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Three Species in the *Vipera kaznakowi* Complex (Eurosiberian Group) in the Caucasus: Their Present Distribution, Possible Genesis, and Phylogeny†

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Abstract.-Three valid species: *Vipera kaznakowi* Nikolsky, *V. dinniki* Nikolsky and *V. darevskii* Vedmedeja, Orlov, and Tuniyev of the "*Vipera kaznakowi* " complex belonging to the Eurosiberian viper group are recognized. The distributions of the closely related species, *V. kaznakowi* and *V. dinniki* are defined. The habitat of *V. kaznakowi* is present along the Black Sea coast, from Khopa Village (Turkey) in the south, to Maikop (USSR) in the north. *Vipera kaznakowi* is associated with montane areas from sea level up to 1000 m. The range of *V. dinniki* covers the northern and southern slopes of the Great (Main) Caucasus Ridge, ranging from the Fisht-Oshten Massive in the west to Shkhara Mountain in the east. *Vipera dinniki* tends to be restricted to alpine and subalpine zones at elevations from 1500 m to 3000 m. *Vipera darevskii* occurs in the southeastern part of the Dzhavachet Mountain Ridge, Armenia, near the border with Georgia. The history of studies on the vipers of the "*Vipera kaznakowi* " complex is summarized. The possible genesis of the present distributions of these vipers and their phylogenetic relationships are discussed. Comparative morphological and ecological characters of the three species are listed.

Key Words: Reptilia, Serpentes, Viperidae, *Vipera*, USSR, Caucasus, systematics, ecology.

Introduction

The study of the following viper species of the Caucasus, *Vipera kaznakowi* Nikolsky 1909, *V. dinniki* (Nikolsky 1913), and *V. darevskii* Vedmederja, Orlov and Tuniyev 1986 and the history of their distributions is of great interest for understanding the phylogenetic links of the Eurosiberian shield-headed vipers from the Caucasus (subgenus *Pelias*, Merrem 1808) and the formation of the present snake fauna in the west Caucasus Isthmus.

Ever since Nikolsky (1909) described the Caucasus Viper, *Vipera kaznakowi,* the understanding of the taxonomic position of this species has constantly varied. Also, ideas regarding the habitats of those forms referred to this species have varied (Orlov and Tuniyev 1986). We recognize at least three closely related species within the *V. kaznakowi* complex. All of them occur primarily in the western part of the Caucasus Isthmus. The eastern boundary of the species range needs to be defined. The Caucasus vipers (Fig. 1) have been recorded from the following localities:

Western Dagestan in the vicinity of Khasav-Yurt (Krasovsky 1929, 1932).

Along the slope of Makh-khokh Mountain from the highlands of Ingushetia (Chernov 1929).

On Legli Mountain in the Gukasyansky region, Armenia (Darevsky 1956).

In the vicinity of Ushguli at the foothills of Shkhara Mountain in Svanetia, Georgia (Muskhelishvili 1959).

In Borzhomi Canyon, Georgia (Bakradze 1969, 1975; Bannikov et al. 1977).

In Lagodekhi, Georgia (Zoological Institute, the USSR Academy of Sciences, Nos. 8389 and 13769).

† This publication combines material previously published in Russian by Orlov and Tuniyev (1986) and Vedmederja et al. (1986) with additional information.

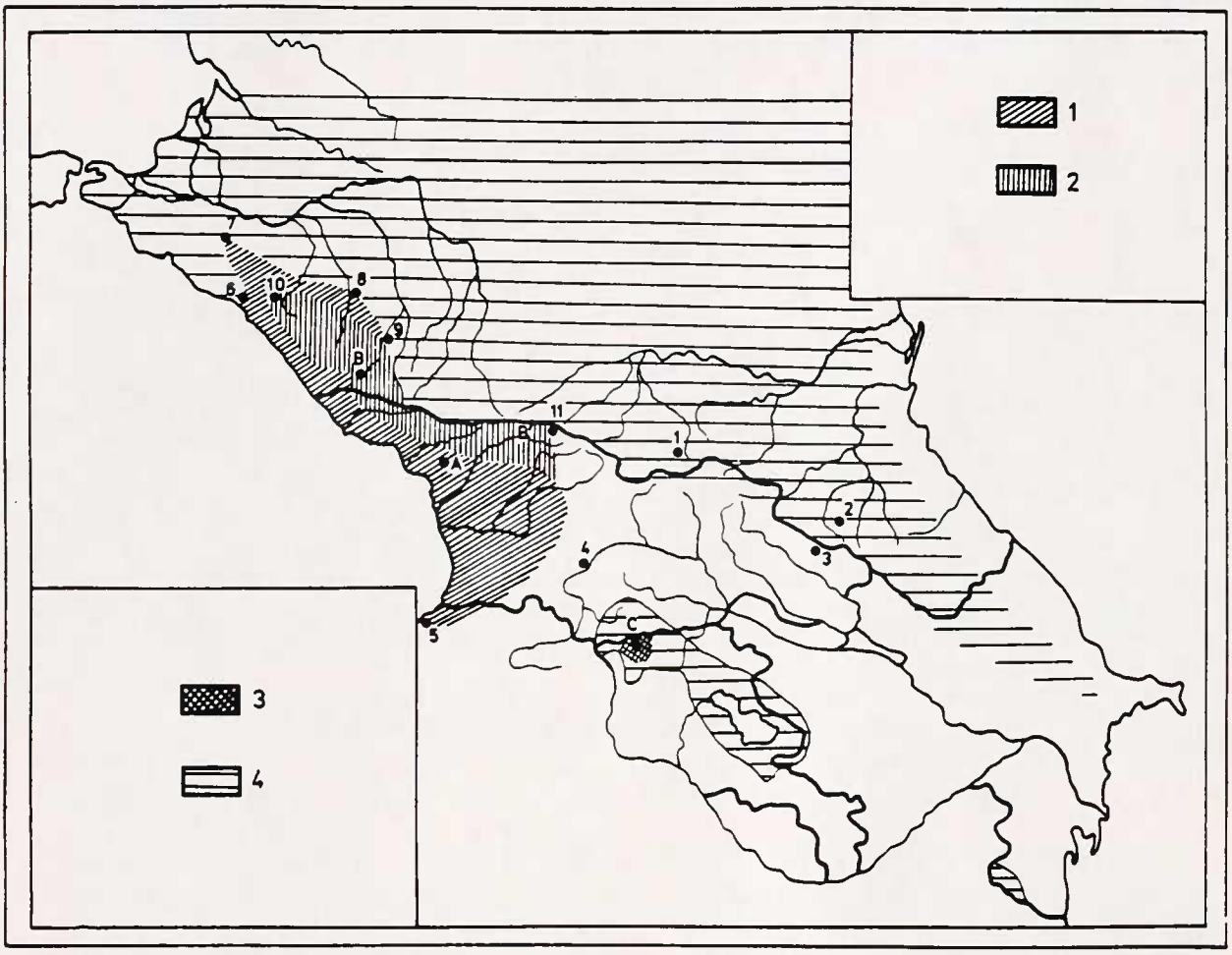


FIG. 1. The distributions of the vipers from the *Vipera kaznakowi* complex and the *Vipera ursini* complex in the Caucasus. 1. *V. kaznakowi*, 2. *V. dinniki*, 3. *V. darevskii*, 4. *V. ursini renardi* (northern population) and *V. ursini eriwanensis* (southern population). Type localities: A –*V. kaznakowi;* B, B' –*V. dinniki;* C –*V. darevskii.* Localities: 1 –Makh-Khokh Mountain; 2 –the settlement of Khasav-Yurt; 3 –Lagodekhi; 4 –Benis-Kheri Canyon; 5 –the settlement of Khopa, Turkey; 6 –Mikhailovsky Pass; 7 –the settlement of Ubinskaya; 8 –the town of Maikop; 9 –the mouth of the Urushten River; 10 –the Fisht-Oshtenovsky Massive; 11 –Shkhara Mountain. Extreme points of the distributions are marked.

All three species, *Vipera kaznakowi, V. dinniki* and *V. darevskii,* differ in morphology and ecology (Vedmederja 1984; Orlov and Tuniyev 1986).

History of the study of the Vipera kaznakowi *complex.*

The taxonomic problems and interrelationships of the viper forms of the Eurosiberian group in the Caucasus has caused contradictions and has confused zoologists for nearly a hundred years. The fragmented highland landscapes within the overall range of the Caucasus vipers isolates even neighboring populations. Hence, there is an accumulation of unique characteristics in populations. Very complex situations emerge in sympatric areas of closely related species of this complex. This may be connected with natural hybridization. Occasionally the identification of some individuals from intergrading populations is difficult. This particularly concerns *Vipera dinniki* in the areas of its interactions with *V. kaznakowi,* and additionally with the vipers of the *V. ursini* complex (Bonaparte). The high

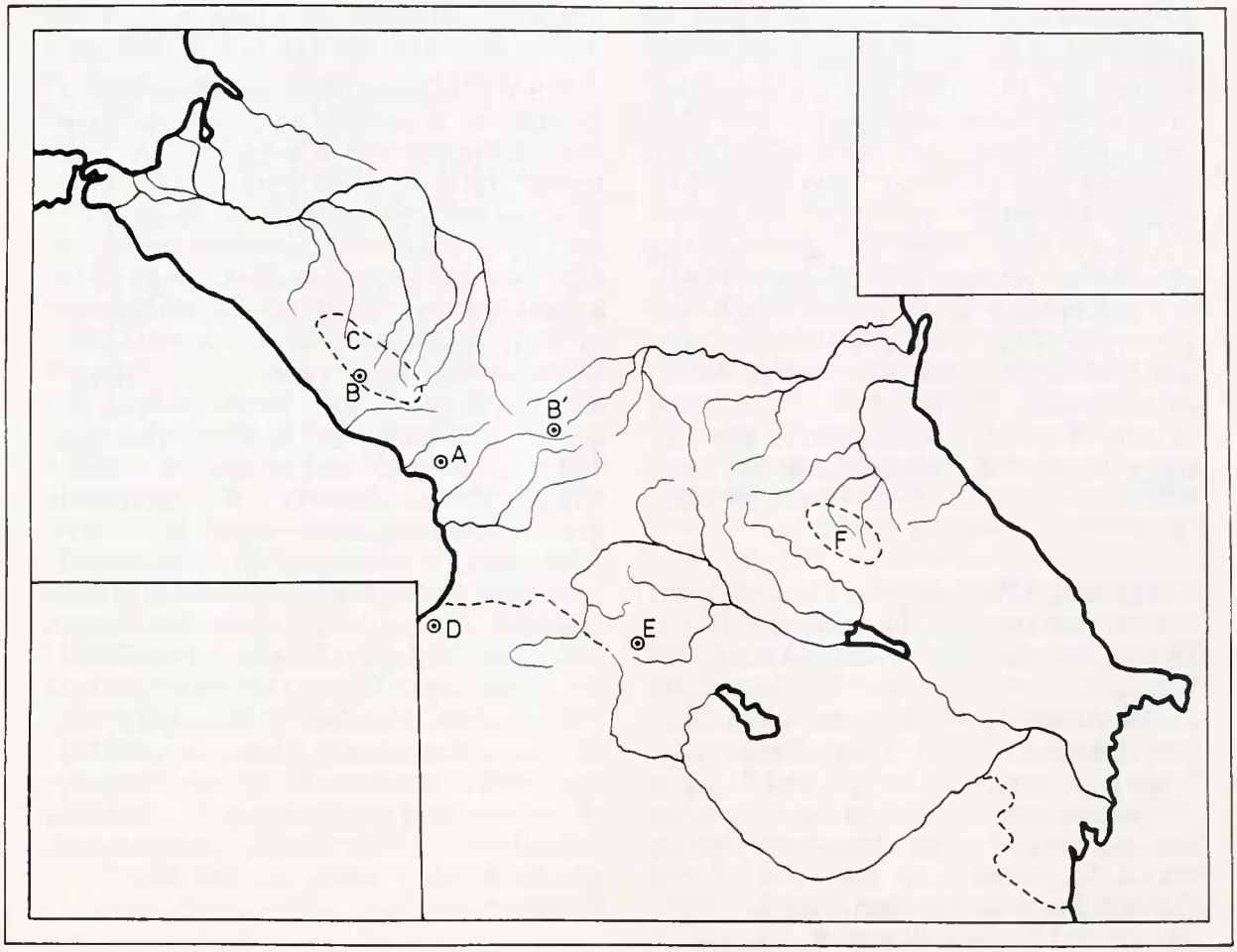


FIG. 2. Type localities of the vipers of the *Vipera kaznakowi* complex proposed over the history of the study. A –*V. kaznakowi* Nikolsky, described in 1909, collected from Tsebelda, the vicinity of Sukhumi, Abkhazia, Georgia. B, B' –*V. Berus dinniki* Nikolsky, described in 1913, from the upper reaches of the Malaya Laba River, the Caucasus Reserve, Krasnodarsky Territory and Svanetia, Georgia (respectively). C –*V. tigrina* Tzarewsky, described in 1916, taken from the Northern Caucasus. D –*V. berus ornata* Basoglu, described in 1947 from the settlement of Khopa, Artviisky Vilayet, Turkey. E –*V. darevskii* Vedmederja, Orlov, and Tuniyev, 1986, from Legli Mountain, the Mokrye Mountains, Gukasyansky Region, Armenia. F –*V. kaznakowi orientalis* Vedmederja, 1984 from the eastern part of the Main Caucasus Ridge.

degree of phenotypic polymorphism in vipers from the *V. kaznakowi* complex also creates additional problems in the evaluation of their taxonomic position.

Due to the complexity in identification of these vipers and the absence of definite localities for specimens an analysis of old literature gives only an approximate idea regarding the relationships of the *Vipera kaznakowi* complex.

Rossikow (1890) mentioned "multi-colored" vipers in the Northern Caucasus defined as *Vipera berus*. Boettger (1893) regarded the dispersal of two closely related viper species, *V. berus* and *V. renardi* from the Caucasus as a phenomenon that deserves attention. Nikolsky (1905) considered *V. berus* to be associated with Transcaucasia whereas *V. renardi* inhabits steppe areas of the Precaucasus and mountains of the Northern Caucasus. Leister (1908a) in his sketch on the geographic distribution of *V. renardi* and *V. berus* within the Caucasus wrote that *V.*

renardi is associated with steppe areas which separate the Caucasus from the habitat of *V. berus*, and also the mountains of the Northern Caucasus. He also confirmed Boettger's and Nikolsky's opinions that *V. berus* also appears in Transcaucasia. In the northern Transcaucasia there is an isolated population. According to Boettger (1899), the individuals of *V. berus* which are preserved at the Caucasus Museum (now the Museum of Georgia) were collected from Suani, Tiflis, Avar, Kodzhori, Khasav-Yurt, and Kazikoparan, whereas those from the Senckenburg Museum (Frankfurt-am-Main, West Germany) were taken from Sukhumi, Georgia.

Leister (1908a,b,c) gives a list of *Vipera berus* specimens in the collection of the Zoological Museum of the Academy of Sciences (now Zoological Institute of the USSR Academy of Sciences) taken from the Caucasus: 1) from Tiflis and Lagodekhi regions, Georgia and 2) from Yelenovka near the Gochka Lake (now the Sevan Lake). Leister then states that he found *V. renardi* on the bank of the Gochka Lake at the same locality where Kessler and Brandt collected *V. berus* (this specimen, ZIN 5478, collected by Brandt we determined to be *V. ursini*). On the basis of the findings of Kessler and Brandt and his own findings, Leister comes to the conclusion that both species, *V. berus* and *V. renardi*, live sympatrically. Concerning the specimens collected by Kessler and Brandt, Nikolsky (1905) writes that their rostral touches only one apical scale like in *V. renardi*. In all other characters they look more like *V. berus*. This led Leister (1908a) to consider that a certain intermediate species is possible—an ancestral form of *V. berus* and *V. renardi*. Nikolsky (1913) referring to the vipers from Transcaucasia listed by Kessler, Brandt and Leister nevertheless concluded that they are *V. renardi*. Leister (1908a,b), having analyzed the collections, concludes that the territory of the Northern Caucasus and Transcaucasia are inhabited by *V. berus* and *V. renardi*. He thought that *V. berus* and *V. renardi* live sympatrically in the Northern Caucasus (for instance, the vicinity of Grozny is a sympatric area).

