

## ON THE MEDITERRANEAN INFLUENCE ON THE FORMATION OF HERPETOFAUNA OF THE CAUCASIAN ISTHMUS AND ITS MAIN XEROPHYLOUS REFUGIA

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The Caucasian Isthmus has common origin within the areas of Ancient Mediterranean and it inherited the united type of mountain belts with Mediterranean mountain systems. On the basing of paleo-areas and recent chorology of Caucasian amphibians and reptiles the analysis was given, including the historical changing of the main characteristic of Mediterranean species-complex, its composition and connection with corresponding phyto-landscapes. The recent refugia of Mediterranean species in the Caucasus are described and made conjecture about stages of colonization the Caucasian Isthmus by these species. The possible ways of preservation of these refugia till now are discussed.

**Key words:** Biogeography, Caucasus, Mediterranean, Herpetofauna, Refugia.

Position of Caucasus in the scheme of biogeographic division of Palaearctic is arguable. Its independence in the formation of peculiar flora and fauna, or belonging to the adjacent areas of Europe and Central Asia are differently interpreted in literature. It is to the significant degree typical and for the separate parts of Caucasian Isthmus. Not aiming to analyze the whole herpetofauna of the Isthmus and partitioning of its territory, we shall stop on the certain fauna of Mediterranean area and make an attempt to estimate the influence of this fauna on the formation of the herpetological complexes of Caucasus.

Zoogeographical works, concerning Caucasus, appeared in the second half of XIX century. Wallace (1876), as well as later on Haake (1886), divided Caucasian Isthmus along the crest of Great Caucasus, referring Precaucasia to the European subregion and Transcaucasia – to the Mediterranean. Severtsov (1877) referred to the Mediterranean area the all Great Caucasus, West Precaucasia and West Transcaucasia, and the rest Transcaucasia – to the West Asian region and North-East Precaucasia – to the Middle Asian region. As a matter of fact in this, very close to the recent, scheme of division, Severtsov have recognized the different of the Caucasus fauna. The most complete description of heterogeneous ori-

gin of the Caucasian fauna was made by Satunin (1910, 1912), what we have pointed already in the previous work (Tuniyev, 1990). Menzbir (1934) included Caucasus and Transcaucasia into the Caucasian subprovince of East Mediterranean province in Mediterranean subregion of Palaearctic. In the opinion of Menzbir, Caucasus was under the influence of two faunogenetic centers – Mediterranean and Central Asian. Puzanov (1938) referred to the Mediterranean subregion all Transcaucasia which together with the Greece archipelago, Asia Minor, Mountain Crimea, enter the East Mediterranean province. The northern slopes of El'brus and Talysh were distinguished by him into the Hyrkan Province.

The numerous following works of 1940 – 1960th were based the main on the theriological and ornithological partitioning where Caucasus was placed either to Mediterranean (Kuznetsov, 1949), either to the province of deciduous forests of Europe (Rustamov, 1945; Kuznetsov, 1949; Bobrinsky, 1951).

The work of great expert and investigator of Caucasian fauna Vereshchagin *Mammals of Caucasus* (1959) deserves particular attention. Criticizing the works of authors, who diminish the significance of Mediterranean area (to which Vereshchagin referred Caucasus too), he wrote: "Mediterranean always gave more possibilities for immigration of animals and plants than Sahara or Kara Kum, but its significance as the independent ancient form genesis center

