

On the Independence of the Colchis Center of Amphibian and Reptile Speciation

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Abstract. -The Colchis region of Western Transcaucasia is characterized by a rather uniform thermal regimen, corresponding to a subtropical climate. The Colchis forests contain an extraordinary abundance and diversity of tree, shrub, and vine species. The herpetofauna of the Colchis forests is surprisingly poor, despite its uniqueness.

Key Words: Amphibia, Reptilia, USSR, Caucasus, biogeography.

Introduction

The herpetofauna of Western Transcaucasia is not homogeneous, due to the different age and genesis of the species distributions. Along with autochthonous and endemic forms, one can find species whose main areas of distribution are in the European part of the USSR and in the Eastern Mediterranean. At the same time, a number of species which have main distributional centers in the Colchis occur beyond the bounds of Western Transcaucasia, in other parts of the Caucasian Isthmus. For these reasons, it is necessary to define the Colchis herpetofauna and to determine its place in the fauna of reptiles and amphibians of the Caucasian Isthmus as a whole.

Research on this issue started with the works of Nordmann (1840), Derjugin (1899), Silantsev (1903), Brauner (1905), and Nesterov (1911). However, the first well-grounded definition of the fauna in question from a zoogeographical point of view was presented in the works of Satunin (1912). Satunin wrote in 1910, "So far I cannot say much about the genesis of the fauna of this region called Western Transcaucasia. This country with its evergreen plants and scanty fauna resembles a piece of the Mediterranean in the narrow sense of the word. True, here are endemic species and forms, but not a single genus of vertebrate is unrepresented in the countries of the Mediterranean.

Often they are inhabited by the same species. The question is whether this fauna has appeared from the west or is it the remainder of the fauna that has populated densely the shores of the Black Sea at one time. It is impossible to answer these questions at the present level of our knowledge. But even now I can definitely say that this fauna by its origin, has nothing in common with the faunas in other regions of the Caucasus."

In 1912, Satunin divided the Caucasian Isthmus into five subregions and 11 districts, including the Colchis in the West-Transcaucasian district of the Littoral subregion.

Among other merits of this work by Satunin, one cannot but mention the fact that for the first time, he defined in an exact way the Colchis region proper. He defined the northern border as the spurs of the Main Caucasian Range up to the basin of the Tuapse River, the southern border as the Pontic Range, and the eastern border as the Arsijanskij Range. The valley of the Rioni River and the adjacent southern slopes of the Main Range were defined as the central part of the region. Satunin emphasized the depauperate herpetofauna of this region on one hand, and the presence of endemic species such as *Vipera kaznakovi* and *Bufo verrucosissimus* on the other hand.

Nikolsky (1911) assigned the entire Caucasus, excluding eastern Precaucasia,

to the Mediterranean. However, he could not differentiate the forest and the alpine belts of the Greater Caucasus, because of the absence of data.

Results and Discussion

Investigations of the last decades made it possible to add the majority of the species of the Colchis herpetofauna to an overall picture of Colchis faunal distributions (Turov 1928; Bartenev and Reznikova 1935; Khozatsky 1941; Milyanovskiy 1957; Bannikov et al. 1977; Negmedzyanov and Bakradze 1977; Orlova 1973, 1978a, 1978b; Golubev 1980, 1985; Tuniyev 1983, 1985). In addition there has been a revision of the taxonomic status of such forms as *Vipera kaznakovi* (Vedmederja et al. 1986; Orlov and Tuniyev 1986a, 1990 this volume), *Lacerta agilis* (Peters 1960), *L. derjugini* (Bartenev and Reznikova 1931; Orlova 1978a; Bischoff 1982, 1984), *L. saxicola* (Darevsky 1967; Darevsky and Vedmederja 1977), *Anguis fragilis colchicus* (Lukina 1965; Scherbak and Scherban 1980), and others.

Accumulation of this information along with works on fossil amphibians and reptiles of the Caucasus (Vekua et al. 1979; Chkhikvadze 1981, 1983, 1984; Bakradze and Chkhikvadze 1977; Zerova and Chkhikvadze 1984; Yefimov and Chkhikvadze 1987) have made it possible to revise the zoogeography of the region.

Darevsky (1957) singled out seven different groups of species and subspecies of the herpetofauna in the Caucasus, based on their origin. Among the species representatives of the region of interest to us, it is necessary to pay attention to *Lacerta strigata* (Asia Minor species), *Emys orbicularis*, *Anguis fragilis*, *Coronella austriaca*, *Elaphe quatuorlineates sauromates*, *Natrix natrix* (European boreal species), *Testudo graeca*, *Natrix tessellata* (Mediterranean species), *Pseudopus apodus*, *Coluber najadum* (east-Mediterranean species), and *Lacerta saxicola*, *L. praticola*, *L. derjugini*, *L. media* (autochthonous species). The

Colchis, however, was not distinguished as an independent center of speciation in this work.

