

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

GÖRAN NILSON¹, BORIS S. TUNIYEV², NIKOLAI ORLOV³, MATS HÖGGREN⁴ AND CLAES ANDRÉN¹

¹Department of Zoology, Göteborg University, Sweden

²Caucasian State Biosphere Reserve, Sochi, Russia

³Zoological Institute, Russian Academy of Sciences, St. Petersburg, Russia

⁴Department of Genetics, University of Uppsala, Russia

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 für 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.
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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
Phosphoglucosmutase	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 intrapopulation 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

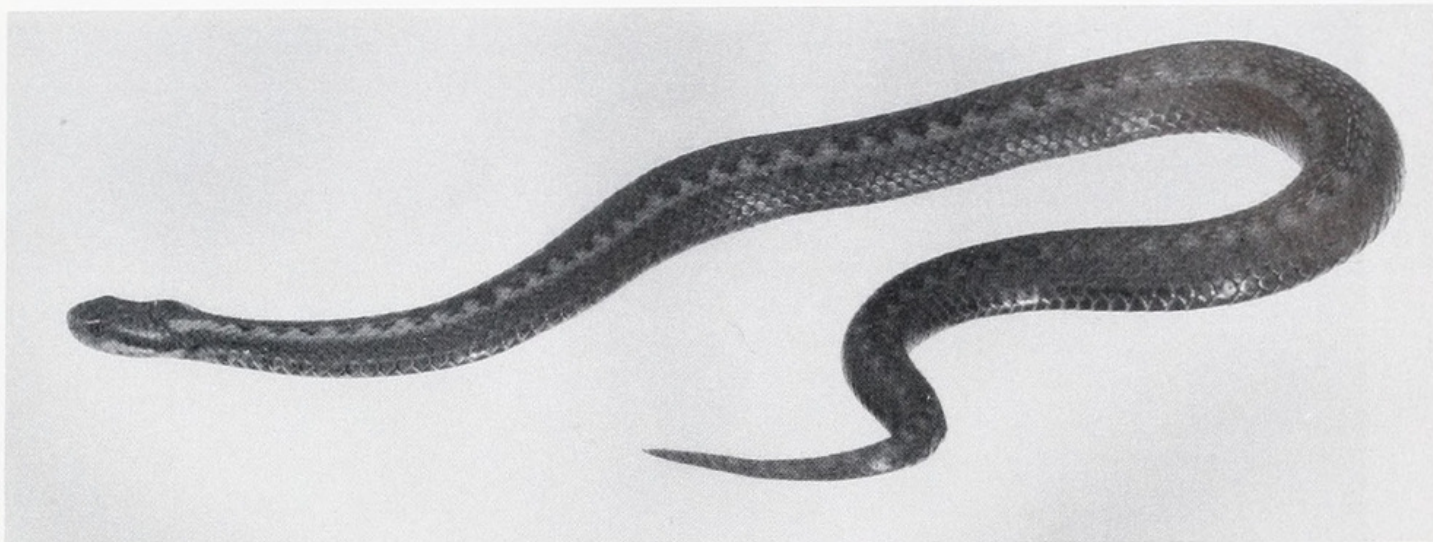


FIG.. 1. The typical "dinniki" pattern type of *Vipera dinniki*, with unicolored lateral sides typical for Fisht/Oshten (ZIG).