Since Nikolsky (1909) described *Vipera kaznakowi*, a number of synonyms have been proposed for this species as new forms have been described and new combinations proposed. A number of forms, primarily from the Northern Caucasus and from the eastern range of *V. kaznakowi* have confused taxonomists as to their relationship to *V. kaznakowi*. These forms were placed in different combinations within *V. berus* and *V. ursini* (Nikolsky 1913, 1916; Basoglu 1947; Knoepfler and Sochurek 1955; Kramer 1961). Nikolsky (1913) assigned the common Caucasus viper to a new subspecies, *V. berus dinniki*. He defined the viper's range as the northern and southern slopes of the Caucasus Ridge from the Malaya (Small) Laba River headwaters up to Elbrus Mountain. Morits (1916) also recorded *V. berus* in the Northern Caucasus. Tsarevsky (1916) described a new form *V. tigrina* that was closely related to *V. renardi* and *V. kaznakowi*. Unfortunately he cited the species locality solely as "the Northern Caucasus."

Nikolsky (1909, 1911, 1913, 1916), the author of *Vipera kaznakowi* and *V. berus dinniki* descriptions, studied the relationships of the species *V. kaznakowi*, *V. berus*, and *V. renardi* (= *V. ursini renardi*) and noted the difficulties in identification of these forms. Nikolsky (1913) described *V. berus dinniki* from a single specimen collected by N. Y. Dinnik at the upper reaches of the Malaya Laba River, and from three specimens found by Shelkovnikov in Svanetia, Georgia. In his next monograph, Nikolsky (1916) discussed both forms: *Coluber berus dinniki* and *Coluber kaznakowi*. The range of the former was defined as the Caucasus Mountains on both sides of the Great Caucasus Ridge. The upper reaches of the Bolshaya (Big) Laba River was designated as a sympatric zone for *V. berus dinniki* and *V. renardi*. In his opinion, *V. renardi* was closely associated with the Caucasus Black Sea coast and the northern slope of the Caucasus Ridge.

Dinnik (1926) noted that *Vipera berus* and *V. kaznakowi* occurred in the Northern Caucasus. Krasovsky (1929) indicated that *V. berus* inhabited Khasav-Yurt and Rutulsky Kanton, Dagestan. Chernov (1929) recorded *Coluber berus dinniki* in the highlands of Ingushetia on the southern slope of Makh-khokh Mountain. The specimens were collected by D. Krasovsky in 1926 (Fig. 1). Krasovsky (1933) included both *V. kaznakowi* and *V. berus* in the fauna of the Caucasus State Reserve. Bartenev and Reznikova (1935) concluded that *V. kaznakowi* and *V. berus dinniki* were distributed in the western Caucasus, whereas in the alpine, *V. ursini renardi* also occurred. Rostombekov (1939) recorded *V. kaznakowi* as part of the fauna of Abkhazia. A new form, *V. berus ornata,* was described from northeast Anatolia (Basoglu 1947). Later on Mertens (1952a) synonymized it with *V. kaznakowi.* Terentyev and Chernov (1949) regarded *V. tigrina* Tzarevsky and *V. berus dinniki* Nikolsky as junior synonyms of *V. kaznakowi* Nikolsky which is, in their opinion, related to *V. ursini renardi.*

Darevsky (1956) presented a new combination of names for the viper from the Gukasyansky region, Armenia: *Vipera ursini renardi.* Fyodorov (1956) recorded *V. berus* in the forests of the premontane area of the Stavropolsky Territory and *V. kaznakowi* in the subalpine belt. In his survey of the snake fauna of Abkhazia, Georgia, Milyanovsky (1957) mentions *V. kaznakowi.* Muskhelishvili (1959) records *V. kaznakowi* on Mount Shkhara from the vicinity of Ushguli, Svanetia, Georgia. Kramer (1961) regards *V. tigrina* a junior synonym of *V. kaznakowi,* whereas *V. berus dinniki* should be synonymized with *V. ursini renardi.* Bakradze (1969) found a female *V. kaznakowi* in the town of Banis-Khevi, near Borzhomi, Georgia. On the basis of this finding, he suggested that the species habitat covered the entire Adzharo-Imeretinsky Ridge and some of the Trialetsky Ridge.

In the field guide of Bannikov et al. (1977) the names *Vipera berus dinniki, V. tigrina* and *V. berus ornata* are mentioned as junior synonyms of *V. kaznakowi.* Vedmederja (1977) recorded *V. kaznakowi* in Adgaria, Georgia. In his opinion (Vedmederja 1984) *V. kaznakowi* is a polytypic species comprising four subspecific forms. Tertyshnikov (1977), in defining ecological and zoogeographic subdivisions of the herpetofauna of the Northern Caucasus, noted that *V. kaznakowi* tends to be restricted to western and southwestern montane regions. The most recent taxonomic works dealing with these vipers state that *V. berus* occurs neither in the Caucasus nor in the Precaucasus. Hence, *V. kaznakowi* is the sole valid name with regard to shield-headed vipers from the western Caucasus Isthmus and northeast Anatolia. The taxonomic status of the eastern populations from Dagestan and Armenia was not discussed (Terentyev and Chernov 1949; Mertens 1952a; Mertens and Wermuth 1960; Klemmer 1963; Bannikov et al. 1977; Baran 1977; Harding and Welch 1980).

The study of old collections and literature shows that the majority of researchers did differentiate the vipers from the *Vipera ursini* complex and the *V. kaznakowi* complex. The major difficulties in defining the systematic position and taxonomic status concerned primarily the vipers from the eastern range of the *V. kaznakowi* complex. References that *V. berus* occurs in the Northern Caucasus and Transcaucasia more often than not concern snakes from the *V. kaznakowi* complex rather than those from the *V. ursini* complex.

An analysis of literature data and morphometric characteristics of 141 viper specimens allowed Vedmederja et al. (1986) to designate three species within the *Vipera kaznakowi* complex:

1. *V. kaznakowi* Nikolsky, 1909

2. *V. dinniki* Nikolsky, 1913

3. *V. darevskii* Vedmederja, Orlov and Tuniyev, 1986

Fig. 2 represents type localities of the forms proposed for the *Vipera kaznakowi* complex over the history of its study.

Systematic Accounts

Vipera kaznakowi Nikolsky, 1909 (Fig. 3, 4, 14a, Plate 1)

Chronology of species description

Vipera renardi (Christoph) - Silantyev, 1903, 30:37 (part).

Vipera kaznakowi Nikolsky, 1909:174; Nikolsky, 1910:81, table 1.

Vipera kaznakowi - Nikolsky, 1913:179-181; colored plate III (=Fig. 3, this paper).

Coluber kaznakowi - Nikolsky, 1916:244-247.

Vipera berus ornata Basoglu, 1947:182-190.

Vipera ursini kaznakowi - Knoepfler and Sochurek, 1955:185-188.

Vipera kaznakowi - Terentyev and Chernov, 1949:270-277 (Map 15); Bannikov et al., 1977:323-324 (map 133; colored plate 31, 4).

Vipera kaznakowi kaznakowi - Vedmederja, 1984:8.

The English common name is the Caucasus Viper, or Kaznakow's Viper.

Lectotype†**:** No. 4408, an adult female. Collected by Y. V. Voronov from Tsebelda, the vicinity of Sukhumi, Abkhasia, the Caucasus. It is stored in the Caucasian Museum (now the Museum of Georgia, Tbilisi).

† Kramer (1961) was mistaken regarding this specimen as the holotype, because Nikolsky (1909) had not singled out a holotype from the five specimens from which he described the species.

Diagnosis: A large snake for the Eurosiberian group. Total length reaches 650-700 mm. Dorsally the head is covered with large scales. In size and shape they differ considerably from body scales. Nostril is cut through either in the middle or slightly closer to the lower edge of the nasal. Upper-lateral edge of snout is pointed. Rostral normally reaches two apical scales on upper snout. Upper edge of the nasalorostral scale is slightly curved at obtuse angles. Scales of anterior frontal have weak longitudinal keels. Head is broad and normally black dorsally. Head is separated from body by a sharp nuchal collar.

Description: The ratio of body length to tail length is 5.7 to 6.4 in males and 7.5 to 10.9 in females. Unlike other species assigned to the *Vipera kaznakowi* complex, red and yellow colors prevail in *V. kaznakowi*. Melanistic specimens are common. However, unlike complete melanistic individuals of *V. dinniki,* those of *V. kaznakowi* preserve yellow or red color on either upper or lower labials. *Vipera kaznakowi* is either black or dark brown striped dorsally and laterally. Often stripes merge so that only red or yellow spots remain between them. Ventrum is black. Head is very broad, impressed dorsally. This fact is emphasized by a slightly pointed upper edge of snout. Cheeks are greatly swollen. Head is well separated from body by a thin nuchal collar. Comparative data on scalation and size characters are listed in Tables 1-4.

Variability and comparative remarks

V. kaznakowi (Fig. 4, Plate 1) is undoubtedly more closely related to *V. berus* and *V. ursini*. Supposedly, when interacting with *V. ursini renardi* and *V. ursini eriwanensis* it forms two species of hybrid genesis: *V. dinniki* and *V. darevskii*. From all listed forms it differs by: 1) the extraordinarily great width of the triangular head, 2) the head width of specimens of this species equals the distance between tip of snout and posterior angle of mouth slot, 3) the "cheeks" are greatly swollen, hence a broad furrow

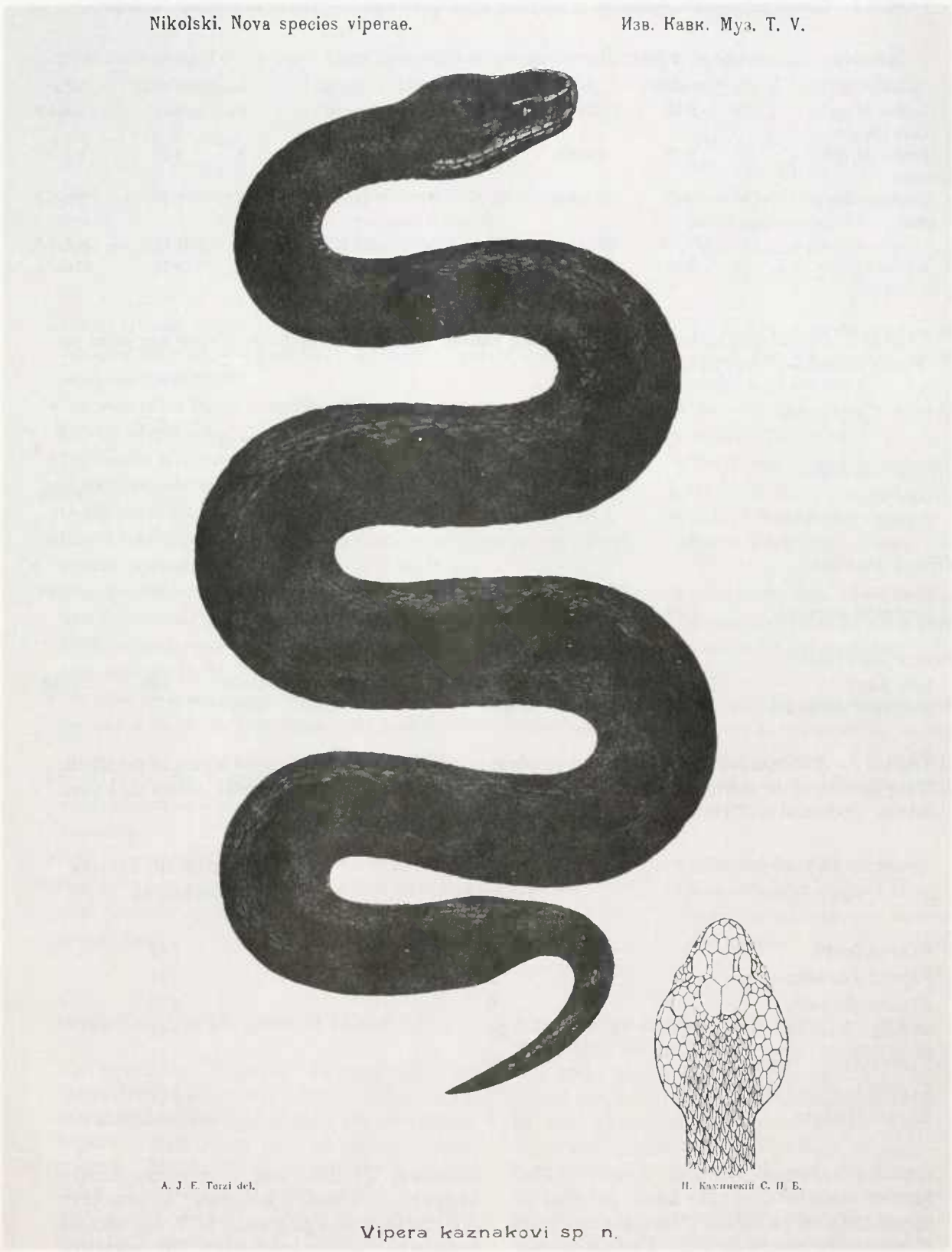


FIG. 3. Type specimen of *Vipera kaznakowi* Nikolsky, 1913 (reproduced from Plate III, originally printed in color, Nikolsky 1913).

TABLE 1. Comparative scale characters of the three viper species of the "*Vipera kaznakowi* " complex.

Species / Characters	*Vipera kaznakowi* n	min-max	x±se	*Vipera dinniki* n	min-max	x±se	*Vipera darevskii* n	min-max	x±se
1. Number of scales round the eye	64	8-12	10.03±0.1	65	9-12	9.6±0.1	9	8-9	8.4±0.2
2. Number of upper labials	64	8-10	9.0±0.1	68	8-11	10.3±1.3	9	9-10	9.2±0.1
3. Number of lower labials	64	8-12	10.9±0.05	68	8-12	10.5±0.1	9	9-10	9.5±0.2
4. Number of ventrals	64	130-143	135.5±0.8	68	126-141	133.9±1.8	9	134-140	135.5±0.8
5. Number of scale rows around body	64	18-21	20.0±0.1	68	21-23	21.1±0.15	9	19-21	20.6±0.2

TABLE 2. Sexual dimorphism of body length and number of subcaudals in the three viper species of the "*Vipera kaznakowi* " complex.

Characters	♂♂ n	min-max	x±se	♀♀ n	min-max	x±se	t♂♀	p
Vipera kaznakowi:								
Body length	23	358-475	415.1±7.5	16	375-600	504.1±118.6	4.5	<0.001
Number of subcaudals	23	31-40	34.8±1.5	20	22-32	25.4±0.9		
Vipera dinniki:								
Body length	29	259-412	331±8.76	20	321-486	441.8±11.4	5.6	<0.001
Number of subcaudals	29	31-37	32.2±0.6	20	18-30	23.7±0.8		
Vipera darevskii:								
Body length	3	236-258	249.3±5.53	5	233-421	331.8±28.2	2.82	<0.05
Number of subcaudals	3	29-35	32.3±1.4	5	25-30	27±0.79		

TABLE 3. A comparison of the number of vertebrae carrying ribs in Shield Headed Vipers of the USSR. X-ray analysis of the vipers indicates that the number of rib-carrying vertebrae is stable, except for *Vipera dinniki*, (indicated by **) in which the number varied from 128 to 140.

Specific and subspecific viper forms	Number of specimens analyzed	Number of rib bearing vertebrae
Vipera berus	10	142
Vipera kaznakowi	8	135
Vipera darevskii	9	138
Vipera dinniki	25	138**
Vipera ursini renardi	10	148
Vipera u. eriwanensis	10	140
Vipera dinniki	2	132 and 135

appears between eye and temple. The furrow goes up to upper head, parallel to upper edge of parietals. Dorsally the head is either impressed or flat. The viper also differs from closely related species in body proportions: 1) it is relatively thicker, more massive; 2) the head is conspicuously bigger. These habitus characters differentiate all age groups of *V. kaznakowi* ranging from juveniles to mature specimens. Comparative data on pholidosis, size, and number of vertebrae

TABLE 4. Comparative morphology of vipers in the "*Vipera kaznakowi*" complex.