Scherbak (1981) included the Colchis in the Caucasian Region of the Mediterranean Province. He suggested that the typical species of the region were *Mertensiella caucasica*, *Pelodytes causicus*, *Lacerta saxicola*-complex and others. However, the Colchis proper was again not distinguished as an independent center of herpetofaunal formation.

For the analysis of the herpetofauna of the Colchis proper, it is necessary to exactly define the term "the Colchis phytolandscapes", and to decide what types of vegetation are universally recognized as "Colchis types". Albov (1885) was the first to clearly depict plant landscapes of the Colchis. He singled out a region, unique for Russia, of mountain limestone flora which had been developing mainly autochthonously in a large refugium with numerous endemic and relict species and even genera. Kolakovskiy (1980) regarded the Colchis flora as basically forest and alpine-meadow, and suggested that its main phytolandscapes had existed since old times with changes only in the composition of their edificators, except for the extinct formation of evergreen subtropical forests in the lower mountain belt. The tertiary-relict character of the forest mesophile flora and vegetation is fully revealed here due to slight changes in this region's climatic conditions (Kuznetsov 1891). The most characteristic features of the tertiary-relict Colchis forest are: extraordinary abundance and diversity of tree and shrub species, impossibility of singling out the dominant species (which is also characteristic of tropical forest with extreme density of trees), abundance of vines and epiphytes, and almost total absence of grass cover. All these attributes make the Colchis forest similar in many aspects to a tropical rain forest (Pavlov 1984). According to Sinskaya (1933), the Colchis forest vegetation underwent three main stages of development: the tropical forest; the forest of Colchis type, but rich and covering a wider area; and last, the modern Colchis

forest.

The Colchis type of vegetation includes a number of phytocenoses differing in structure, composition, and ecological peculiarities: it may be mixed (polydominant), or may be presented by cenosis of one or two species, but the common and obligatory attribute of phytocenosis of the Colchis type is an abundance of tertiary relicts. The area with Colchis type vegetation is characterized by a rather monotonous thermal regimen, corresponding to a subtropical climate, but with highly diverse soils (Gulisashvili et al. 1975).

The herpetofauna of the Colchis forests is surprisingly poor, despite its uniqueness. The species composition is different in the southeastern and northwestern parts of the Colchis compared to the other portions of its territory. Species such as *Mertensiella caucasica*, *Lacerta clarkorum*, *L. parvula*, and *L. mixta*, whose distributions are connected with forests growing on acid soils above volcanic rocks, are found on the western slopes of the Adzharo-Imeretinsky, Shavshetsky and Lazistansky (Pontic) mountain ranges. Similarly, floristic endemics of this part of the Colchis (*Rhododendron ungerii*, *Osmanthus decorus*, *Betula medwedewii*, *Epigaea gaultherioides*, and others), are Adzharo-Lazistan endemics, sometimes with slight radiations to the adjoining regions, but are not Colchis endemics in the broad sense of the word. The same applies to *Lacerta saxicola darevskii* and *L. saxicola brauneri* which are widespread in the northwestern part of the Colchis, but are absent in the central and southeastern Colchis. These animals, by analogy with floristic endemics (*Allium candolleianum*, *Campanula mirabilis*, *C. bzybica*, *C. calcarea*, *C. jadvigae*, *Genista abchasica*, *Gentiana paradoxa*, *Omphalodes kusnetzovii*, and others) are northern-Colchis endemics. For example, of the 450 endemic Colchis species of flora, 83 (25%) are endemics of the northern Colchis (Adzinba 1980). *Triturus vittatus ophryticus*, *T. vulgaris lantzi*, *Bufo verrucosissimus*, *Pelodytes caucasicus*, *Lacerta derjugini*, *L. agilis*

grusinica, *Natrix megalcephala*, and *Vipera kaznakowi* are Colchis endemics in the broad sense of the word.

In addition to the Colchis endemics, there are three more ecological-geographical groups of amphibians and reptiles in the region. They have similar ecological characteristics (habitat first of all), and overlapping geographic distributions.