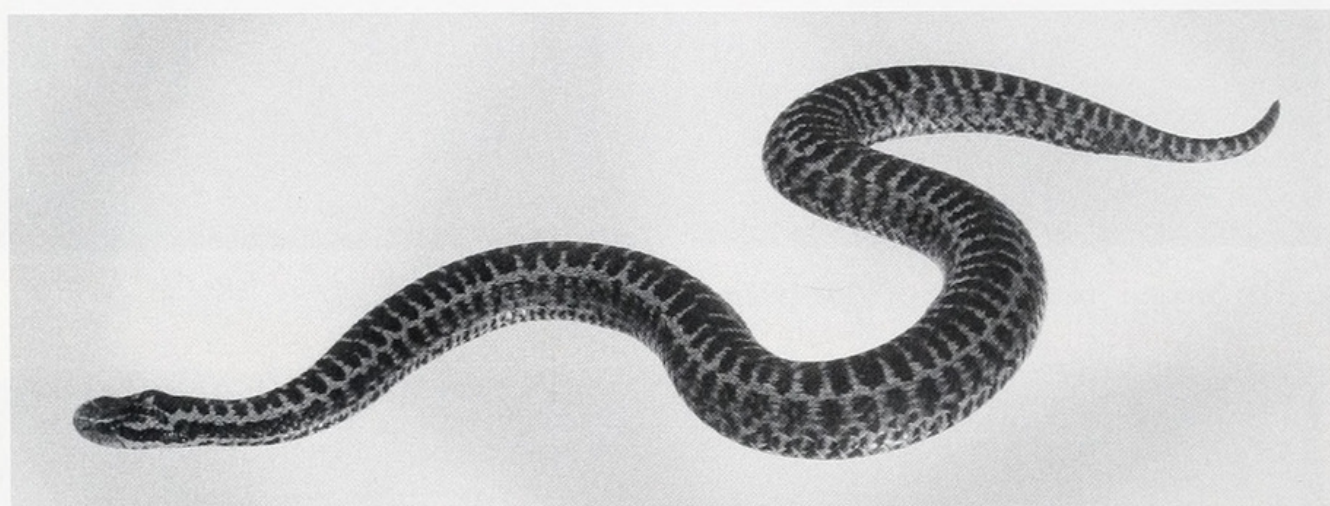


FIG. 2. The "dinniki" pattern type of *Vipera dinniki*, with a tendency towards the "tigrina" morph. From Kardyvach (ZIG).

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.