Vipera kaznakowi, 64 specimens	*V. dinniki*, 68 specimens	*V. darevskii*, 9 specimens
• SVL ♂♂ ≯ 475 mm SVL ♀♀ ≯ 600 mm	• SVL ♂♂ ≯ 412 mm SVL ♀♀ ≯ 486 mm	• SVL ♂♂ ≯ 258 mm SVL ♀♀ ≯ 421 mm
• SVL ♂♂/ CL ≈ 5.6-6.4 SVL ♀♀/ CL ≈ 7.5-10.9	• SVL ♂♂/ CL ≈ 5.9-7.4 SVL ♀♀/ CL ≈ 7.9-13.5	SVL ♂♂ / CL ≈ 6.0-6.5 SVL ♀♀ / CL ≈ 8.4-9.3
• Head is either impressed or flat dorsally	• Head is either flat or slightly protuberant dorsally	• Head is either flat or slightly protuberant dorsally
• Edge of snout is slightly rounded	• Edge of snout is rounded	• Edges of snout are slightly pointed laterally. Anterior edge is a little rounded
• Rostral is broad. Usually touches two apical scales (in 91% specimens) rarely one apical (in 9%)	• Rostral is narrow reaching either one (in 48.6%) or two (in 51.4%) apicals	• Rostral is more narrow and touches one (in three specimens) or two (in six specimens) apical scales
• The width of the frontal is equal to 1.21-1.72 of its length	• The width of the frontal is equal to 1.13-1.83 of its length	• The width of the frontal is equal to 1.48-1.71 of its length
• The distance between anterior edge of the frontal and the rostral is equal to 0.75-1.05 of the frontal edge	• The distance between anterior edge of the frontal and the rostral is equal to 0.77-1.35 of the frontal edge	• The distance between anterior edge of the frontal and the rostral is equal to 0.67-1.07 of the frontal edge
• Frontal is either smaller than parietals or equals them	• Frontal is either smaller than parietals or equals them	• Frontal is larger than parietals
• Large lower oculars are separated from frontal either by one row (in 87.0%) or rarely by two rows of small scales (in 12.4%)	• Large lower oculars are separated from frontal either by one row (in 58.5%) or two rows (in 41.5%)	• Large lower oculars are separated from frontal only by a single row of small scales (in all nine specimens)
• The upper pre-ocular does not touch the nasal in 96.1%. In 3.9% it does	• The upper pre-ocular does not touch the nasal in 86.6%. In other cases it reaches the nasal	• The upper pre-ocular does not touch the nasal in two specimens. In seven specimens it does
• Nostril is either cut through in the middle of nasal or is slightly shifted downwards	• Nostril is cut through in the center or nasal. It may be shifted downwards exceedingly rarely	• Nostril is cut through in the lower part of the nasal
• Nasal does not touch rostral	• Nasal does not touch rostral	• Nasal does not touch rostral
• Body scales with expressed keels; some scale rows that reach ventrals have no keels	• Body scales have expressed keels. 76% of scales that reach ventrals have no keels, 18.4% have slightly expressed keels, 5.6% have well-expressed keels	• Body scales have expressed keels. Some scale rows that reach ventrals have no keels

supporting ribs are given in Tables 1-4.

Coloration. Vipera kaznakowi are incredibly diverse in color and extraordinarily bright among shield-headed vipers. Red hues prevail in the color pattern. Newborns are similarly bright in color, primarily red brown, unlike the gray young of *V. dinniki*. The typical intensive red color appears in *V. kaznakowi* after they have shed twice. Complete melanists are frequent in populations. Often the black dorsal stripe merges with lateral stripes so that either red or yellow spots arranged in two rows along the dorsum remain. The dorsal stripe can be either zig-zag shaped or in the shape of an even broad line. Ventrum is black. Head pattern of adult specimens normally blends with the dorsal stripe. In immature specimens, the head pattern may be separated from the dorsal stripe by a light interval that disappears after maturation.

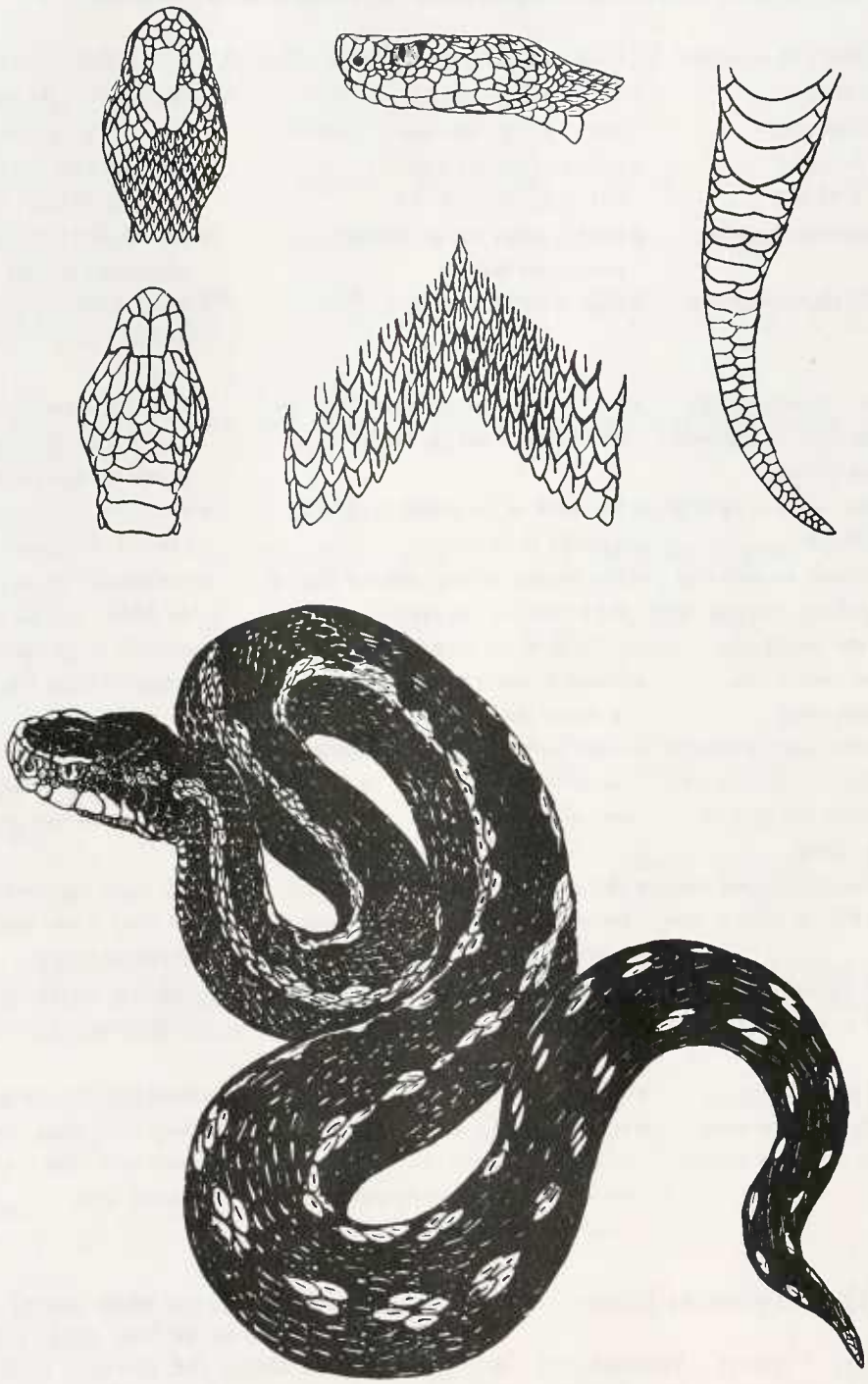
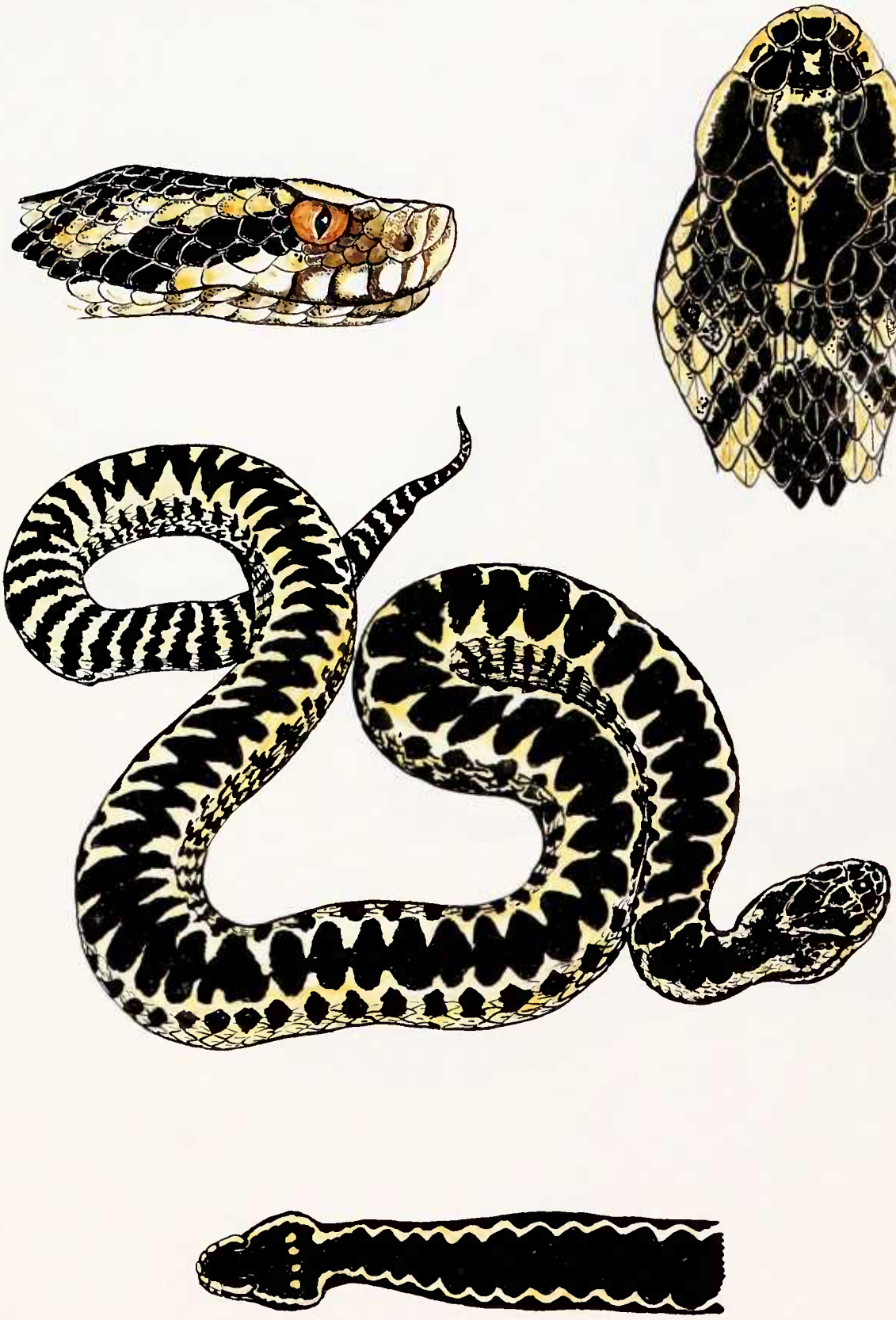


FIG. 4. *Vipera kaznakowi* (ZIN 11529) from the isolated forest of Babuk-Aul.

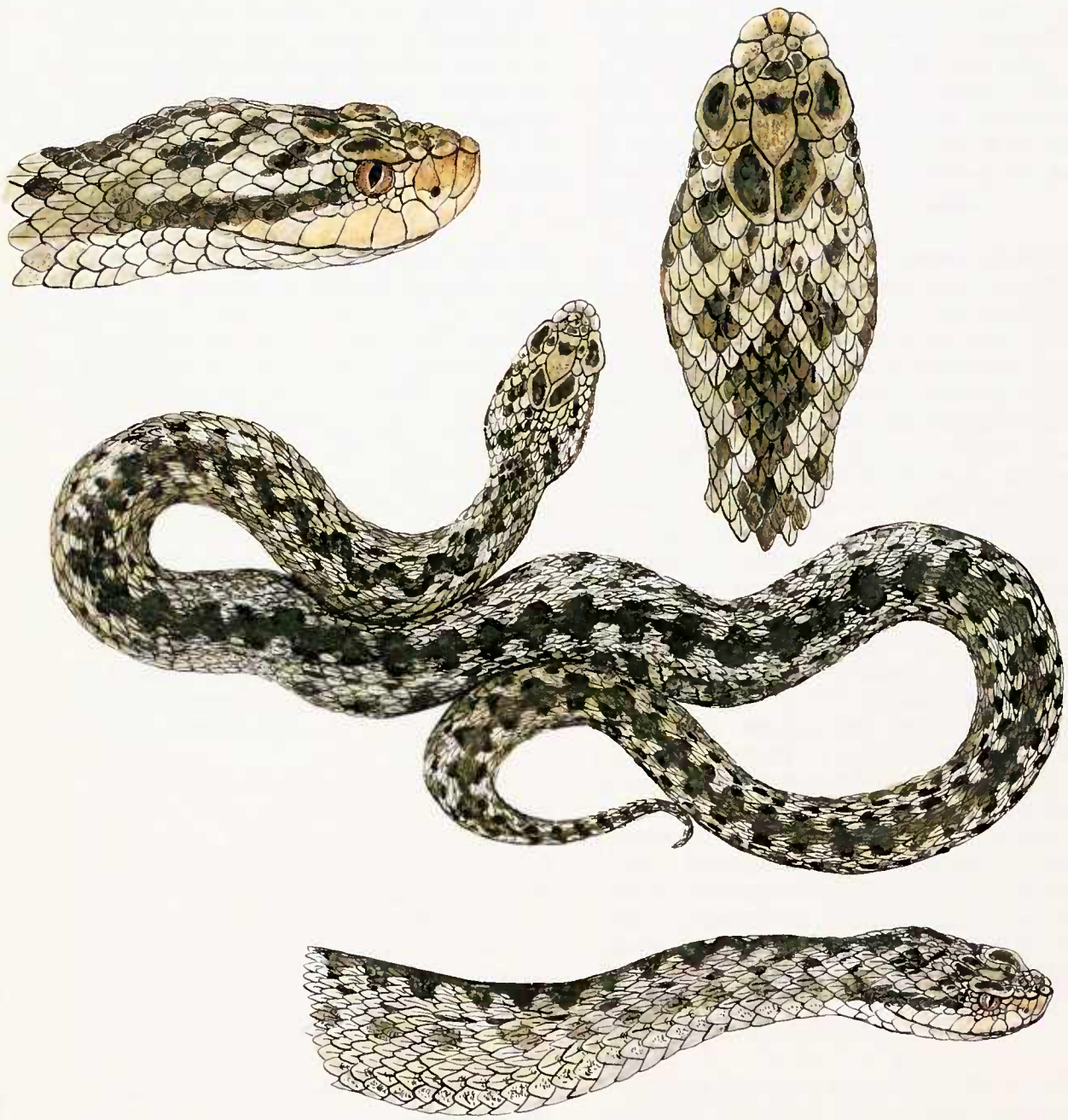
PLATE 1. *Vipera kaznakowi* (ZIN 11529) from the isolated forest of Babuk-Aul.
PLATE 2. One pattern variation of *Vipera dinniki* from Krasnaya Polyana (ZIN 12153), a male.
PLATE 3. *Vipera ursini eriwanensis* from the valley of Kassach, the foothills of the Ara-Fler Mountains.

Vipera kaznakowi



Vipera dinniki

Данов 1988



Vipera ursini eriwanensis

Данов 1987

Sexual dimorphism. Maximum body length is longer in females (up to 600 mm) than in males (does not exceed 457 mm). Males have longer tails (Table 2). Accordingly, the number of ventrals is greater in females, whereas the number of subcaudals is greater in males. Males are more slender. Sexual dimorphism in coloration is feebly marked. Melanistic individuals are more frequent among females.

Age variability. Vipera kaznakowi are born with the typical adult color and pattern. However, in newborns these characters are less pronounced than in adults. Newborn snakes may be either pinkish or reddish. According to our observations on birth and development of snakes from the Sochi-Khosta populations, the coloration becomes stronger with each subsequent shedding. Maximal color intensity is achieved by the season after the first hibernation.

Melanistic specimens are born with the typical species pattern, but their coloration is darker. The coloration becomes darker during subsequent sheddings and elements of the pattern merge.

New born litters are homogeneously colored. On maturing, the coloration becomes diverse. Phenotypic polymorphism in mature vipers of a litter is great. Either partial or nearly complete melanism is observed in all vipers from this population. This is typical for a number of other animals from humid subtropic areas adjacent to the Black Sea coast (Bartenev and Reznikova 1935). Specimens showing maximal melanism always preserve elements of orange and red on the throat scales and chin shields, the rostral, upper labials and subcaudals. Melanistic specimens of *V. dinniki* can have completely black coloration by maturity.

Geographic range and ecology. The species ranges along the Black Sea coast from the town of Khopa, Turkey and Suramsky Pass in the east, then throughout Kolchida (Colchis) up to Mikhailovsky Pass in the west. It is then found up to the northern slope of the Main Caucasus Ridge. Here *Vipera kaznakowi* occurs along the foothills from the settlement of Ubinskaya in the west to the town of Maikop, USSR in the north and the mouth of the Urushten River in the east (Fig. 1 from Vedmederja et. al. 1986). The species generally occurs up to an elevation of 800 m. Along the river valleys of the Black Sea coast, it may occur up to an elevation of 1000 m or even higher.

