proteins I: Isoenzyme electrophoresis. Pp. 45-126. *In* D.M. Hillis and C. Moritz (eds.), Molecular Systematics. Sinauer, Sunderland, Massachusetts.

NEI, M. 1978. Estimation of average heterozygosity and genetic distance from small number of individuals. Genetics 89:583-590.

NIKOLSKY, A. M. 1913. [Reptiles and Amphibians of the Caucasus]. The Caucasus Museum Press, Tiflis, Georgia. 272 pp. (In Russian).

NIKOLSKY, A. M. 1916. Fauna of Russia and adjacent countries, Reptiles, Vol. 2. (1964: Israel Program for Scientific Translations, Jerusalem, vi+247 pp.).

NILSON, G. 1995. Venomous snakes in west Asia: -Applicability of current species concepts. Proceedings of the Asiatic Herpetological Congress. In Press.

NILSON, G. AND C. ANDRÉN. 1986. The mountain Vipers of the Middle East- The *Vipera xanthina* complex (Reptilia, Viperidae). Bonner Zoologische Monografien 20:1-90.

NILSON, G. AND C. ANDRÉN. 1994. The meadow and steppe vipers of Europe and Asia, the *Vipera ursinii* complex. Submitted.

NILSON, G., M. HÖGGREN, B. S. TUNIYEV, N. L. ORLOV AND C. ANDRÉN. 1994. Phylogeny of the vipers of the Caucasus (Reptilia, Viperidae). Zoologica Scripta. (In press).

ORLOV, N. L. AND B. S. TUNIYEV. 1986. [The recent areas, their possible genesis and the phylogeny of three viper species of Eurosiberian group of the *Vipera kaznakowi* complex in the Caucasus]. Pp. 107-135. *In:* N. Ananjeva and L. Borkin (eds.), Systematics and Ecology of Amphibians and Reptiles. Proceedings of the Zoological Institute, Leningrad, 157. (In Russian).

ORLOV, N. L. AND B. S. TUNIYEV. 1990. Three species in the *Vipera kaznakowi* complex (Eurosibirian group) in the Caucasus: their present distribution, possible genesis, and phylogeny. Asiatic Herpetological Research 3:1-36.

RIDGWAY, G. J., S. W. SHERBURNE AND R. D. LEWIS. 1970. Polymorphism in esterase of Atlantic herring. Transactions of the American Fisheries Society 99:147-151.

SELANDER, R. K., M. H. SMITH, S. Y. YANG, W. E. JOHNSON, AND J. R. GENTRY. 1971. Biochemical polymorphism and systematics in the genus *Peromyscus*. I. Variation in the old-field mouse *(Peromyscus polionotus)*. Studies in Genetics VI. University of Texas Publications 7103:49-90.

SHAW, C. R. AND R. PRASAD. 1970. Starch gel electrophoresis of enzymes - a compilation of recipes. Biochemical Genetics 4:297-330.

SNEATH, P. H. A. AND R. R. SOKAL. 1973. Numerical Taxonomy. W.H.Freeman and Co., San Francisco. 573 pp.

TUNIYEV, B. S. 1990. On the independence of the Colchis Center of Amphibian and Reptile speciation. Asiatic Herpetological Research 3:67-84.

VEDMEDERJA, V. L., N. L. ORLOV AND B. S. TUNIYEV. 1986. [On the taxonomy of the three viper species of the *Vipera kaznakowi* complex]. Pp. 55-61 *In:* N. Ananjeva and L. Borkin (eds.), Systematics and Ecology of Amphibians and Reptiles. Proceedings of the Zoological Institute, Leningrad, 157. (In Russian).