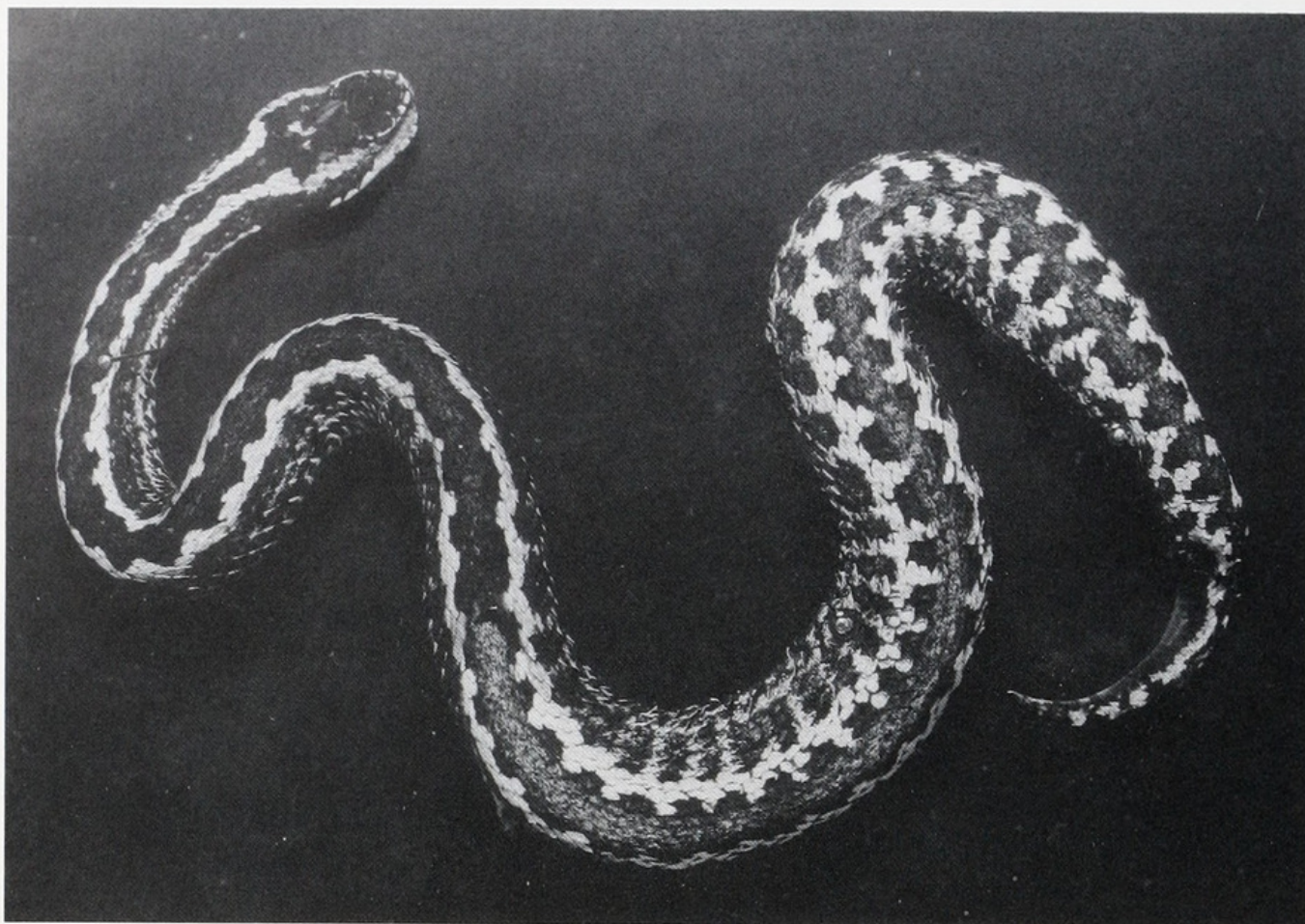


FIG. 3. The "kaznakovi" morph of *Vipera dinniki*, from Fisht/Oshten (Mt.Oshten - Armenian pass).