Vipera kaznakowi is a forest dwelling species. It occurs on montane wooded slopes, in the bottoms of humid canyons, and in meadows adjacent to forests. It is recorded in *Quercetum azaleorum* and *Quercetum coggygriosecornosum* oak groves, in mixed subtropic forests with evergreen subforests of *Quercus hartwissiana, Quercus iberica, Alnus barbata, Fagus orientalis, Taxus baccata, Laurocerasus officinalis, Buxux colchicus, Castanetum colchicum, Fagetum nudum, Salictum fontenale,* and *Alnetum struthiopteridorsum.* In addition, this species is found in polydominant forests in river terraces and large overgrown outcroppings. At the upper limits of its elevational range, the species reaches coniferous forests. It is recorded within the ecotone of *Fageto-Abieta athyridosa-maxtoherbosa,* but the viper never penetrates deep into coniferous forests. *Vipera kaznakowi* is also present within transformed areas such as meadows formed after forests are cut, fruit orchards, kitchen gardens, vineyards, and dilapidated parks (Red Data Book of the USSR 1978, 1984). As a rule, vipers occur within sites where the density of lizards is high.

Typical biotypes are as follows: small meadows and other illuminated spots in forests with an exposure providing high solar radiation in conditions of humid subtropical climate of the Black Sea coast of the Caucasus. The sites are located in the vicinity of standing water, where rocks exit that are suitable for hibernation. The climate of the Caucasus coast is greatly dependent on topographic conditions of the area that forms a narrow line between the Caucasus Ridge and the Black Sea. It is

situated from northwest to southeast along the coast. The wall of the Ridge starts from Anapa. Near Novorossiisk it reaches an elevation of up to 600 m. Near Tuapse, the wall exceeds 1000 m above sea level. At the latitude of Sochi, it is 3000 m high. The Great Caucasus Ridge presents a barrier for cold northeastern winds. This barrier separates the warm humid coast from the comparatively cold continental Prekuban area (Korostelyov 1933). In the east the Adzharo-Imeretinsky Ridge separates the humid subtropical Kolchida (Colchis) from the arid regions of the Eastern Precaucasia. The climatic zone of the Black Sea coast of the Caucasus appears to be extremely favorable for *Vipera kaznakowi*. The northwestern most localities for this species (Mikhailovsky Pass and Stanitsa Ubinskaya) coincide with Pontic and northwestern floristic regions. In relief, climate, and vegetation the northwestern region is a continuation of the southern coast of the Crimea.

The Pontic region is marked by 1) subtropical vegetation in the foothills, 2) great temperature stability, and 3) high humidity (Korostelyov 1933). The limited dispersal of the species along the northern slope of the Big Caucasus is in the region of the "Kolchidian (Colchis) Gates." Due to the lowering of the western portion of the Main Caucasus Ridge, interchange of flora and fauna of Kolchida (Colchis) and the Prekuban area occurred in the past and presently occurs. Warm humid air from the Black Sea breaks through in this part of the Ridge. On the northern slope of the Big Caucasus, it creates a small refugium on a Kolchidian (Colchis) type associated with *Castanea satyra, Buxux colchicus, Ostrya carpinifolia, Corylus colurna,* and others (Galushko 1974; Kharadze 1974; Kholyavko et al. 1978). Of the herpetofauna of Kolkhida *Bufo verucossimus, Triturus vittatus ophryticus, Pelodytes caucasicus,* and *Lacerta derjugini* occur along with *V. kaznakowi*. Along the entire area of of the Black Sea coast of the Caucasus, the viper is rare. In a number of spots it has disappeared. In some situations, only single specimens of *V. kaznakowi* might be encountered.

The highest density of *Vipera kaznakowi* that have been observed are in rocky outcroppings within the forest belt in the mountains of the Caucasus Reserve. In beech forests along a road in the valley of the Achipse River, we have recorded three specimens per kilometer of road. Single specimens have been recorded in the vicinity of Khosta, Babuk-Aul, Guzeripl, and Kisha Kordons. The density of the viper is also low in the southern habitats in Adzharia and Lazistan, Georgia (Basoglu 1947; Vedmederja 1977; Basoglu and Baran 1977).

Anthropogenic factors are responsible for declining numbers and populations of *Vipera kaznakowi*. There are pressures due to recreational use of health resorts along the Black Sea coast, ploughing of sites near the foothills, and to a smaller extent, hay-mowing (Red Data Book of the USSR 1978, 1984). Within some resort areas *V. kaznakowi* is completely extinct.

Diet. Vipera kaznakowi feeds on various animals. Different populations show specific feeding patterns with regard to prey available. According to data recorded in captivity, individual preference is observed. When stimulated to regurgitate, the following food species were recorded in the field: *Apodemus sylvaticus,* a forest mouse, *A. agrarius,* a field mouse, *Microtus majori,* a juvenile specimen, *M. gud, Sorex raddei, Lacerta saxicola, L. derjugini, L. praticola* and *L. agilis*. In the collection of the Zoological Museum of the Moscow State University a viper specimen from Bebysyry Lake is preserved. In its stomach a juvenile grass snake (*Natrix natrix*) was found. Immature individuals feed on juvenile lizards of the above mentioned species, and to a lesser extent, on Orthoptera.

In captivity adult vipers readily take any small rodents, fledgling sparrows, lizards, and pieces of chicken. Young vipers usually start on small lizards and crickets (*Grillus bimaculatus* and *Achaeta domestica*). After some months they usually take newborn mice. After the viper's bite a prey normally dies in 5-7

minutes. The snake never persecutes its prey. It finds the prey some time later using its olfactory organs. Swallowing ranges from one minute to 3.5 hours depending on prey size and the state of a snake. Complete digestion in the wild takes up to five days. In captivity digestion may take 30 to 40 hours at stable temperature. Optimal day temperature is 26-30°C, and night temperature 18°C during activity period.

Shedding. Mature vipers normally shed 2 to 3 times during the activity period. General shedding is observed in June. New born vipers shed in the first hours after birth. Before entering hibernation, they shed again.

Reproduction. Mating is recorded from late March to April. Birth occurs in late August. Females give birth to 3 to 5 young. The observed time of birth lasts for about two hours with intervals of 20 to 40 minutes (Zinyakova and Trofimov 1977). In captivity, the majority of females give birth at night, between 2400 and 0600 hrs. Some individuals are born in transparent capsules, which the neonates leave in the first minutes after birth. Females reproduce annually. Gravid females continue to take food right up to birth.

Development of young. Neonate *Vipera kaznakowi* have a mean body length of 144.75 mm, tail length of 14.0 mm. Mean body weight is 4.1 g (n=8). After first shedding on the second day after birth, newborns start actively feeding on insects or small lizards. After birth the activity period is 1.5 to 2.5 months, whereas newborns of *V. dinniki* never take food and almost immediately enter hibernation, during which snakes increase in length from 10 to 20 mm. *Vipera kaznakowi* lose 0.3 g of initial weight during the first month after birth. In the second month they restore their initial weight and then increase it approximately 1 g before entering hibernation. One year old specimens have a body length of 200 mm and a tail length of 24 mm. Vipers reach sexual maturity by the third year at a SVL of 350-400 mm.

Territoriality. Like other vipers, *Vipera kaznakowi* is conservative in territory use. The same individuals can be encountered in the same places during different seasons. *Vipera kaznakowi* utilizes considerably larger individual ranges than *V. dinniki*.

Seasonal and daily activity. Along the Black Sea coast of the Caucausus, *Vipera kaznakowi* emerge after hibernation in March at an altitude of 600 to 800 m. On the northern slope of the Big Caucasus the vipers appear in the second half of April to early May when the mean day temperature is 13°to 16°C. In the foothills the vipers enter hibernation at the beginning of November at an altitude of up to 600 m. In the upper elevational limits of its range *V. kaznakowi* hibernate in late September to early October. New born vipers are more active than those of other age groups.

Two sharply marked peaks of daily activity can be observed in *Vipera kaznakowi*. In the morning the period of daily activity ranges from 0730 to 1130 hrs, and in the evening from 1630 to 1830 hrs. At those times the soil temperature does not exceed 30-32°C in the sites inhabited by *V. kaznakowi*.

Sympatric species. Along with *Vipera kaznakowi* the following species of reptiles occur: *Lacerta derjugini, L. saxicola, L. praticola, L. agilis, Anguis fragilis, Pseudopus apodus, Coluber najadum, C. jugularis, Elaphe longissima, Natrix natrix, N. tessellata,* and *Coronella austriaca*. Narrow sympatric areas appear with *Testudo graeca, Lacerta trilineata, L. caucasica, L. rudis, L. parvula, L. mixta, Elaphe hohenackeri, Vipera ursini,* and *V. dinniki*.

Vipera dinniki Nikolsky, 1913
(Fig. 5, 6, 7, 12, 14ab,16, Plate 2)

Species description in chronology

Vipera berus - Boettger *in* Radde, 1899:286; Nikolsky, 1905:304 (ad Caucasus).

Pelias chersea - Menetries, 1832:73 (part).

Vipera xanthina - Dinnik, 1902:34.

Vipera renardi - Silantyer, 1903, 30:37 (part).

Vipera berus dinniki Nikolsky, 1913:176-179.

Coluber berus dinniki - Nikolsky, 1916:240-244.

Vipera tigrina Tzarevsky, 1916:32-37.

Vipera ursini renardi - Kramer, 1961:715.

Vipera ursini kaznakowi - Knoepfler and Sochurek, 1955:185-188.

Vipera kaznakowi - Terentyev and Chernov, 1949:270-271 (map 5); Bannikov et al., 1977:323-324 (map 133, colored plate 31,4).

Vipera kaznakowi dinniki - Vedmederja, 1984:8.

Vipera kaznakowi orientalis - Vedmederja, 1984:9, nomen nudum.

The English common name is Dinnik's Viper or the Caucusus Subalpine Viper.

Lectotype: No. 26044, an adult female collected by N. Y. Dinnik (Fig. 5) from the upper reaches of the Malaya (Small) Laba River, Northern Caucasus and Svanetia, Georgia (Fig. 2: B, B'). The specimen is preserved at the Museum of Natural History, Kharkov State University, Ukraine.

Diagnosis: Total length reaches 500 to 550 mm. Dorsally the head is covered with large scales. Nostril is cut through in the center of the nasal. Upperlateral snout edge is rounded and slightly pointed. Rostral touches either one or two apical scales on upper head. Three to four scale rows with no keels are between the rostral and frontal. Head is not broad. Nuchal collar is not expressed.

Description: In males body length is not greater than 412 mm; in females it does not exceed 486 mm. The ratio of body length to tail length is 5.9 to 7.4 in males; 7.8 to 13.5 in females. General coloration is not as bright as in *Vipera kaznakowi*. However, specimens with bright yellow and orange elements can be observed. Normally *V. dinniki* (Fig. 6,.Plate 2) have light brown, grey, silver greyish or green greyish color which never occurs in *V. kaznakowi*. Some specimens have a dark even dorsal stripe along the center of the body. The latter substitutes for the zig-zag shaped stripe typical for the majority of plate-headed vipers. Ventrum is either dark and light spotted or light grey and dark speckled. Neonates of *V. dinniki* occasionally don't have the red color of the body typical for *V. kaznakowi*. They can be born grey brown. The head is relatively narrower than that of *V. kaznakowi*. The nuchal collar is not expressed, unlike in *V. kaznakowi*. Upper edge of snout is either rounded or slightly pointed. Head can be either protuberant or flat dorsally, but never impressed like that of *V. kaznakowi*. Body is thinner and more delicate. Comparative data on pholidosis and size characters are listed in Tables 1-4.

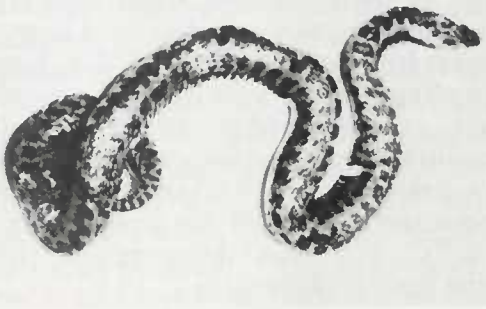


FIG. 5. Lectotype of *Vipera dinniki* (The Museum of Natural History of Kharkov State University 26044).

Remarks and variability.

Vipera dinniki greatly resembles morphologically *V. kaznakowi, V. ursini renardi* and *V. berus*. In size *V. dinniki* is smaller than *V. kaznakowi* and larger than *V. ursini renardi* (Table 2). The head normally is slightly protuberant, seldom flat and never as broad as that of *V.*

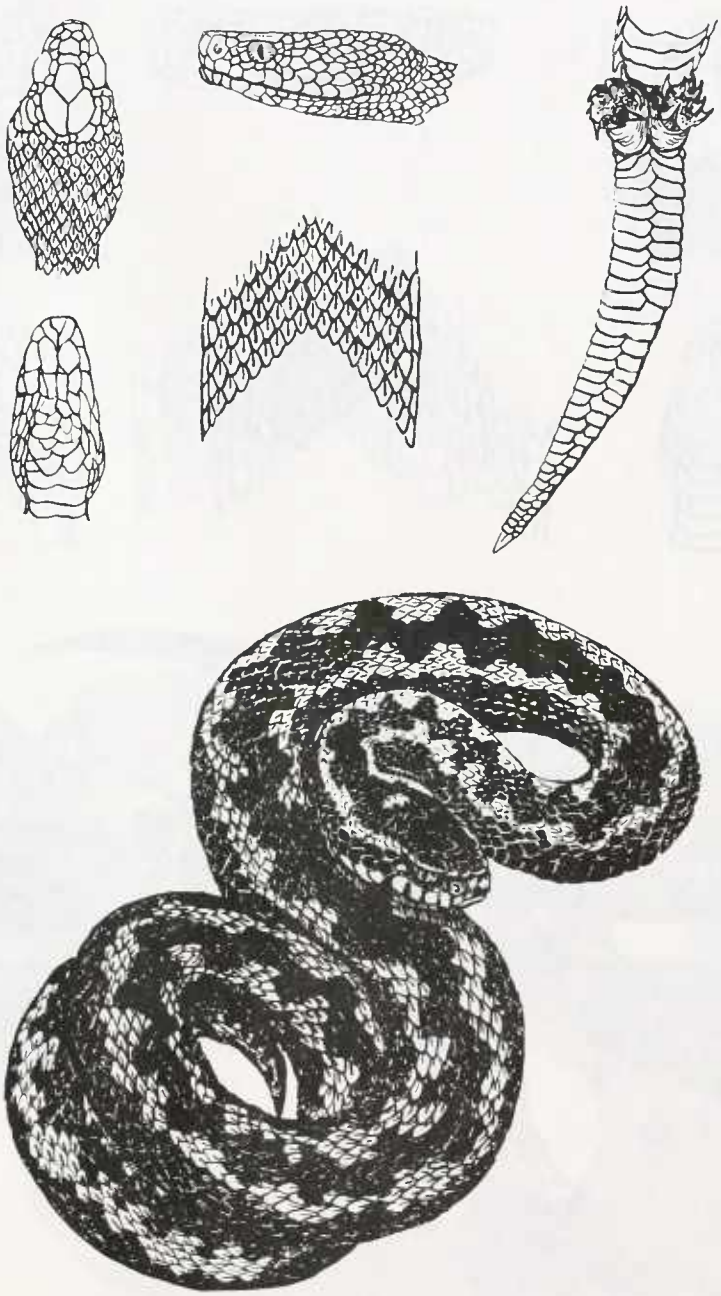


FIG. 6. A Female *Vipera dinniki* from the upper part of the Laba River (ZIN 17281).

kaznakowi. Hence, the nuchal collar is hardly marked. In body proportions it primarily resembles *V. berus*. Normally the parietals are shorter than the frontal. Three to four lower labials reach the lower jaw scale.