1. The East-Mediterranean group consists of *Triturus cristatus karelini*, *Testudo graeca nikolskii* (Fig. 1), *Lacerta media*, *L. praticola pontica*, *L. strigata*, *Pseudopus apodus tracijs*, *Natrix tessellata*, and *Coluber najadum*. This group's distribution includes either the Balkans and the Caucasus or the Balkans, Crimea, and the Caucasus. According to ecological characteristics, these are xeromesophiles or hemixerophiles whose spreading is related to dry foothills of Western Transcaucasia up to 200-300 m above sea level with an annual sum of temperatures exceeding 5000°C. Thus, *Testudo graeca*, *Pseudopus apodus*, and *Coluber najadum* occur in the Colchis on a narrow seaside strip of land with enclaves of Mediterranean vegetation from Tuapse to Pitsunda-Sukhumi. A local population of *L. strigata* occurs in the Pitsunda region, and a local population of *L. media* occurs in the environs of Pitsunda and Salme. The majority of localities of *L. praticola* and *Natrix tessellata* in the Colchis are in the seaside hills up to 400 m above sea level. It is only along the valleys of large rivers like the Shakhe River, the Mzymta River, the Bzyb River, and others that *N. tessellata* penetrates into the Colchis up to 600 m above sea level. Thus the majority of these species are found either in places with vegetation of the Mediterranean type, or in places where the initial Colchis vegetation has been reduced to zero and the landscapes resemble the Mediterranean ones by their thermo-biotope conditions (substitute shibliaks and tomillares, Pitsunda pine groves, foothill post-forest glades, and landplots with *Erica tetralix*, *Juniperus oxicedrus*, *Pinus pityusa*, and *Arbutus andrachne*).



FIG. 1. *Testudo graeca nikolskii* is a Mediterranean species, and in the Colchis it is found only in the seaside strip of land with enclaves of Mediterranean vegetation.

2. The Caucasian group includes *Hyla arborea schelkownikowi* (Fig. 2), *Rana macrocnemis*, *Lacerta caucasica alpina*, *L. rudis*, and *Vipera dinniki*. Distributions of these species in the Caucasian Isthmus are broader than those of the Colchis group. At the same time, the majority of them are Colchis autochthons. These species are mesophiles and occur in mesophillous forest and mountain meadow formations. This group seems to be of Colchis origin, retaining close connections with the main center of the formation. Broader ecological tolerance in comparison with typical Colchis species makes it impossible to include them within the Colchis group.

3. The European group consists of *Bufo viridis*, *Rana ridibunda*, *Emys orbicularis*, *Anguis fragilis*, *Natrix natrix*, *Coronella austriaca*, and *Coluber jugularis caspius*.

The composition of this group is not homogeneous. It includes both species typical for the steppe areas (*Bufo viridis* and *Coluber jugularis*) and those that are widely distributed in Europe (all the rest). Only *Anguis fragilis* and *Coronella austriaca* are widely distributed in the Colchis. This makes it difficult to definitely consider them late migrants to the Caucasus. Other species either occur in several spots along the Colchis seashore (*B. viridis* and *Natrix natrix*) or populate a narrow strip of land along the sea together with the Mediterranean species (*C. jugularis*) or a somewhat wider strip (*Emys orbicularis* and *Rana ridibunda*). Despite the possibility of finding these species in the typical Colchis forest formations, the majority of them are still attributed to the Mediterranean type of vegetation.



FIG. 2. *Hyla arborea schelkownikowi* seems to be of a Colchis origin, but because of its broad ecological tolerance, it is found in a large part of the Caucasian Isthmus.

Let us consider the dispersal and distribution of the representatives of the Colchis group in detail. *Triturus vittatus* occurs in the territory from the seashore to the subalpine meadows in all the forest types. In the place called "the Colchis Gates" (lowering of the Main Caucasian Range between Mt. Fisht and Mt. Chugush) the species crosses over to the northern slope of the Western Caucasus, reaching the environs of Goriachij Klutch and Krasnodar in the northwest and the basin of the Laba River in the northeast. In the eastern part of the area, the species crosses the Adzharo-Imeretinskij mountain range and reaches the outskirts of Tbilissi-Oni. It occurs in the Lagodekhi region as an isolate. Outside the boundaries of the Colchis this species occurs either in the Colchis type forests or in their derivatives.

Triturus vulgaris lantzi (Fig. 3) occurs in the same places in the Colchis as *T. vittatus ophryticus* does. Very often both species are symbiotopic (Tuniyev and Beregovaya 1986). On the northern slope of the Western Caucasus, its home range is wider than that of the previous species, but it is only through the mesophillous forests and subalpine meadows that it penetrates into the Eastern Transcaucasia up to the Trialet Ridge. The isolated population in Talysh occurs in the Hirkan forests which are ecologically and genetically close to the Colchis forests.