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

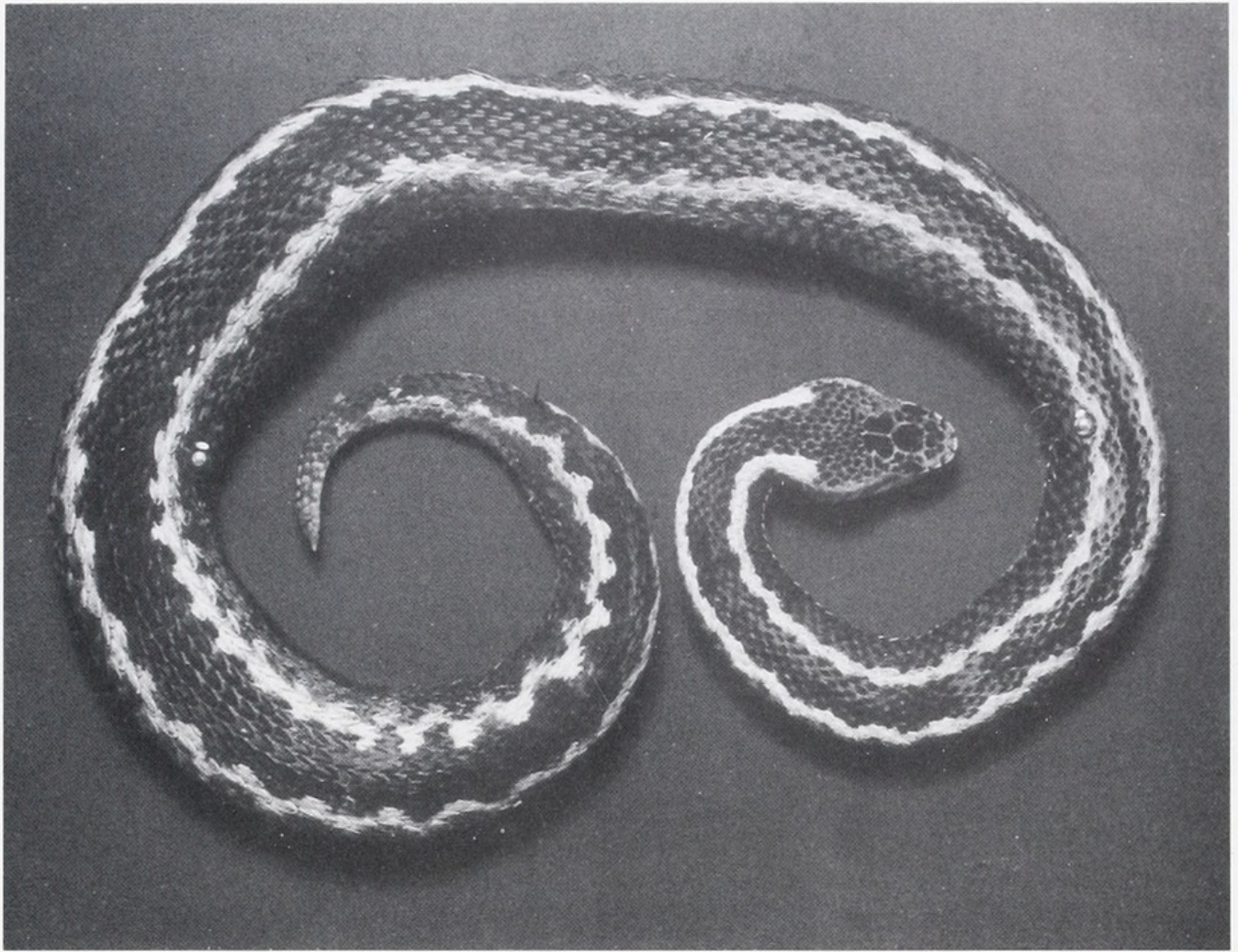


FIG. 4. A typical *Vipera kaznakovi* from the inland locality cordon Babuk-Aul at the foothills of Mt. Fisht (ZIG).

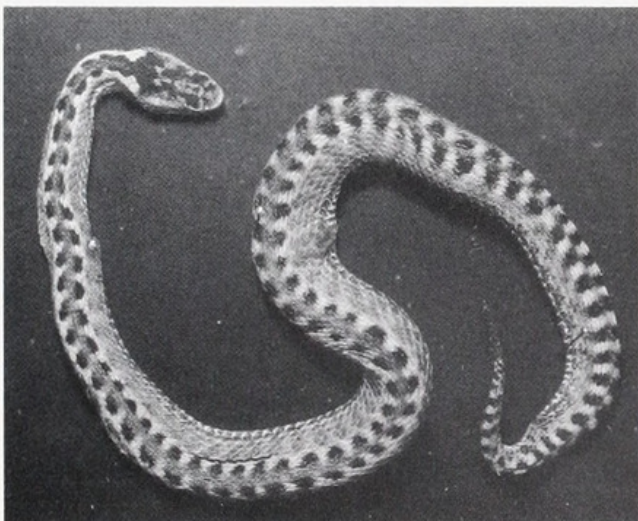


FIG. 5. The "ursinii" pattern type of *Vipera dinniki*, with more unicolored lateral sides from Mt. Fisht (ZIG).

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.