Color. Normally *Vipera dinniki* is not as brightly colored as *V. kaznakowi*. However specimens with either bright yellow or orange elements occur. Often *V. dinniki* have greyish, silver greyish or green greyish color. This is never recorded in *V. kaznakowi*. For all shield-headed vipers a zig-zag shaped dorsal stripe is a common pattern element. In *V. dinniki* the stripe is often an even broad dark line which runs along the dorsum. This is occasionally seen in *V. kaznakowi*, where it is usually represented by a row of oblique

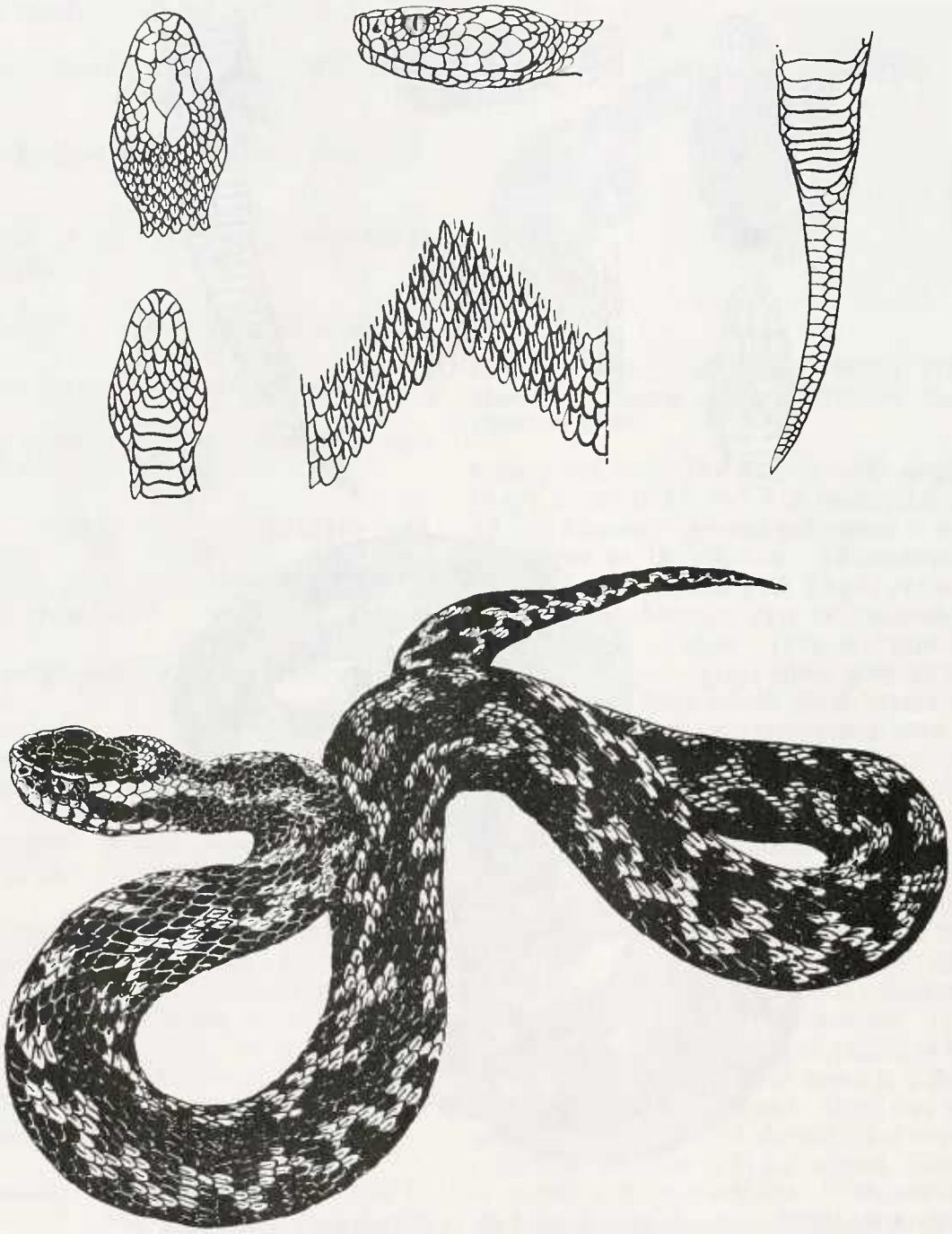


FIG. 7. A male *Vipera dinniki* from the vicinity of Krasnaya Polyana (Red Meadow), [ZIN 12153].

diametrical spots. The dorsal stripe is separated from the dark sides by lighter lateral stripes. The ventrum is either dark with light spots or light grey. The number of melanistic specimens in populations ranges from 20 to 25%. Complete melanistic individuals of *V. dinniki* do not have a single light spot in color, unlike melanists of *V. kaznakowi*.

Sexual dimorphism. Maximum body length is greater in females (up to 486 mm), and smaller in males (up to 412 mm). Males have longer tails, characteristically

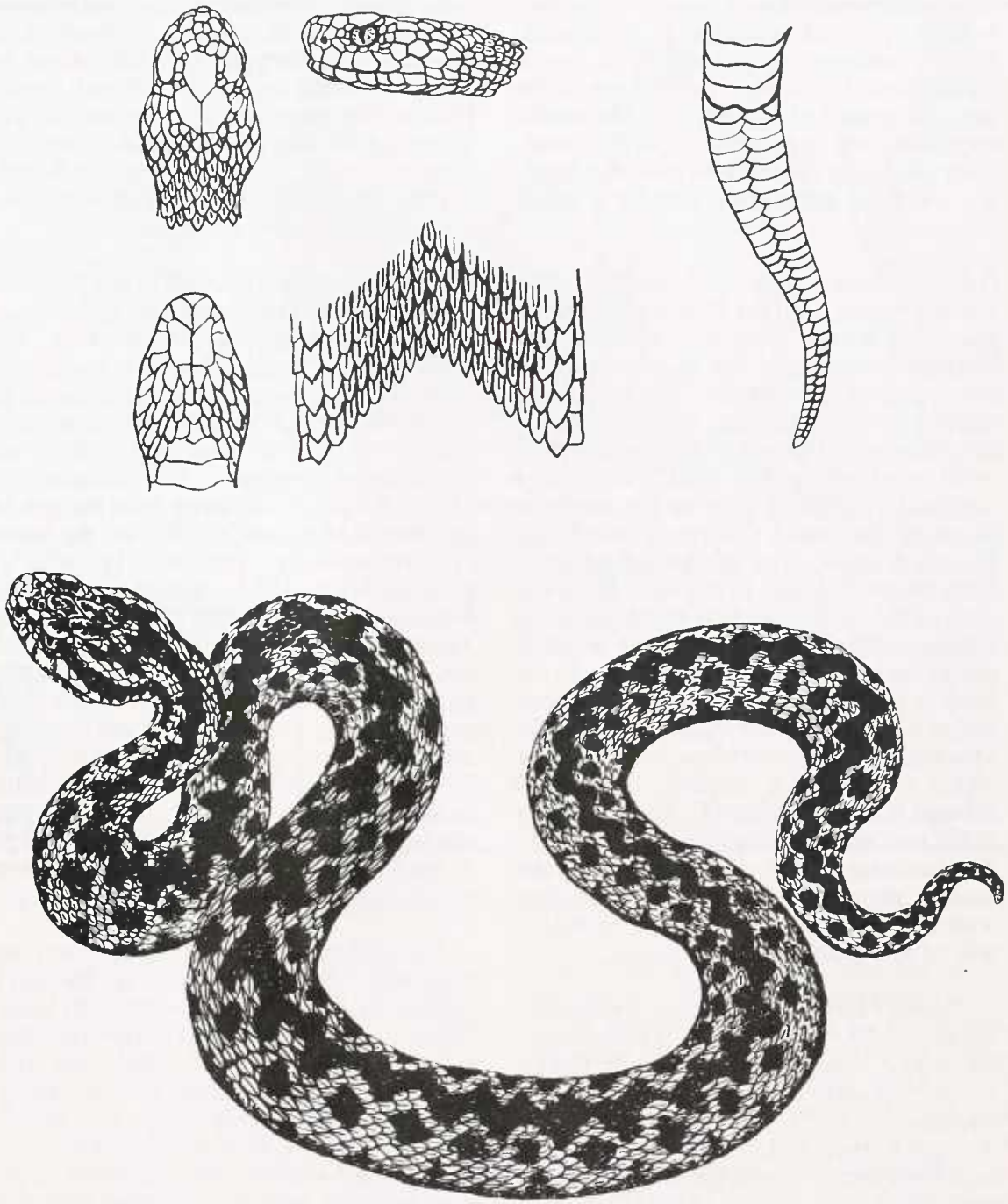


FIG. 8. A *Vipera dinniki* from Lagodekhi, an eastern population (ZIN 13769).

thicker at the tail base (Table 2). The number of ventral scales is greater in females. The number of subcaudals is greater in males. Males are more delicately built than females. Sexual dimorphism in color is hardly expressed. Coloration in males is generally brighter and more contrasting.

Age variability. Neonate vipers are patterned like adult individuals. However, the general color is normally grey, unlike bright red neonates of *Vipera kaznakowi.* Only after the third shedding, faint

coloration typical for the species (yellow, reddish, greenish) emerges in *V. dinniki*. Color becomes stronger with each subsequent shedding. Maximum color strength is reached by maturity. Melanistic specimens are born with a specific color. They gradually darken with each shedding. By the third year, they acquire a black velvet color.

Geographical range and ecology. The species ranges from the Fisht-Oshtenovsky Mountain Range in the west up to Mount Shkhara in the east. The eastern limits of this species distribution has not been worked out and additional eastern localities are probable. The southern distributional limit runs along the dark coniferous highland ecological belt on the southern slope of the Main Caucasus and South Frontal Ridges. The northern limit goes from Mount Shkhara to the west along the crest of the Main Caucasus Ridge up to the Bolshaya (Big) Laba River head where it passes on to a northern macroslope. In the north it occurs on the Peredovoy (Frontal) Ridge and reaches the Fisht-Oshtenovsky Mountain Massive (Orlov and Tuniyev 1986). Research during 1987-1989 showed that *Vipera dinniki* occurs further to the east than previously known (Fig. 9). The problem of subspecific status of the eastern populations and their interaction with the vipers of the *V. ursini* complex will be addressed in a future paper.

The elevational distribution is generally between 1500 and 3000 m. Occasionally the viper may descend slightly lower. *Vipera dinniki* is a subalpine montane-meadow species. It tends to be restricted to the upper forest belt, subalpine and alpine meadows, rocky outcroppings and montane moraines.

Vipera dinniki can be observed in vegetation associations of *Betuletum calamagrostidosum, Pinetum mystillosum subalpinum, Fageto Betuleto-Sorbetum altherbosa-subalpinum,* also in *Aceretum trantaltherbosum subalpinum.* It is associated with rock outcrops interspaced with shrubs of *Rhodoretum caucasicus subalpinus,* subalpine highland herbs and rock debris. It occurs widely in moraines overgrown with moss, lichens and *Thymus*. The biotype of *V. Kaznakowi* is always located in the vicinity of water. Hibernation sites are also located in the immediate vicinity of summer biotypes. All types of rock outcrops are inhabited. *Vipera dinniki* can be found in limestone, slate, and crystalline outcrops.

Climatic conditions within the range of *Vipera dinniki* are much more severe than those of *V. kaznakowi*. However, the viper's distribution in severe highlands coincides with the mildest climatic places in this severe area. *Vipera dinniki* commonly occurs on slopes with a southern or southeastern exposure. For instance, on Mount Aibga, 23 km away from the sea, at an altitude in excess of 1800 m, the mean temperature in January is -0.1°C (Korostelyov 1933; Shkadova 1979). Mean temperature in July is only 13.7°C on Mount Achisko at an altitude of 1750 m (37 km away from the sea). However, great temperature drops never occur in this area, even in winter. As regards to soil freezing, minimum temperature in January is -7°to -8°C (Selyaninov 1933). Due to solar radiation on slopes with southern and southeastern exposures, the vipers manage to maintain high body temperatures during activity periods.

Vipera kaznakowi reaches the edge, but does not penetrate deep into the dark coniferous belt. *Vipera dinniki,* at its lower limits, reaches the edge but never penetrates the dark coniferous belt. Thus, the dark coniferous belt is a barrier between them. Occasionally, in spots where this belt is either absent or is fragmented, for instance along river valleys, both species occur sympatrically, forming a narrow line with intergrading characters. The valley of the Mzymta River may serve as an example of a site where the two species come in contact. The limited distribution of the species on the northern slope of the Main Caucasus Ridge might be connected with the increase of the mountain's aridity and severe climate towards the east. Xerophytization is observed from west to east in the subsequent change of beech

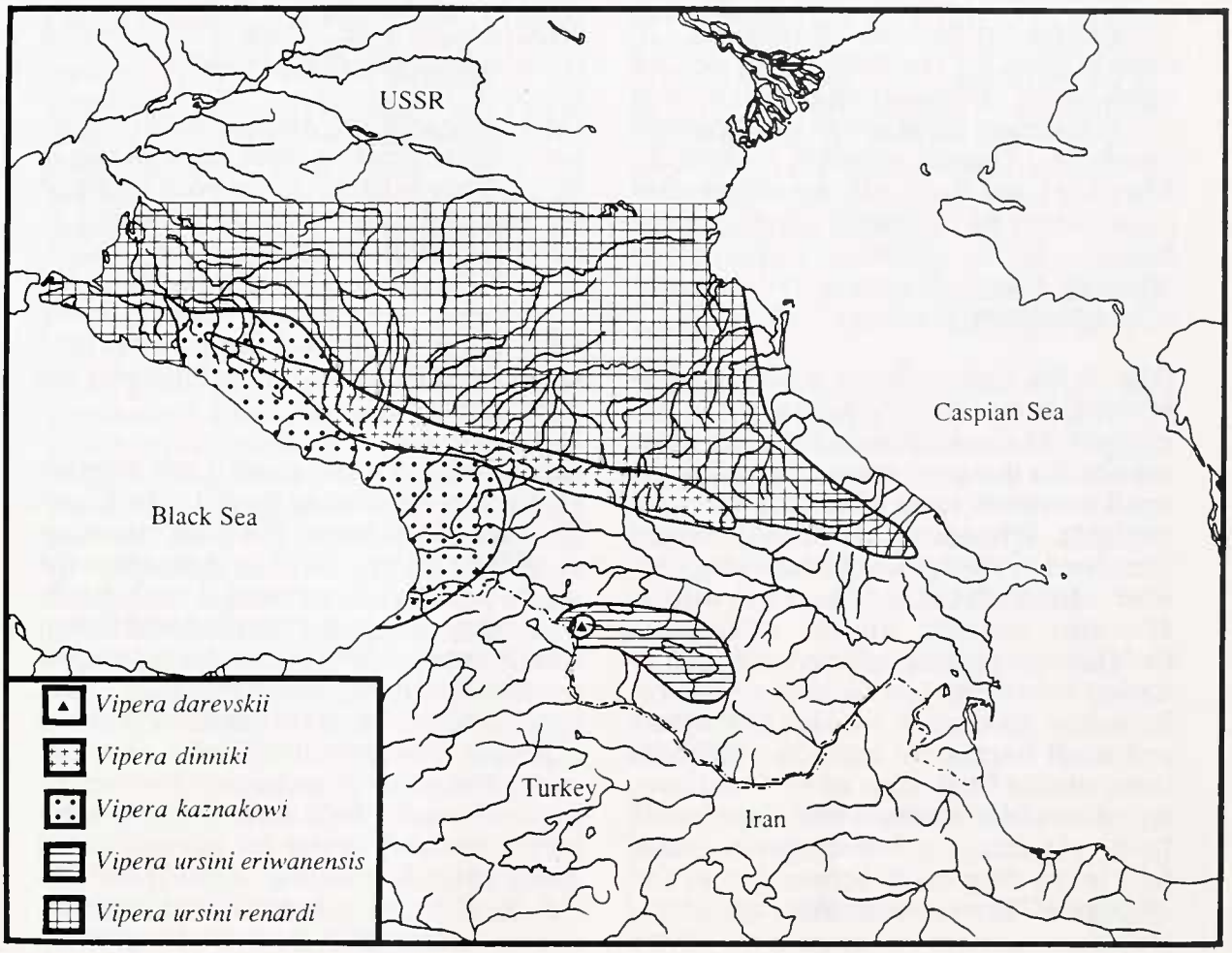


FIG. 9. Distribution map of shield-headed vipers in the Caucasus.

forests and *Abies* forests to pine forests, and further east, to steppe areas (Adamyants 1971, Kharadze 1974, Lavrenko 1980; Agakhanyants 1981). This change is noted in amphibians and reptiles. Along with *V. dinniki, Lacerta derjugini* and *Pelodytes caucasicus* fall out and more xeric species such as *Bufo viridis, Lacerta agilis,* and *Vipera ursini renardi* dominate.

Population density is different in various parts of the habitat. It is maximal on rock outcrops and moraines in the subalpine belt of the Caucasus Reserve. In July, in subalpine meadows of the Gertsen Ridge and along the valley of the Bezymyanka (Without name) River, 1700 to 1900 m, we have recorded as many as 5 to 7 vipers per 1 km of a route. At the same time, on an area of 500 m², we have recorded up to 6 specimens. This is at an elevation of 1800 m on the Aishkha Ridge in a subalpine meadow of *Aceretum trantaltherbosum subalpinum*. In late June to early July along the Moloshnaya (Milk) and Sumasshedshya (Crazy) rivers of the Mzymta River basin, up to 4 specimens per 100 to 500 m of a route were recorded. In August, on a bank of the high altitude Kardavych Lake, we recorded up to 8 specimens per 300 m of a route. On the Aspidny Ridge, 2000 m above sea level, we recorded 5 to 6 specimens per 300 to 400 m of a route.