Bufo verrucosissimus (Fig. 4) occurs in all parts of the Colchis from the sea shore up to the subalpine forests. On the northern slope of the Western Caucasus, it is found on the territory from the environs



FIG. 3. *Triturus vulgaris lantzi*. This subspecies is widespread throughout the Colchis.

of Krasnodar in the west to the Psebj settlement and the Shakhgirej Canyon in the east, where it is found in the derivatives of the Colchis forests from 400 m to 1000 m above sea level. In the Eastern Caucasus it is found in the Borzhomy Gorge, the Lagodekhi-Zakataly, and the Talysh region, where its distribution is limited to the mesophilous forests, which are abundant in the Colchis and Hirkan floral elements.

The distribution of *Pelodytes caucasicus* (Fig. 5) in the Colchis is more restricted. It does not occur in the coastal belt and oak-forests. It is found both in the mesophilous beech, chestnut, and fir-tree forests, and in mixed broad-leaved forests with an evergreen understory. On the northern slope of the Western Caucasus, its distribution coincides with that of *B. verrucosissimus*, but unlike the latter, it is not found in deforested places. Its

southeastern distributional limits also coincide with that of *Bufo verrucosissimus*. *Pelodytes caucasicus* does not occur east of the Trialet Ridge. There is an isolated population in the mesophilous forests in the Lagodekhi-Zakataly region.

Lacerta derjugini has a distribution in the Colchis similar to *P. caucasicus*. It reaches the sub-alpine belt. On the northern slope of the Western Caucasus, it is found in the Colchis forest derivatives from the Belaja River to the Small Laba River (the Shakhgirej Gorge). The species penetrates through the Eastern Transcaucasia up to the Trialet Ridge. Separate populations occur in north-eastern Georgia up to Lagodekhi-Zakataly.

Lacerta agilis grusinica (Fig. 6) is known to occur only on the territory of the Colchis and the adjoining sea coast up to



FIG. 4. *Bufo verrucosissimus*. This Colchis endemic occurs in the four Colchis refugia.

Novorossijsk. Its vertical distributional limit is 700 m above sea level, though local populations can be found in the sub-alpine belt (Mt. Aishkho and Mt. Uglovoj).

The distribution of *Natrix megalcephala* is similar to that of many Colchis species. It is found from the environs of Tuapse and Gorjachij Kljutch in the west, to the region between the Belaja Laba River and the Small Laba River in the north, eastwards through the whole territory of the Colchis up to the Borzhomy Gorge and separately in the Lagodekhi-Zakataly region (Orlov and Tuniyev 1986b). In the Colchis it reaches the sub-alpine belt. In the rest of the area it does not exceed 1000 m above sea level.

Elaphe longissima (Fig. 7) occurs in the region of Novorossijsk and throughout Western Transcaucasia, except for the mid-

mountains and highlands. There are isolated populations in the Borzhomy Gorge, the Lagodekhi-Zakataly region and the Belaja River basin on the northern slope of the Western Caucasus.

Vipera kaznakowi (Fig. 8) occurs throughout the territory of the Colchis up to 1000 m above sea level. On the northern slope of the Western Caucasus it occurs between the Belaja River and the Small Laba River. Separate populations are known in the Borzhomy Gorge and the Lagodekhi region.

The dispersal and distribution of *Lacerta saxicola darevskii* (Fig. 9), *L. s. brauneri*, *L. mixta*, *L. parvula* and *Mertensiella caucasica* have been analyzed above.

A comparison of the endemic Colchis species, whose distributions are associated



FIG. 5. *Pelodytes caucasicus* occurs in all four Colchis refugia.

with forest and meadow formations of the Colchis type, makes it possible to identify three more regions in the Caucasian Isthmus, besides the Western Caucasus (the Colchis proper), in which the Colchis herpetofauna occurs. The three regions are: the Bjelo-Labinskij region on the northern slope of the Western Caucasus, the Kakhetinskij (Lagodekhi-Zakataly) region on the southern slope of the Eastern Caucasus, and the Borzhomskij region in Eastern Transcaucasia (Fig. 10). The comparative composition of the herpetofauna of these regions is shown in Table 1.

It is evident from Table 1, that the most significant differences are found between the Colchis and the Kakhetinskij regions and the least significant differences are between the Colchis and the Borzhomskij and the Belo-Labinskij regions. Taking into

account the above mentioned peculiarities of distribution of herpetofauna within the Colchis refugium itself, the differences become even less significant. In this case, we deal with three regions smaller in space, and a wealth of species of the Colchis herpetofauna that occur in refugia and have survived off the main territory of the Colchis.