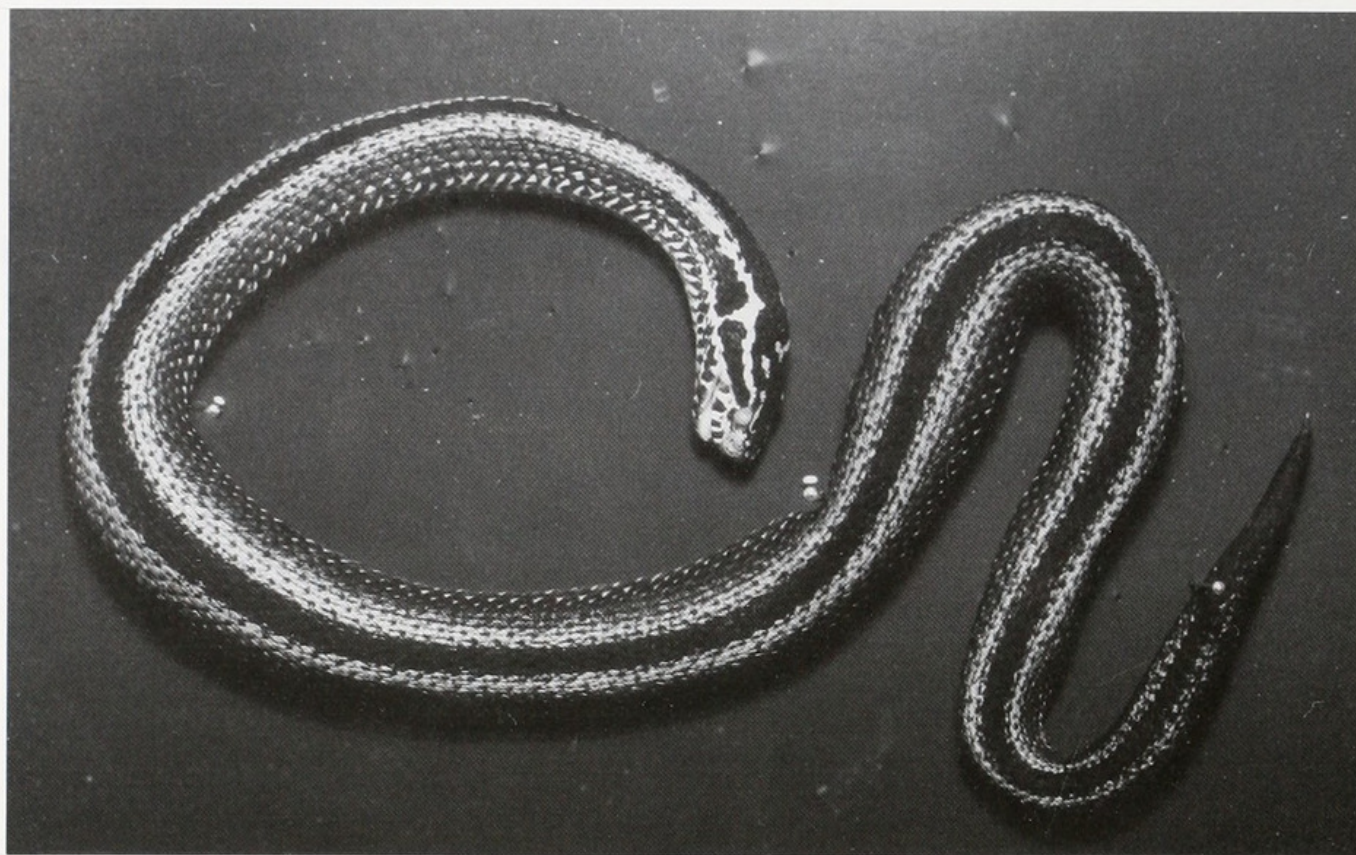


FIG. 7. The "bronze" morph of *Vipera dinniki*, from Mt. Loyub (ZIG).

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.

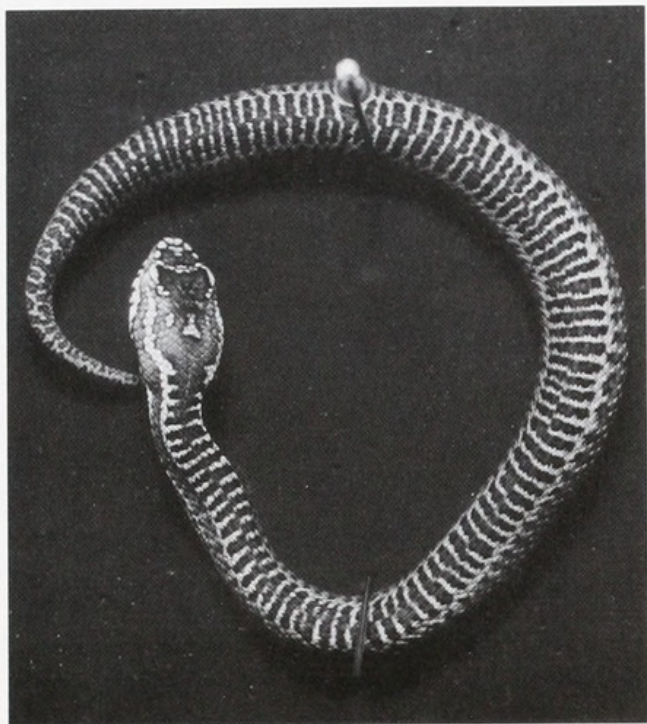


FIG. 6. The narrow-banded "tigrina" morph of *Vipera dinniki*, from Kardyvach (ZIG).