According to Bozhansky (1979), the density in the subalpine belt is 2 to 6 specimens per hectare. Occasionally, seasonal accumulations of up to 30-40

individuals per hectare are possible. In other regions the population densities are much lower. Degradation of localities is due to intensive cattle grazing in subalpine meadows. Overall numbers of both *V. kaznakowi* and *V. dinniki* are estimated at some dozens of thousands (Bannikov and Makeyev 1976). Apparently the figure may primarily concern *V. dinniki* as the number of *V. kaznakowi* is rather small.

Diet. Adult *Vipera dinniki* eat fewer types of food items than *V. kaznakowi.* For instance, in the highlands there are viper populations that prey either on lizards or on small mammals as no other food items are available. When field collected vipers were stimulated to regurgitate, the following prey were observed: *Apodemus sylvaticus, Microtus majori, Sicista caucasica,* fledglings of ground nesting birds such as *Anthus spinoletta,* and *Lacerta caucasica.* Immature specimens feed on Orthoptera and small lizards. In captivity *V. dinniki* takes similar food items as *V. kaznakowi.* It is often observed that a bitten mouse or a field-vole makes a few desparate leaps, falls into a deep crack between rocks and dies there. The viper skillfully catches its prey between its teeth, drags it out onto a level spot, then drops it, examines it from all sides and having found the prey's head, swallows it. This behavior is typical for other rock dwelling vipers from the Caucasus, such as *V. raddei,* and *V. ammodytes.*

Shedding. Overall, shedding is observed in June and in late August to early September. Neonate vipers shed during the first hours after birth. Some days later they enter hibernation.

Reproduction. Copulation occurs in late April to May (Bozhansky 1984). Birth of neonates on the northern slope of the Main Caucasus Ridge occurs in August. On the southern slope it occurs throughout September. Bozhansky (1983) found two groups of specimens during the summer. One group containing males and females which do not reproduce that year, and the other group containing gravid females. Bozhansky suggests that in montane conditions, female *Vipera dinniki* have a reproductive cycle of many years.

Development of the young. In late July to early August viper embryos reach 70 mm in length (Orlova 1973). Mean body length of the neonates is 131.0 mm, tail length is 14.8 mm, mean weight is 3.1 g (N=28). In the highlands almost right after birth the vipers enter hibernation. Unlike newly born *Vipera kaznakowi,* they do not feed until the next season. By the third year the vipers become mature.

Territoriality. Gravid females tend to move on small areas ranging from 1-4 to 51 m^2. Their individual places to a great extent (up to 98%) overlap. Within their sites the vipers actively utilize only 2 or 3 places where they may be encountered at different times and under various weather conditions. During the morning the vipers can be found in places with a western exposure. Normally, this place is on a rock surface shaded by a bush. The vipers utilize direct sun for a short time, leaving a part of the body under the sun and a part under a half shaded area. From 1100-1200 the vipers retreat to burrows and normally appear after 1500 hours. In gloomy weather they lie flat on a rock during the entire period of activity. This increases the surface of the body contiguity with the rock. On rare hot days, after midday the vipers never reappear on the surface. Males and non-reproducing females emerge much more seldom, normally after they have taken food. Bozhansky (1984) observed some specimens using the same territories for three seasons.

Insolation is of great importance in the viper's life. Gravid females take food rarely and two months before giving birth, they stop eating. Territory utilization is entirely dependent on optimal insolation patterns. Absence of aggressiveness allows all adult females in a territorial group to utilize the warmest microhabitats (Bozhansky 1983, 1984). These data were collected by Bozhansky during three summers at an elevation of 2000 m along the border between the forest and subalpine belts on Aishkha Ridge, the right ridge of

the Mzymta River valley, the western Caucasus. It is amazing that *Vipera kaznakowi* from the low altitudes of the coast have considerably larger individual sites. The females do not have a multi-year cycle and never stop taking food while gravid. The adaptations in the highland *V. dinniki* are very important in relatively low temperatures, rainy periods, and when it suddenly becomes cold.

Seasonal dynamics in populations. Biological monitoring in highland populations from the Caucasus Reserve testify to their climax state (the collections of the Zoological Museum of the Moscow State University and the Zoological Institute, the USSR Academy of Sciences were adopted as a zero counting point). Seasonal dynamics within climax populations is monotypical. At the beginning of spring, males emerge first. Then the percentage of female occurrences gradually increases. By early-mid June the sex ratio is 1:1. In mid-late summer males are seen on the surface less frequently than females. During the period of pre-hibernation at the end of summer, males become more common again. From late August to mid September, 80% of the snakes observed are gravid females and new born individuals. The later can be observed on the surface even when adults have entered hibernation. During this period, the location of new born individuals does not necessarily correlate with rock outcrops which are used as winter shelters. The newborn snakes migrate much more than adult snakes.

Seasonal and daily activity. In the spring vipers emerge from mid April to May when mean day temperature on the surface reaches 11°C. Seasonal activity is dependent on weather conditions. In the highlands of the Caucasus Reserve the first snow usually falls in the second half of September and snow is present until May. Snow cover is 7-8 m thick. Hence, *Vipera dinniki* inhabiting the subalpine belt enter hibernation in the second half of September. At elevations of 1800 to 2400 m morning activity is hardly expressed, whereas evening activity is shifted from 1700 to 2000 hrs. In gloomy weather snakes are active throughout daylight at temperatures higher than 10°C. At 8°C vipers are not seen on the surface. Gravid females are seen on the surface even in drizzling rain. Even if the temperature is 10°C, body temperature in vipers is 30°C, and cloacal temperature is 26-28°C due to accumulation of warmth from solar radiation. This is an important thermal adaptation of a number of highland reptiles.

Sympatric species. Throughout nearly the entire range *Vipera dinniki* is sympatric with *Lacerta caucasica, L. saxicola, Anguis fragilis,* and *Coronella austrica.*

Vipera darevskii Vedmederja, Orlov, and Tuniyev, 1986 (Fig. 10, 11, 12, 13)

Chronology of species description

Vipera kaznakowi dinniki - Darevsky, 1956:128.

Vipera kaznakowi darevskii - Vedmederja, 1984:8, *nomen nudum.*

The English common name is Darevsky's Viper.

Holotype: ZIN 19934, an adult female from Legli Mountain, the Mokrye (Wet) Mountains, Gukasynsky region, Armenia. The specimen was collected in June, 1980 by I. S. Darevsky. The specimen is preserved at the Zoological Institute, the USSR Academy of Sciences, Leningrad (Fig. 10).

Paratypes: ZIN 16546 a and b. The specimens were collected May 28, 1954; ZIN 17545, the specimen was collected August 6, 1955; ZIN 19935, the specimen was collected June, 1980 by I. S. Darevsky (Fig. 11).

Holotype description: Body length is 421 mm, head included. Tail length is 46 mm. A female. Head is slightly impressed dorsally. Lateral snout edges are slightly pointed. Anterior edge of snout is slightly rounded. Rostral is narrow. Frontal is

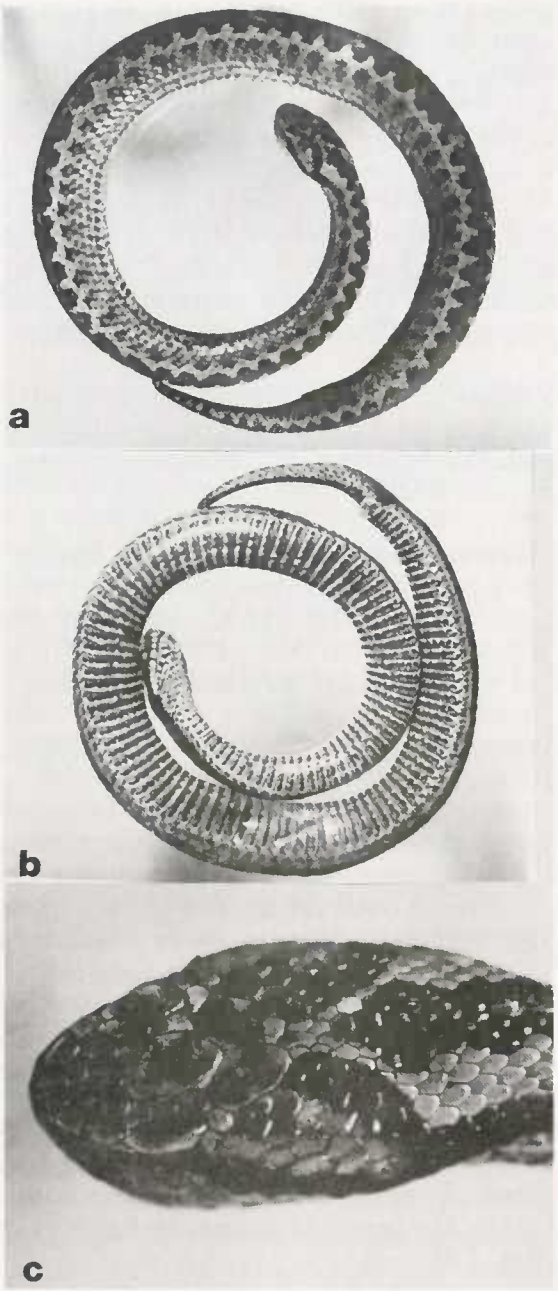


FIG. 10. Holotype of *Vipera darevskii* (ZIN 19934). a. dorsal view, b. ventral view, c. head.

narrow. Its length is equivalent to 1.66 times its width. Parietals are slightly longer than the frontal. The frontal is separated from supraoculars, which protrude over lateral edge of the snout, by a row of three scales. Prefrontal is triangular, three times shorter than the frontal, and is separated from the rostral by 2 scale rows. Nostril is cut through in the lower part of the nasal. The latter is separated from the rostral by a broad scale. Upper labials and lower labials are both 9 to the right and 8 to the left. There are 5 rows of throat scales. Around the center of the body there are 21 scale rows with strongly expressed keels, except for two scale rows on both sides adjacent to the ventrals, which are smooth. The number of ventrals is 138. There are 25 pairs of subcaudals.

The color is yellowish grey. A zig-zag shaped brown stripe runs along the dorsum. At the center of the body its width is nearly 8 mm. A row of hardly conspicuous spots is present laterally. The spots merge into a light brown stripe. Dorsally, the head has light yellowish spots along the edges of the frontal, parietals and lower oculars with yellowish temporals. Ventrum is blackish marked by light contours of ventrals (Fig. 10).

Paratypes: Morphological characters of 8 paratypes are listed in the tables 1-4. General color resembles that of the holotype, except for 2 specimens. In the latter the dorsal stripe is interrupted in the anterior part of the body (Fig. 11).

Diagnosis: This viper is not large. SVL reaches 460 to 489 mm. Head is slightly impressed dorsally, covered by big scales. Lateral edges of snout are slightly pointed. Anterior snout edge is rounded. Nostril is cut through in lower part of the nasal. Head is narrow, hardly separated from body.

Remarks and variability.

Morphologically, *Vipera darevskii* occupies an intermediate position between *V. kaznakowi* and *V. ursini eriwanensis*. To be more precise, morphologically *V. darevskii* occupies a middle position between the two species of the "*Vipera kaznakowi* " complex (*V. kaznakowi* and *V. dinniki*), on the one hand, and the steppe vipers from the "*V. ursini* " complex, on the other hand. This viper is considerably smaller in body size than *V. kaznakowi*. The head is narrower and the nuchal collar is less expressed. It differs

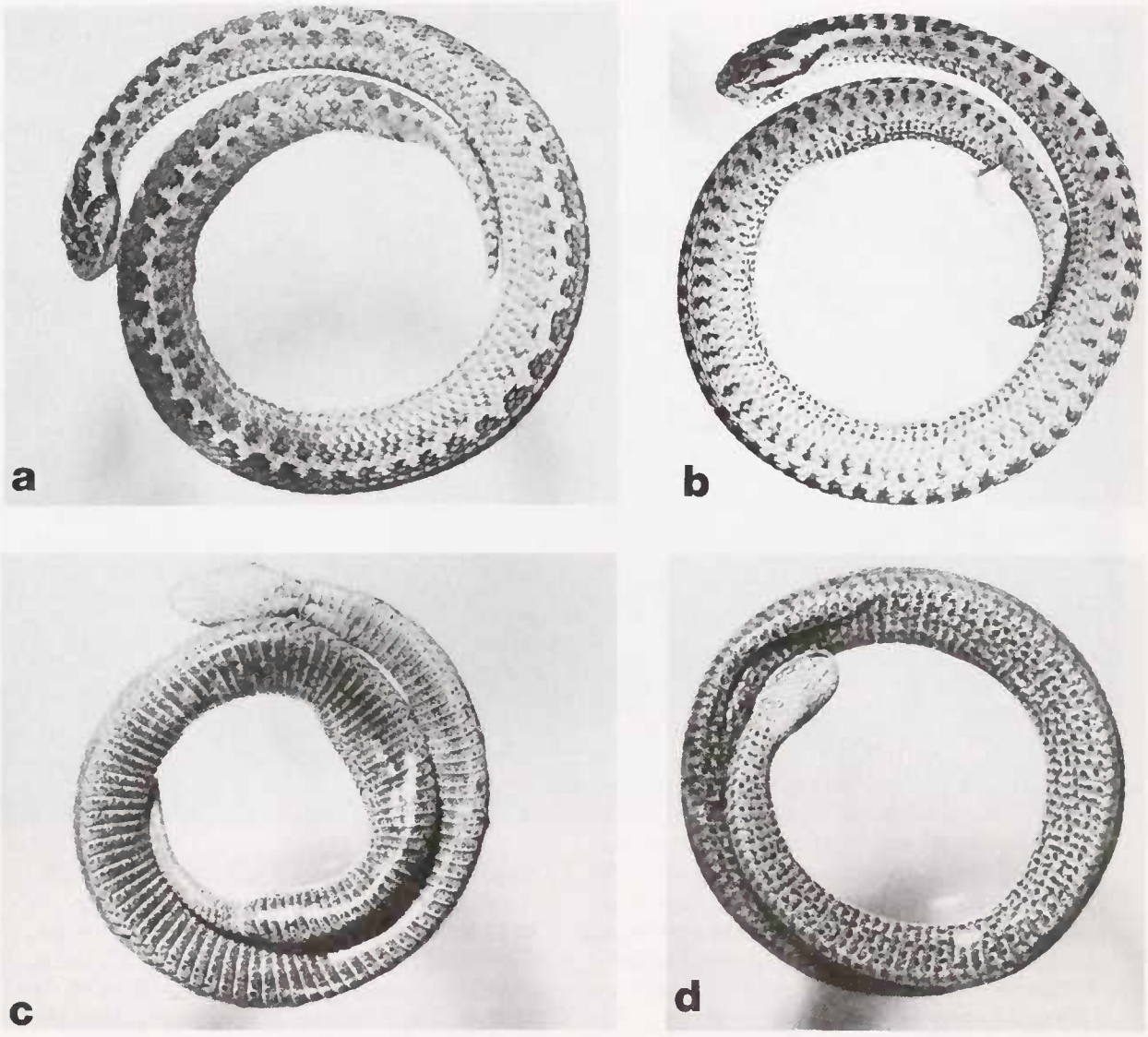


FIG. 11. The paratypes of *Vipera darevskii* (ZIN 19935). a., b. dorsal view. c., d. ventral view.

from *V. ursini eriwanensis* by greater head height and much less pointed upper anterior snout edge. Pholidosis data are listed in Tables 1-3.

Coloration is yellowish or yellowish grey, which never occurs in *Vipera ursini*. Along the dorsum a contrasting zig-zag shaped brown stripe is present. The ventrum is dark grey, speckled black and white. Of the small number of known specimens, no melanistic individuals have been found. The coloration of *V. darevskii* is evidently more stable than that of the polymorphic and motley colored *V. kaznakowi* and *V. dinniki* (Fig. 13). Yellow-greyish hues are prevalent. The pattern is more homogeneous. The neck transition is hardly expressed, like in *V. dinniki*. It differs from *V. ursini eriwanensis* by 1) a relatively high head, 2) yellowish general coloration, 3) clear contrasted pattern, and 4) special pholidosis.

Sexual dimorphism. Maximum body size is greater in females than males (Table 2). Males have longer tails. Number of ventral scales is greater in females (Fig. 14). Number of subcaudal scales is greater in males. Sexual dimorphism in color is not recorded.