The Belo-Labinskij region is only conventionally separated from the Colchis by the crest of the Main Caucasian Mountain Range. All the northern Colchis species, except *L. a. grusinica*, occur on the northern slope of the Western Caucasus in the Belaja and the Small Laba river drainages. It should be stressed that this unity is based on the fact that the characteristic Colchis elements of flora and vegetation cross over the Main Caucasian Range in the place known as "the Colchis Gates" to its northern slope. The basins of



FIG. 6. *Lacerta agilis grusinica* is found throughout the main Colchis refugium.

TABLE 1. Distribution of the endemic Colchis herpetofauna in the main refugia of the Caucasian Isthmus.

Species	R	E G	I O N	
	Colchis	Bjelo-Labinskij	Kakhetinskij	Borzhomskij
<i>Triturus vittatus</i>	+	+	+	+
<i>T. vulgaris lantzi</i>	+	+	-	+
<i>Mertensiella caucasica</i>	+	-	-	+
<i>Bufo verrucosissimus</i>	+	+	+	+
<i>Pelodytes caucasicus</i>	+	+	+	+
<i>Lacerta derjugini</i>	+	+	+	+
<i>L. agilis grusinica</i>	+	-	-	-
<i>L. saxicola darevskii</i>	+	+	-	-
<i>L. s. brauneri</i>	+	+	-	-
<i>L. mixta</i>	+	-	-	+
<i>L. parvula</i>	+	-	-	+
<i>L. clarkorum</i>	+	-	-	-
<i>Natrix megalcephala</i>	+	+	+	+
<i>Elaphe longissima</i>	+	+	+	+
<i>Vipera kaznakowi</i>	+	+	+	+
Total:	15	10	7	11



FIG. 7. *Elaphe longissima*. The Colchis refugia populations are disjunct from the main distribution in Europe.

the Belaja, Tsitse and Laba rivers abound in those elements. To the north of these watersheds their distributions are continuous up to the Skalistij (Rocky) limestone ridge. Malejev (1939) has noted that a part of the Maikop district abounds in Colchis elements and is inseparable from the Colchis according to the character of its flora and vegetation.

The Borzhomskij region is also conventionally separated from the Colchis by the Adzhara-Imeretinskij Mountain Ridge. The flora and vegetation of the Baniskhevskoje Gorge, the Likanskoje Gorge, and the upper belt of Mt. Lomis-Mta, as well as the environs of Bakuriani, hardly differ from those of the Colchis.



FIG. 8. *Vipera kaznakowi* occurs throughout the territory of the Colchis up to 1000 m above sea level.

In the isolated eastern Kakhetskij region a considerable number of the ancient Tertiary vegetation representatives survived due to the warm and humid climate (Gulisashvili et al. 1975).

Modern distributions of eco-geographic groups of amphibians and reptiles distinguished by our scientists have distinct altitudinal-ecological limits owing to natural and historical reasons.

Migration of ancestral species of the Colchis and the Caucasian groups from the south apparently took place in the Miocene when the Caucasian island joined vast territories of Asia Minor. Colonization of the Caucasus from the south by different species of mammals during the early Miocene has been studied by Vereschagin (1958), and that of lizards of the *Podarchis-Archaeolacerta* group by Darevsky (1967).

The early Miocene was about the time of the formation of the Caucasian Mountains (Bogachev 1938).

The warm subtropical climate and vegetation in the Caucasus favored the evolution and dispersal of heat and mesophilic forms (*Triturus vittatus ophryticus*, *T. vulgaris lantzi*, *Pelodytes caucasicus*, *Bufo verrucosissimus*, *Lacerta saxicola darevskii*, *L. s. brauneri*, *L. derjugini*, *Elaphe longissima*, *Natrix megalcephala*, and *Vipera kaznakowi*), as well as species with a broader ecological tolerance (*Rana macrocnemis*, *Hyla arborea schelkownikowi*, *Lacerta rudis*, and *L. agilis grusinica*).