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.

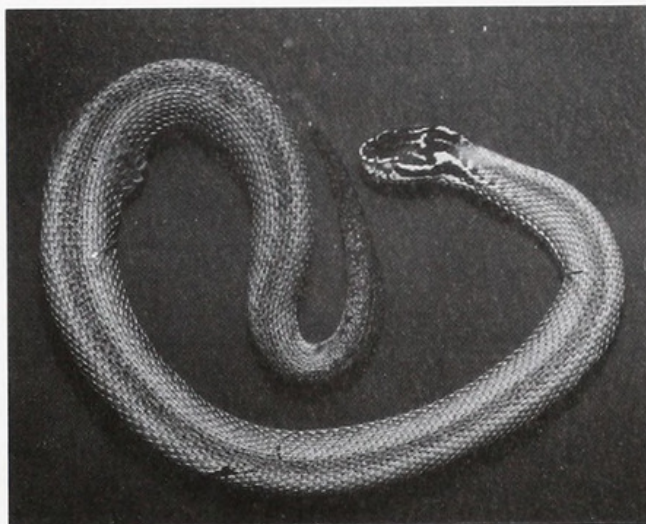


FIG. 8. The "bronze" morph of *Vipera dinniki*, from Mt. Loyub (ZIG).

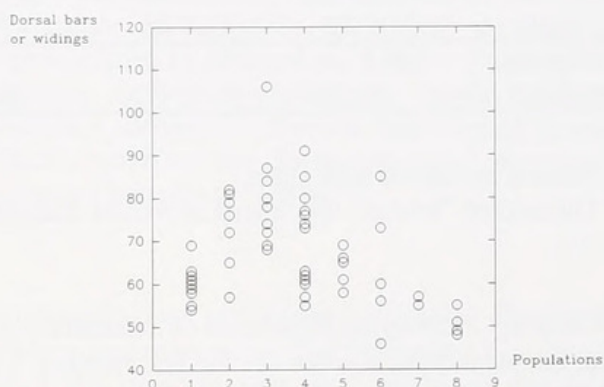


FIG. 9. Distribution of number of bars and/or windings in the dorsal zig-zag band in the different *Vipera dinniki* populations, running from west towards east in high Caucasus (1: Fisht, 2: Loyub, 3: Kardyvach, 4: Impsi, 5: "central Caucasus" (=Elbrus and surroundings), 6: "east Caucasus" (=mountains above Lagodechi, Georgia), and *V. kaznakovi* populations (7: Sochi-Adler, 8: Hopa, Artwin).

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 prefrontal 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 prementals 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
<i>kaznakovi</i> (DAGOMYS)	"kaznakovi"	3	8 "kaznakovi"
<i>dinniki</i> (FISHT)	"melanism"	1	6 "dinniki" 1 "ursinii"
<i>dinniki</i> (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"
<i>dinniki</i> (IMPSI)	"dinniki"	6	1 "dinniki/bilineate" 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"

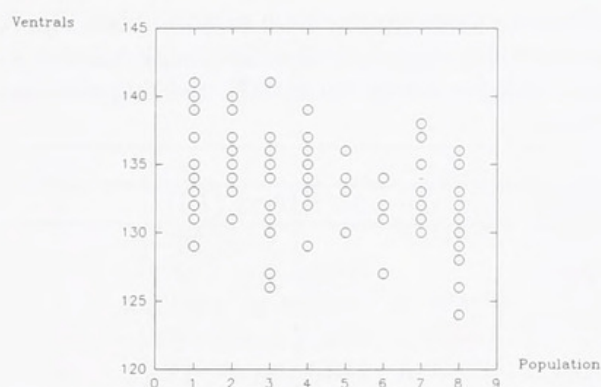


FIG. 10. Distribution of ventral numbers in the different *Vipera dinniki* populations, running from west towards east in high Caucasus (1: Fisht, 2: Loyub, 3: Kardyvach, 4: Impsi, 5: "central Caucasus" (=Elbrus and surroundings), 6: "east Caucasus" (=mountains above Lagodechi, Georgia), and *V. kaznakovi*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