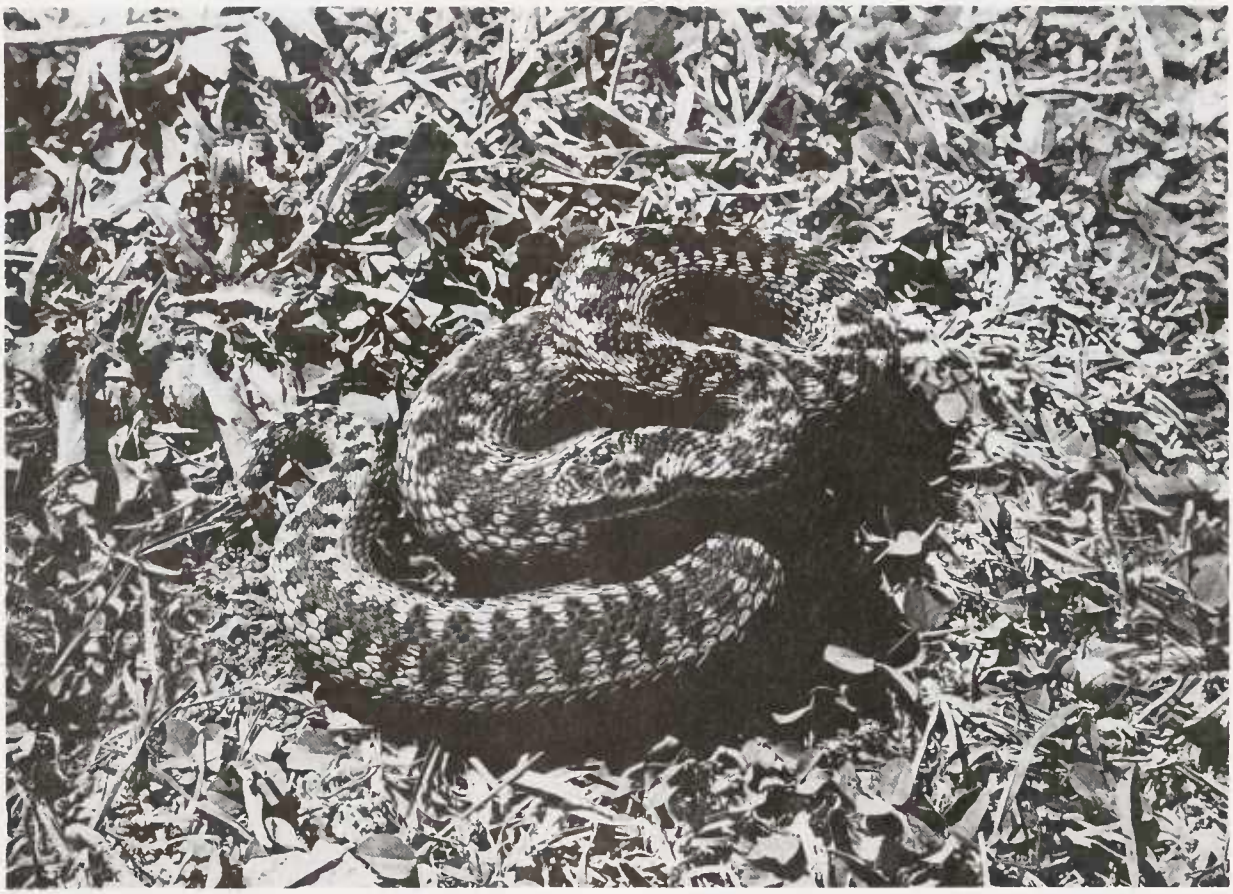


FIG. 12. *Vipera darevskii* in the field.

Age variability. Newly born vipers are uniquely colored.

Geographic range and ecology. The species range shows relict characters. It covers the southeast part of the submeridian Dzhavakhetsky Ridge within the territory of Armenia (here this ridge has the name Mokrye (Wet) Mountains) and evidently adjacent regions of Georgia (Fig. 1: 9). Vertical distribution lies within a narrow interval at elevations from 2600 (rarely 2500) to 3000 m on Mount Legli, Georgia. It is a montane meadow subalpine species inhabiting detritus slopes with great amounts of big black outcrops of volcanic rocks at angles of 35°-45° (Darevsky pers. comm.). At recorded elevations, according to Tumadzhanov (1980), subalpine meadows (so called Transcaucasian oats outcrops) are widely represented. It is a leading formation on steep slopes with all exposures which form the first stages of invasion of bare rock outcrops. Characteristic components of these meadows are as follows: *Festuca woronowii, F. ovina, Bromopsis variegata, B. villosula,* and *Carex tristis*. Lower along the slopes at elevations from 2300 to 2400 m the formations of transition montane-meadow steppe are replaced by montane *Festuca valesidea* and *Stipa* (feather grass). From elevations of 2200 m down to 1000 m *Festuca valesiaca* steppes occur (Lavrenko 1980). Here in the montane-steppe highland ecological belt, *Vipera ursini eriwanensis* occurs in contact with *V. darevskii* in the transition zone of the meadow steppes.

The numbers of *Vipera darevskii* are not great. To date it is known only from the type locality cited as "Mount Legli", where it occurs within a narrow band in subalpine meadows. The species biology is nearly unknown.

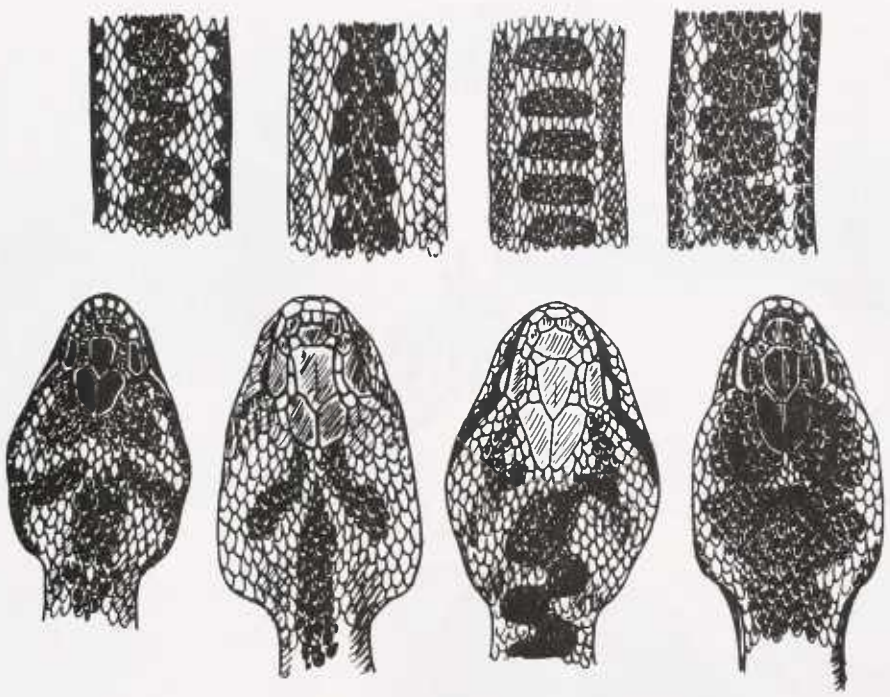


FIG. 13. Polymorphism in *Vipera dinniki* from the population that occurs in the valley of the upper part of the Mzymta River.

Discussion

Phylogeny and the history of present viper distributions in the Vipera kaznakowi *complex in the Caucasus Isthmus.*

The head of the vipers assigned to *Vipera berus, V. ursini,* and the *V. kaznakowi* complex (Fig. 15) is covered with rectangular scales (the rostral, nasals, nasal-rostrals, upper oculars, parietals, and the frontal), unlike in *V. lebetina, V. xanthina, V. raddei,* and *V. persica.* In the latter species, small scales on the upper head are typical.

Marx and Rabb (1965) consider these characters important in the assessment of phylogenetic relationships of the vipers. On the basis of body vertebrae close relationships and isolation of *Vipera berus, V. ursini* and *V. kaznakowi* within the genus *Vipera* have been proposed (Chkhikvadze and Zerova 1983). They restore the prior generic name of *Pelias* to the vipers. Reuss (1935) noted the isolation of the vipers that have large regular head plates, on the basis of skull kinesis and analysis of the head muscles. Without going into extensive detail on the taxonomic position of these vipers with large regular head scales from the Euro-Siberian group, we shall simply refer to them as shield-headed vipers. These vipers show great morphological resemblance. They are share a common color pattern, behavior, and reproductive biology.

We consider *Vipera berus* and *V. kaznakowi* to be close relatives. These vipers probably diverged from a mesophilic form in the Miocene. Northern populations tend to be restricted to humid biotypes up to tundra areas, whereas for southern populations, humid subtropical forests are inhabited. In Kramer's (1961) book concerning the taxonomy of *V. ursini* and *V. kaznakowi,* in the chapter on phylogeny and history of the vipers distribution, he regards *V. berus* and *V. ursini* as a united circle of races, a rassenkreis. Such facts that *V. ursini renardi* was subspecifically included in *V. berus* also emphasizes close relationships of shield-headed vipers.

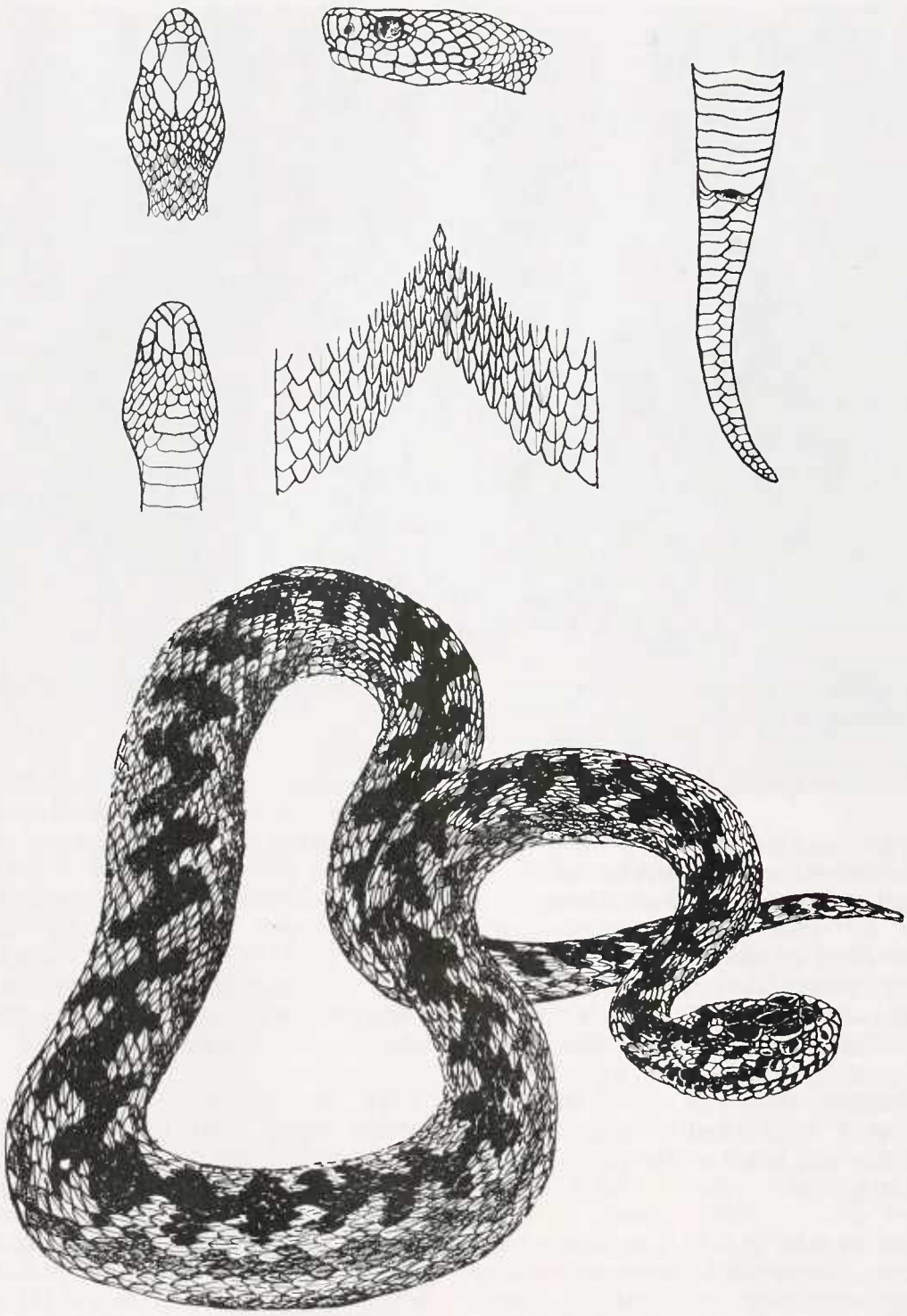


FIG. 14. A female *Vipera darevskii* from the vicinity of Gukasyansky Region, Armenia (ZIN 19934).

Basoglu (1947) recognized the following varieties within *V. berus: berus, renardi, ornata.* His view point was criticized and the *V. ursini renardi* was restored (Terentyev and Chernov 1949; Mertens 1952 a, b). Kramer (1961) noted great morphological resemblance in *V. berus* and *V. kaznakowi.* He considered them

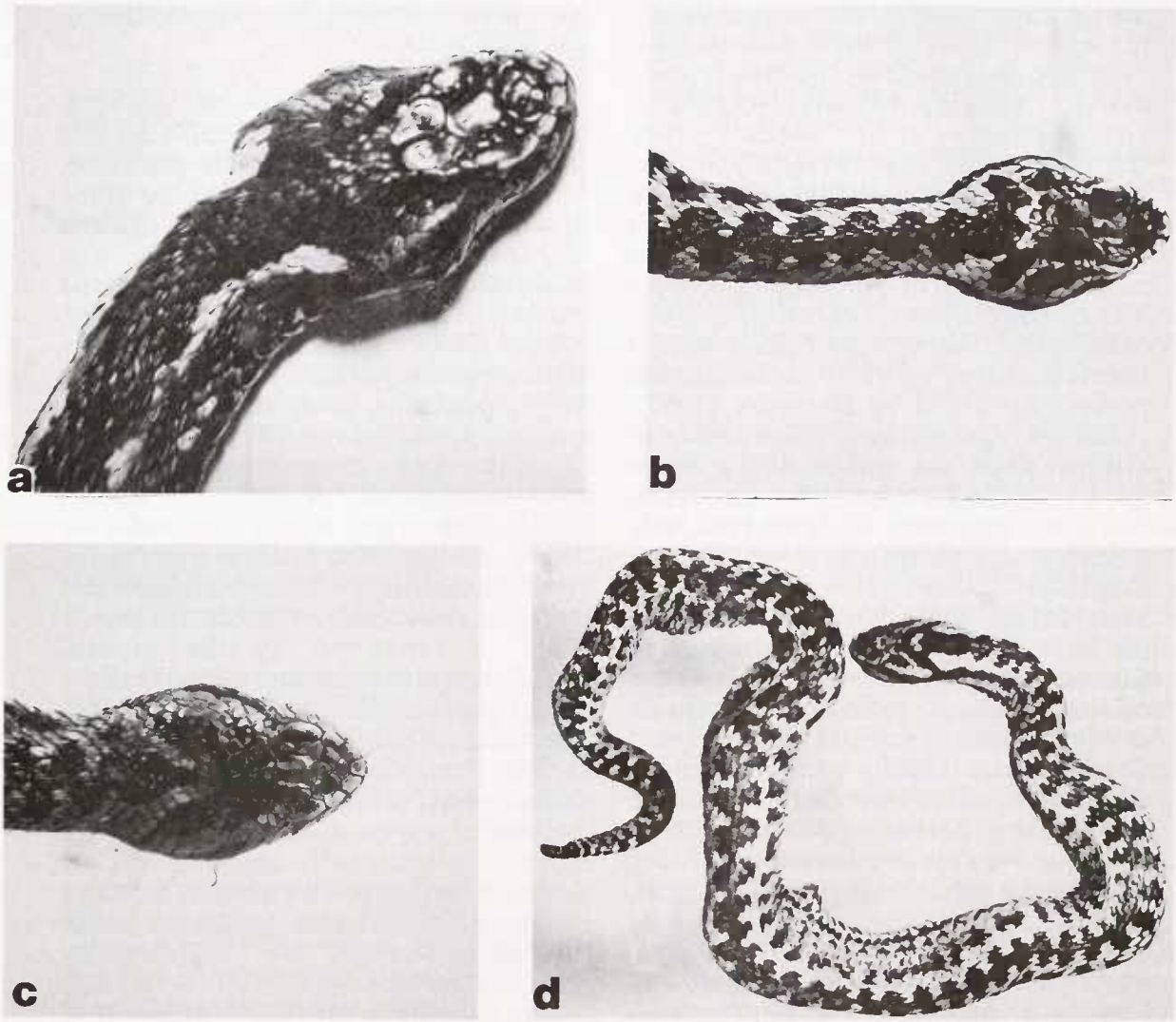


FIG. 15. The shield-headed vipers from the Caucasus. a. *Vipera kaznakowi*, b. *V. dinniki*, c. *V. ursini renardi*, d. *V. dinniki* (Lagodekhi, Georgia. ZIN 8389).

phylogenetically close species and felt that montane populations of the vipers played a big role in the formation and isolation of the forms. In his opinion, when it became cold they were forced out of the mountains onto the plains by glaciers. When the climate became warm again, they retreated into the mountains. In the mountains it was easy to choose temperature and humidity optima, whereas on the plains this was not possible. Kramer felt that in some places on the plains where refugia might be present, the climate remained more or less stable. For the vipers in the *V. ursini* complex, Kramer suggests first separation in the Miocene and Pliocene and later independent development of the eastern and western forms. The complex formation of the climate and relief in the Caucasus coincides with regular regressions and transgressions of the sea. Breaks in links between the faunas of the Caucasus and the European platform, the Balkans and Turkey stipulate emergence and isolation of original viper forms, beginning with the Miocene and Pliocene. At this time the formation of the Caucasus as a montane country occurred (Bogachev 1938). Schwarz (1936) suggests that the viper fauna of the Mediterranean islands are Miocene relicts.