Fossil remains of mammals (*Mesocricetus*, *Prometheomys*, *Sorex*, *Talpa*) [Vereschagin 1958] and insects (Orthoptera, Hemiptera, Blattoidea, and

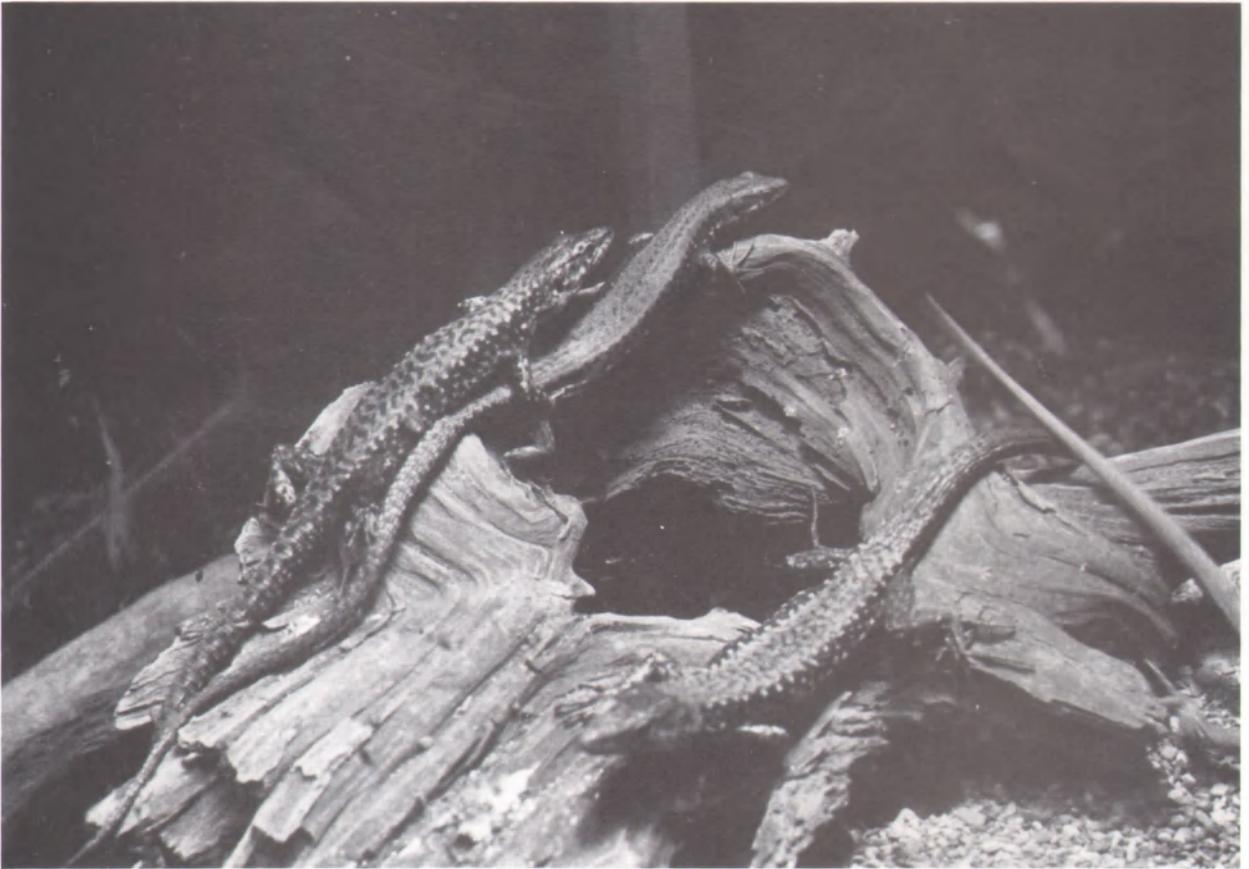


FIG. 9. *Lacerta saxicola darevskii*. This lizard is a Colchis endemic whose distribution is restricted to the northwestern part of the Colchis.

Coleoptera) [Rodendorf 1939] suggest a good food supply for amphibians and reptiles during the Miocene. It was also in the Miocene that the majority of these species reached the eastern-most parts of the Greater Caucasian Range along its southern slopes and penetrated from there into the Talysh across the so-called "Karabakhi Bridge". Safarov (1966), and other scientists, have studied the former direct relations between the Colchis and the Hirkan floras. Even at the present time, the floristic composition of the Kakhetsinskij region and of the Karabakh has many common features with that of the Colchis and the Talysh forests (Arushanyan 1973; Sokolov 1977; Takhtadzhan 1978; Gadzhiyev et al. 1985).

The end of the Tertiary period was characterized by damping of tectonics due

to the broad correlation of the Caucasus and the Balkans (Vereschagin 1958) and the formation of the steppe landscapes along the northern Black Sea coast (Pidoplichko 1954; Scherbak 1966). During that period, such South-European species as *Rana ridibunda*, *Bufo viridis*, *Emys orbicularis*, *Anguis fragilis*, *Coluber jugularis*, and *Coronella austriaca* seem to have penetrated to the Precaucasia from the west. At the same time, such species as *Testudo graeca*, *Pseudopus apodus*, *Triturus cristatus karelini*, *Lacerta praticola pontica*, *L. media*, *Coluber najadum*, and *Natrix tessellata* got into the Colchis from the west along the Black Sea coast.