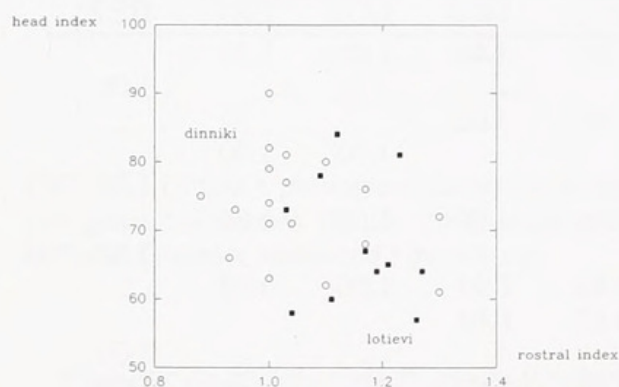


FIG. 12. Head index (breadth/length) and rostral index (height/ breadth) in sympatric sibling species of east Caucasus. White circles= *V. dinniki* ("east-dinniki"); black squares= *V. lotievi*.

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

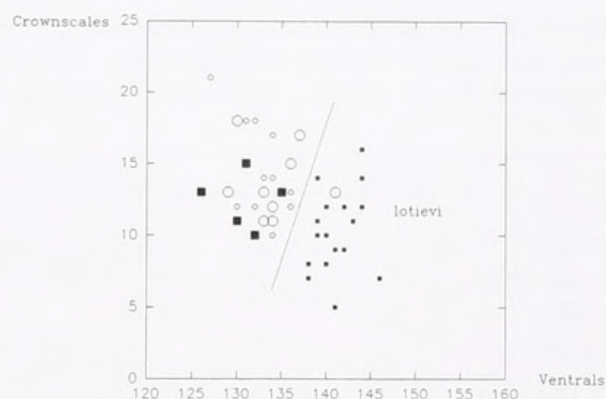


FIG. 11. Numbers of crown scales and ventral plates in "ursinii/bronze" and "dinniki" morphs and sympatric sibling species of west and east Caucasus. The dotted line indicate the main separation between *V. lotievi* and the *V. dinniki* from different regions. Big white circles= the "dinniki" morph of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

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).

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 prefrontals and apicals). Number of specimens in parentheses.

	Sochi - Adler (17)	Hopa (13)
Prefrontals	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	

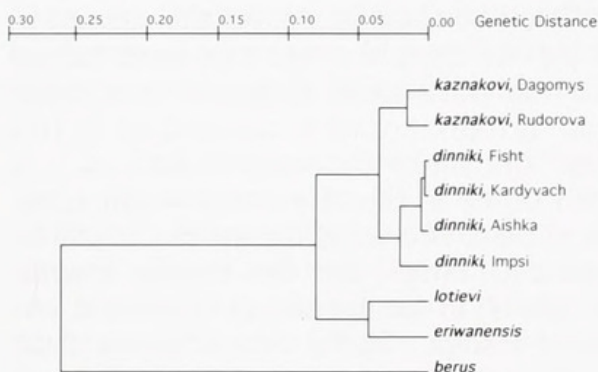


FIG. 13. UPGMA phenogram clustering modified Nei genetic distances (Hillis 1984) among eight OTUs of Caucasus vipers and *Vipera berus*.

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.

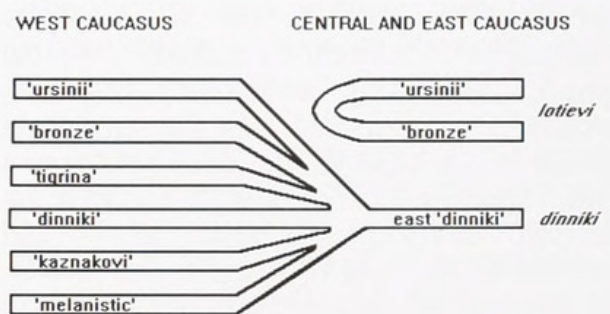


FIG. 14. The different types of morphs and species found in west and east high Caucasus.

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



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