Present ranges of shield-headed vipers in

the Caucasus have precise altitudinal and ecological limits to their distributions. They are supported by natural historic events. Overlap of ranges occurs in comparatively small areas. The "*kaznakowi* "like vipers evidently invaded the Caucasus during the Miocene from the south, when the Caucasus island was connected with Middle Asian land. The southern invasion of the Caucasus in upper Miocene by different mammal species was observed by Vereschagin (1958); that of lizards from the *Podarchis-Archaeolacerta* groups was noted by Darevsky (1967). Fossils of *Vipera* have been known in Europe since the Miocene (Tatarinov 1964). Of the European Miocene fossils, *Provipera boettgeri* Kinkelin 1892, was described. Of those from lower Pliocene, *V. gedulyi* Bolkay 1913, was described by Marx and Rabb (1965). This was at about the time the Caucasus Mountains were formed (Bogachev 1938). A warm subtropical climate which stimulated rich development of mesophilic vegetation, and contributed to the formation and wide distribution of warmth and mesophilic species like *V. kaznakowi* in the Caucasus, including the Adzharo-Imeretinsky Ridge where even until the Pliocene, bay trees, rubber plants, araucarias and palms were preserved (Vereschagin 1958). Different mammal fossils: Middle Asian and Caucasus hamsters, *Mesocricetus, Prometheomys, Sorex,* and *Talpa* (Vereschagin 1958) and also those of insects: Orthoptera, Hemiptera, Blattoidea, Coleoptera (Rodendorf 1939) testify to the presence of good foodstuff for the shield-headed vipers in the Miocene.

The end of the Tertiary period was marked by a decrease in tectonics and with the emergence of a broad link between the Caucasus and the Balkans via the Crimea (Vereschagin 1958). Steppes arose in northern areas adjacent to the Black Sea coast (Pidoplichko 1954; Scherbak 1966). During this period an arid adapted "*urisini* "–like viper associated with steppe areas penetrated into western Precaucasia from the east. It might have already separated from *Vipera ursini renardi* and have become widely distributed throughout the plains area along the northern slope in the Big Caucasus.

The middle-upper Pliocene, when the ridges of both the Big and Small Caucasus were subjected to considerable glaciation, should be considered the beginning of the initial break in the range of *Vipera kaznakowi* (Markov et al. 1965). The Kolchida (Colchis) had become a basic nucleus in *V. kaznakowi* dispersal. There, even in the epochs when it became severely cold in the Pleistocene, a relatively warm-loving vegetation of a Caucasus type was preserved (Vereschagin 1958). Along with Kolchida (Colchis) much smaller refugia were sporadically preserved along the Black Sea coast up to the town of Lazorevskoye. The same is true for the northern slope of the Main Caucasus Ridge between the Pshekha and Malaya rivers. This is supported by the present distribution of the Tertiary vegetation of the Kolchida (Colchis) type in the western Caucasus (Adamyants 1971; Kharadze 1974; Pechorin and Lozovoy 1980; Kholyavko et al. 1978; Tuniyev 1990, this volume).

It is in the narrow humid canyons with a relatively regular thermal regime that *Vipera kaznakowi* is preserved. Also, isolated populations might be preserved in midlands where the refugia with Kolchida (Colchis) vegetation are known in regions of the Fisht-Oshterovsky Massive, the Lago-Naki Plateau, and even in the Central Caucasus (Kharadze 1974; Kholyavko et al. 1978). Small refugia might also be preserved along the southern slope of the eastern Big Caucasus. Similar refugia for *Archaeolacerta* were recorded by Darevsky (1967). Most highland populations of *V. kaznakowi* undoubtedly went extinct during the glacial period. Those that were preserved in refugia have been accumulating unique characters. Data obtained by Takhtadzhan (1946) and Maruashvili (1956) reveal that in glacial epochs, mean annual temperature never dropped lower than 1.5-2.0°C, and the amount of precipitation was never less than 1500-2000 mm. These data support the proposed preservation of relictual *V.*

kaznakowi populations in the mountains.

Darevsky (1967) regards this argument as proof that due to the development of montane glaciers, a fundamental reconstruction of all animals and plants in these areas occured from premontane and montane refugia. Lizards for example, might have been preserved in the Gagrinsky and Bzybsky ridges facing the sea, along with other regions. The end of the Pleistocene was marked by the development of steppe landscapes on the Zakubauskaya sloping plain along with already formed landscapes and a characteristic biological community of the present type along the Black Sea coast of the Caucasus (Vereschagin 1958). This situation contributed to a much wider dispersal of *Vipera ursini renardi* and further preservation of *V. kaznakowi*.

During the xerothermal epoch in the Holocene, intensive glacial melting and the upwards elevational shift of vegetation belts along the mountain slopes occurred throughout the area. Within a considerable area of the Caucasus, steppe landscapes became prevalent. This allowed the steppe animals, including the steppe viper, *Vipera ursini renardi,* to ascend into the mountains (Vereschagin 1958). At that time an initial contact of *V. ursini renardi* with montane relict populations of *V. kaznakowi* might have occurred in the midmountains of the Western Caucasus. This region is presently inhabited by *V. dinniki* which shows mixed morphologies of both *V. kaznakowi* and *V. ursini renardi*. The approximate ways of possible interaction and characters are shown in Fig. 16.

Darevsky (1967) writes about the form-building role of hybridization in the Caucasus. He observes the genesis of new forms in the lizard group *Archaeolacerta*. Hybridogenity in *Vipera dinniki* is problematic, whereas introgressing hybridization in the zones of contact between *V. kaznakowi* and *V. dinniki* is presently not doubted, age interbreedings apparently occurring in midmontane populations of *V. dinniki*. For example, in one of these populations associated with the Mzymta River head, all the initial types of vipers can be found (Fig. 15). In premontane populations of *V. kaznakowi* we have not found specimens which have hybrid characters. Generally all premontane populations of *V. kaznakowi* show great homogeneity. In the eastern range of *V. dinniki* the species is presently disjunct geographically from the closely related *V. ursini renardi,* but rare individuals with an intermediate morphology between these species are present.

Mayr (1968), Borkin and Darevsky (1980) and Solbrig and Solbrig (1982) report on various types of hybridization. For instance, it is recorded that hybrids possessing vital capacity occur between sympatric species. Some of these hybrids are capable of recurrent crosses with one or both parental forms. The fate of both species between which hybridization occurs is partially dependent on 1) the intensity of hybridization occurring between them and 2) the level of genetic and ecological sterility of hybrids (Solbrig and Solbrig 1982).

In most cases the hybrids themselves do not have greater evolutionary significance. Rather it is the products of recurrent interbreeding between the hybrids and the parental forms, i.e. the process of introgressive hybridization, that may form new taxa; i.e. the blending of genomes of ancestral taxons, or "borrowing" of parts from other genomes by means of introgression of genes as a variant of hybridogenic species formation (Mayr 1968; Borkin and Darevsky 1980).

After the xerothermal epoch, the climate again became more humid. This fact contributed to the restoration of the former limits of the forest belt (Vereschagin 1958). Throughout the subalpine belt along the southern slope of the Main Caucasus Ridge within the area from the Central Caucasus up to the Fisht-Oshtenovsky Massive in the west, subalpine meadows and montane curved forests are widely developed (Galushko 1974; Dolukhanov 1974; Kharadze 1974; Kholyavko et al. 1978).

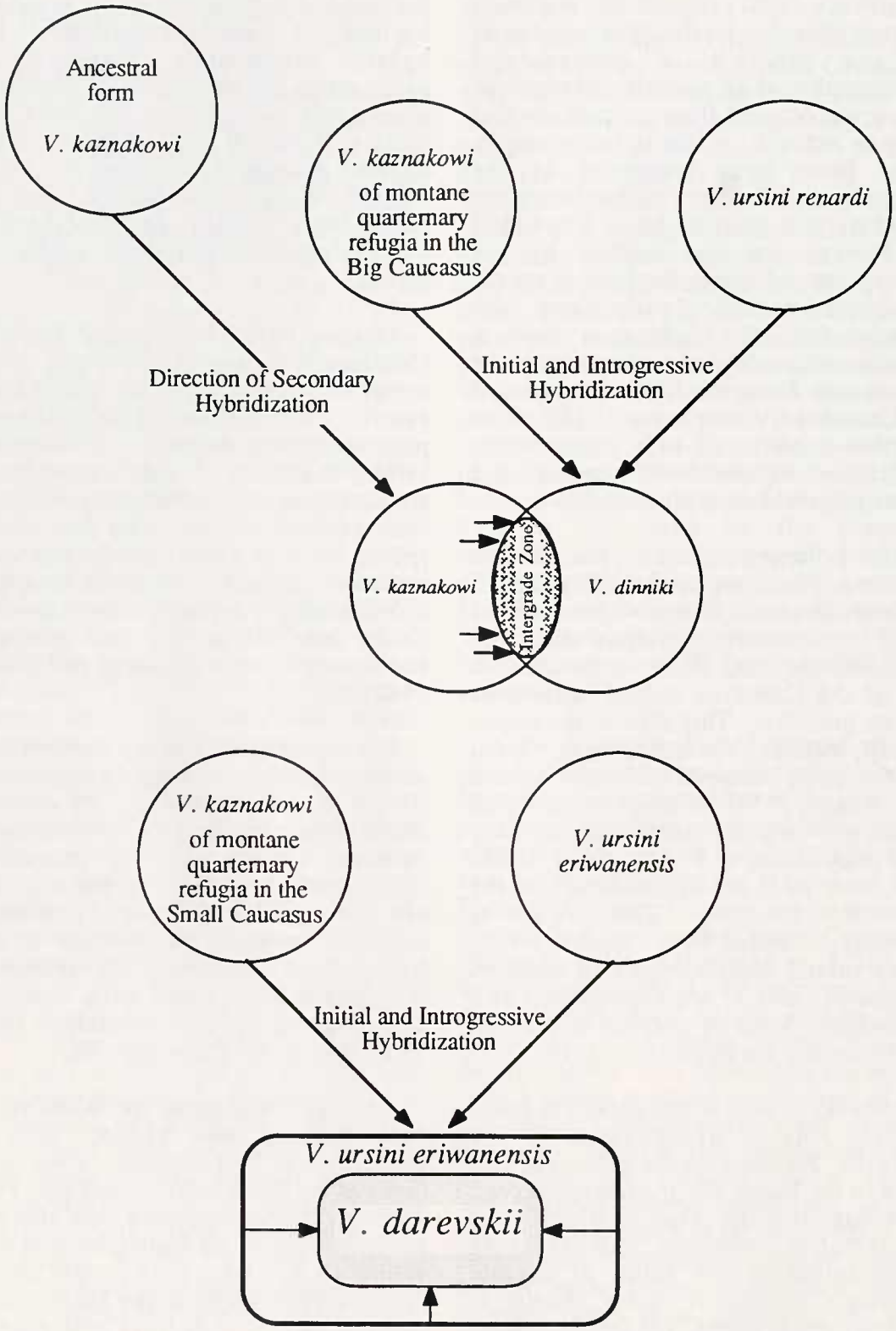


FIG. 16. Model of the proposed genesis of the vipers from the *Vipera kaznakowi* complex.

In the western part, this vegetation is present along the northern slope. To the east, it gradually changes to steppe (Lavrenko 1980). Definite limits of the subalpine belt in the area influenced by the warm Black Sea mark the present distributional limit of *Vipera dinniki*.

The final establishment of the present climate stabilized the range of *Vipera kaznakowi* and allowed the joining of scattered populations from the refugia within the given region. The favorable conditions along the Black Sea coast made it possible for *V. kaznakowi* to disperse along warm river valleys up to midmountains and for *V. dinniki* to disperse along the northern slope of the Big Caucasus to the east up to the Belshaya Laba River head. Where *V. kaznakowi* and *V. dinniki* distributions meet, and those of *V. dinniki* and *V. ursini renardi*, zones of secondary hybridization emerged. In these zones the following is observed: intergradation of characters, a high degree of polymorphism, and the "plucking" of specimens from the "initial" type. In these populations the specimens are hard to define.

Phenotypical diversity is great with regard to the Mzymta River valley (Fig. 15). Non-identified individuals having characters of both *Vipera ursini renardi* and *V. kaznakowi* are known from a number of localities in the complex eastern range of these vipers. We think that the history of *V. darevskii* is also connected with the invasion of *V. kaznakowi* from the south during the Miocene and its further wide dispersal throughout the Caucasus. *Vipera kaznakowi* apparently used to inhabit the majority of the Maly (Small) Caucasus area, including the Adzharo-Imeretinsky, Meskhetsky, and Dzhavakhetsky ridges. The fact that this range did exist in the past is demonstrated by a relict population of *V. kaznakowi* that occurs in Baniskhevsky Canyon, Georgia and by the proposed distribution of the vipers along the Trialetsky Ridge (Bakradze 1969). The latter might be a link between the areas presently inhabited by the closely related species, *V. kaznakowi* and *V. darevskii*.

In middle Pliocene, *Vipera kaznakowi* apparently invaded the Dzhavakhetsky Ridge (the Mokrye [Wet] Mountains). At that time the hot, arid climate of the region was replaced by a more humid, cool climate. Later on, however, beginning with the middle Pleistocene, processes of aridization and glaciation caused the final degradation of forests (Agakhanyants 1981). By that time the diverged vipers were restricted to the highest places in the mountains where maximum humidity could be found. At the same time the newly formed steppe areas were actively invaded by *V. ursini eriwanensis* (Reuss 1935) from the Anatolyskoye Plateau. Later on the viper became widely distributed throughout the entire montane-steppe belt in the Small Caucasus and the Armyanskoye Plateau. At that site one more source of hybridization, including further form-building, evidently existed. The genesis of *V. darevskii* can be explained by the hybridization of *V. ursini eriwanensis* and *V. kaznakowi* that split from its major range in the vicinity of the Mokrye Mountains (Plate 3).

Apparently, introgression of genes from *Vipera ursini eriwanensis* which essentially surrounded a small Pleistocene population of *V. kaznakowi* was very substantial. Morphological propinquity of *V. darevskii* to *V. ursini eriwanensis* and *V. kaznakowi* support its possible hybrid genesis (Borkin and Darevsky 1980). It goes without saying that further ecological, ethological, cytological and biochemical research of these vipers is needed to prove it. Similarly, Agakhanyants (1981) explains the floristic richness of the region by a complex interaction of invaders from the south and north in the highlands of the Small Caucasus. Further aridization of the climate caused the mesophilic form of *V. darevskii* to ascend into the mountains. Ecological disconnection in the present high-altitude belts caused complete separation of *V. darevskii* and *V. ursini eriwanensis*.

The presence of "*kaznakowi*" -like

vipers in Lagodekhi and other regions of the Big Caucasus may be accounted for solely by changes in climate in refugia that preserved populations and further divergence in isolated montane canyons. A number of isolated populations might by modified due to hybridization with *Vipera ursini renardi* in a manner similar to the above listed scheme.

During the period of xerophytization in the Holocene, breaks within the range of *Vipera kaznakowi* occurred. At that time isolated populations existed over a long period. A number of populations in hydrophilous epochs to follow, would have been capable of connecting many times. This is supported by the restoration of the former forest belt after Holocene xerophytization (Galushko 1974; Kharadze 1974). Pleistocene glaciation obviously also influenced the emergence of isolated populations and changes in the distributional limits (Markov et al. 1965).

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