Early and Middle Pliocene should be considered the beginning of initial fragmentation of the Colchis faunal areas when the Greater and the Lesser Caucasian

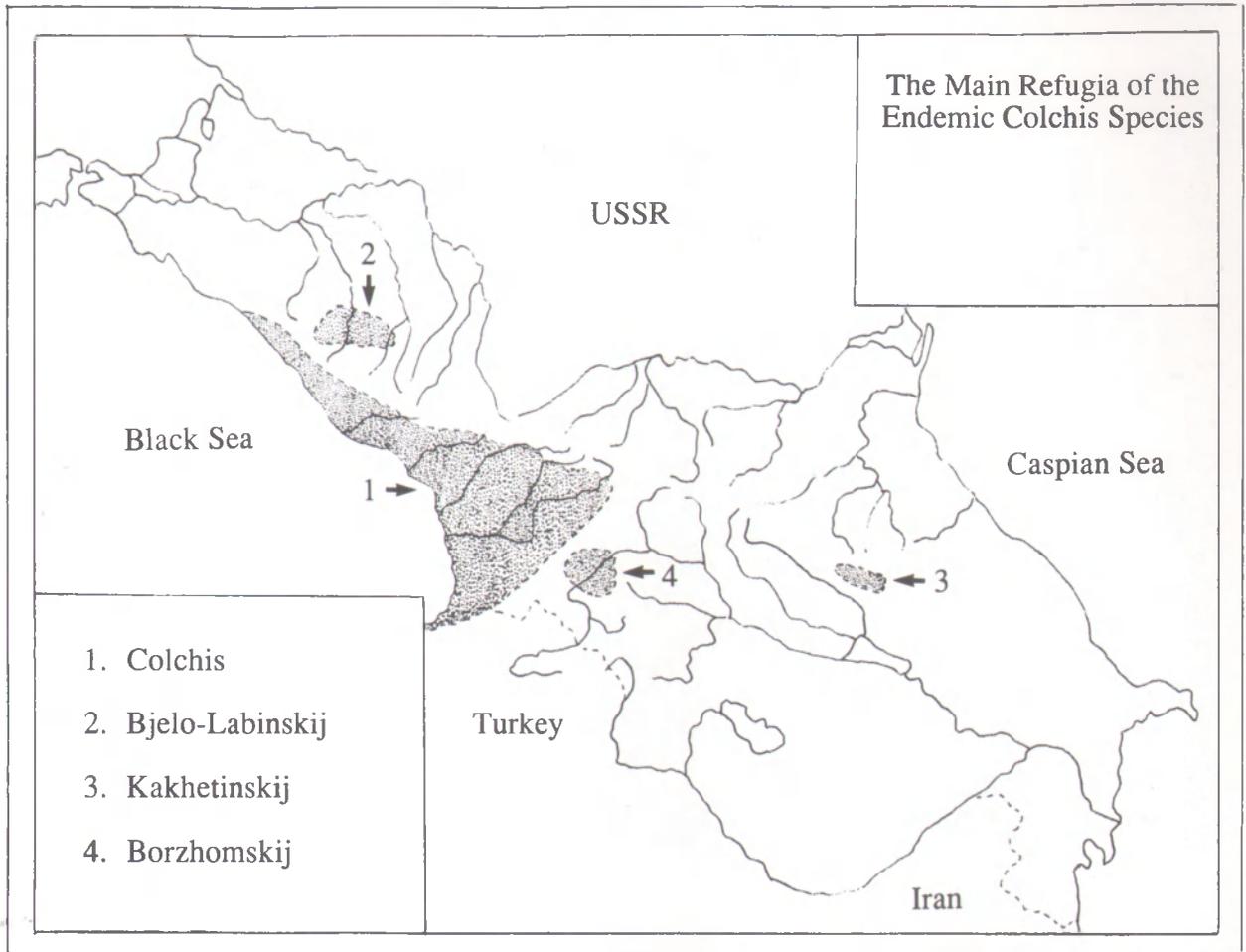


FIG. 10. The main refugia of the endemic Colchis herpetofauna.

Mountain ranges underwent substantial glaciation (Grozdetzkiy 1954; Markov et al. 1965). The main center of dispersal of these species was the Colchis, where relatively heat-loving vegetation of the Caucasian type survived even during the periods of the extreme Pleistocene cooling (Vereschagin 1958; Adamyants 1971). Along with the Colchis, smaller refugia sporadically survived on the territory of the Caucasus Black Sea coast, and also on the northern slope of the Main Caucasian Range between the Pshekha River and the Small Laba River. The present distribution of the Tertiary vegetation of the Colchis type in the western Caucasus testifies to this (Kharadze 1974; Pechorin and Lozovoy 1980; Kholyavko et al. 1978; Adamyants 1971; Koval and Litvinskaya

1986).

It was in the narrow humid gorges with a relatively constant thermal regimen that the representatives of the Colchis group remained intact. At the same time, independent populations might also have been preserved in mid-mountain areas where refugia of the Colchis vegetation exist in the vicinities of the Fisht-Oshtenskij Mountain Massive, the Lagonaki Plateau and even in the Central Caucasus (Kholyavko et al. 1978; Kharadze 1974). Small refugia seem to have also remained on the southern slope of the eastern part of the Greater Caucasus and in the Kuru River Gorge. It is indisputable that the majority of the mountainous populations of Colchis species perished during the Pleistocene and

that the ones that survived in refugia have been accumulating unique characteristics which led to different geographical forms (subspecies) on different slopes of the Main and the Adzharo-Imeretinskij mountain ranges. The data presented by Takhtadzhan (1946) and Maruashvili (1956) support the hypothesis concerning the preservation of relict Colchis species in the mountains. According to their data, the average annual temperature during the glacial periods decreased not more than 1.5-2.0°C, while precipitation amounted to not less than 1500-2000 mm.

Darevsky (1967) considers that this argument supports the possibility of foothill refugia of reptiles existing on the sea facing slopes of the Gagrinskij and the Bzhybskij mountain ranges, and in other regions, despite radical reorganization of the distributions of all the species of plants and animals in connection with glaciation.

During the interglacial and especially the postglacial periods, reconstruction of all vegetation belts took place (Vereschagin 1958). This favored the isolation of the species of the Colchis and the Caucasian groups in the above-mentioned refugia, but favored wider dispersal of the European and the Mediterranean groups in Transcaucasia. In the northwestern part of the Caucasus Black Sea coast, mesophilic vegetation gave way to xerophytic vegetation of the Mediterranean type. Plant formations of this type with the prevalence of *Juniperetum*, *Querceto*, *Pinetum carpinulosum*, *Pinetum fruticosum* and shibliaks are characteristic of the Anpa-Gelendzhik region. Enclaves of Mediterranean vegetation remained still further to the south, up to Pitsunda (Takhtadzhan 1978; Kolakovskiy 1961).

When the xerothermic period ended, the climate became more humid again. This favored the reestablishment of the former borders of the forest belt (Vereschagin 1958). Subalpine meadows and elfin woodlands were expanding throughout the whole subalpine belt of the southern slope of the Main Caucasian Mountain Range from the Central Caucasus to the Fisht-

Oshtenskij Mountain Massive (Kholyavko et al. 1978; Kharadze 1974; Dolukhanov 1974; Galushko 1974). On the northern slope such vegetation is present in the western parts and changes its character to the east, transforming into a steppe type (Lavrenko 1980). Modern areas of *Vipera dinniki* and *Lacerta caucasica alpina* have fixed distributional limits in the subalpine belt influenced by the warm Black Sea. Final settling of the present-day climate favored fixation of the Colchis species distributions, with their distinct populations exceeding the bounds of the refugia. This was coupled by simultaneous depression and reduction of the European and especially of the Mediterranean species distributions.

Concluding this review of the Colchis herpetofauna and their main refugia, it is necessary to enumerate the most important characteristics. The Colchis species are characterized by antiquity (conservation since the Tertiary period), Autochthony, depression—for some species (*Vipera kaznakovi*; *Lacerta clarcorum*, *L. a. grusinica*), existence of the northern-Colchis limestone, and the southern-Colchis volcanic centers of formation of narrow-endemic forms. Reptiles have a common tendency toward melanism, while amphibians approach their low temperature thresholds. These are the adaptive features acquired during the glacial period. As a rule, the modern distribution of the Colchis species does not exceed the bounds of the Colchis vegetation refugia or their derivatives.

The maximal vertical distribution is in the center of the Colchis up to 1800 m above sea level, while in the other portions of the refugia it does not exceed 1000 m above sea level as a rule. The existence of four refugia of the Colchis herpetofauna in the Caucasian Isthmus is determined by natural factors of high order—these are the areas with slightly changed climatic conditions characterized by modern crossing of the January -3°C isotherm and 800 mm isohyet.

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