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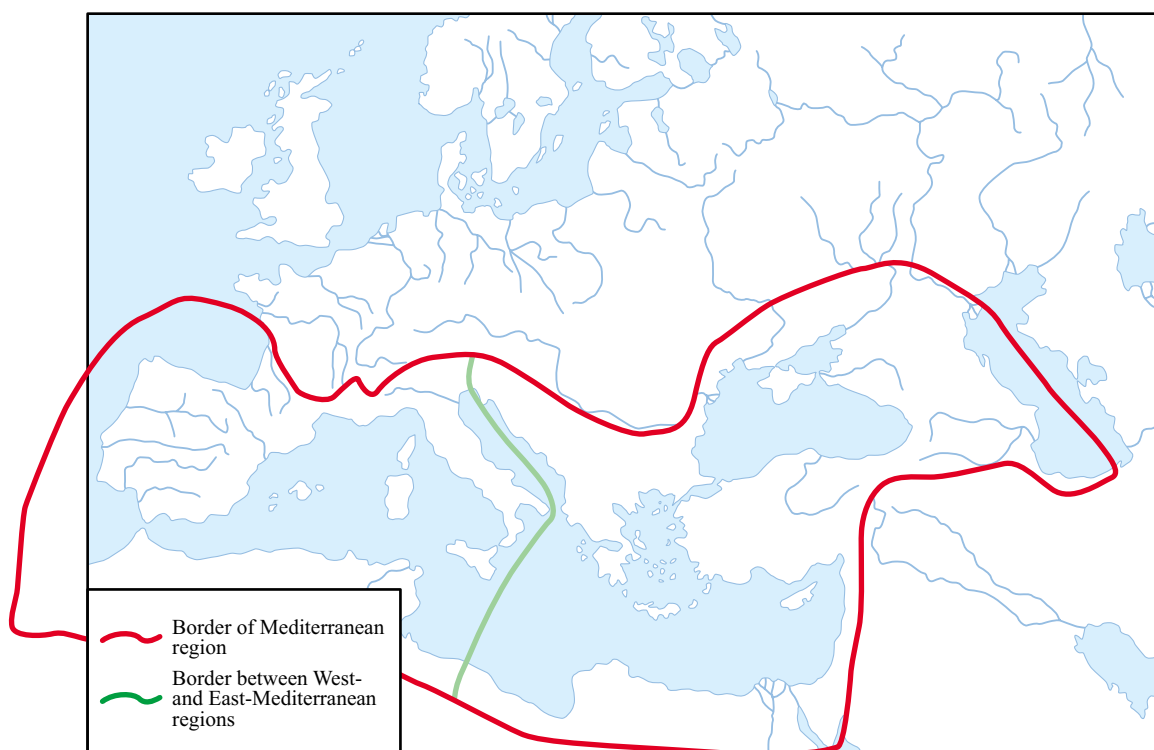


Fig. 1. Botanical borders of Mediterranean region (after Rikli, 1946).

was not decreasing due to this. The correct interpretation of the concept of “Mediterranean,” and, therefore, and Mediterranean type of fauna could be achieved only with the complex analysis of natural transformation which took place in the Cenozoic in the limits of Mediterranean geosynclinal. As it is known, the Sarmatian sea, which stretched from Gibraltar up to Transcaspien, later on in the Pliocene and Pleistocene not once disintegrated on the chain of isolated basins, being connected sometimes in the epochs of transgressions. The Aral coast and the northern part of Caspian Sea due to the conditions of relief and high continental climate were early deserted and come out of the united system of zones of Mediterranean type. Nevertheless, the rest plots of this chain of Cenozoic basins, among this and Caucasus, inherited a number of single primitive features of landscapes, flora and fauna, the roots of which are going into Miocene. Just because of this as the Mediterranean, taking in account its paleogeographical essence should be meant the southern vicinities of Europe (including the south of Ukraine and Crimea), Northern Africa, Asia Minor, Caucasian Isthmus (excluding Premanych), Talysh, and El’brus ridge” (p. 462). Ve-

reshchagin’s interpretation of Mediterranean coincides as a whole with the boundaries of floristic Mediterranean of Rikli (1946) (Fig. 1), though in botanists the position of Caucasus also was a subject of a long discussions. Thus, Boissie (1867) in his book *Flora Orientalis* referred the forest Caucasus, occupied by deciduous and, partly by the dark coniferous forests north Anatholiya and some regions of European Turkey to the region of Middle Europe. To the “Mediterranean region” he, besides the countries, adjoining the Mediterranean seacoast, referred and southern Crimea. Not only mountain Crimea, but the whole Caucasus was included in the Mediterranean subregion (province) on the territory of the former USSR by Alekhin (1938) and Vul’f (1944). Grossgeim (1948) and Maleev (1946) pointed on the affinity of the Caucasian formations of macquis, garigue, phrygana broad-leaf forests with the same formations of Mediterranean. Isachenko and Lavrenko (1980) did not agree with them, referring Caucasus to the two botanical-geographical areas: European broad-leaf and Afro-Asian desert. Lavrenko (1958) considered also earlier that phytogeographically sense the forest area of Caucasus in the origin and ecology is

related to the broad-leave forests of Europe, but not to the Mediterranean. Takhtadzhyan (1978) having analyzed significant amount of published data, referred to the Mediterranean area the foothill part of West Caucasus between the Anapa, Krasnodar, and Tuapse, the rest parts of Caucasus he referred to the Euxine and Caucasian province of the Boreal subrealm and Armenian – Iranian, Hyrkanian, and Turanian provinces of Iran – Turanian region.

Stanyukovich (1973) refers the North Caucasus and Transcaucasia to the type of belting of the mountains of the subtropical zone. Vereshchagin considered (1959) that the similarity and close affinity of theriological complexes of the West Mediterranean with Caucasus (up to Talysh – El'brus on the east) is connected with the common time of origin and formation of high mountain landscape. As reasonably wrote Il'insky (1937) the landscape of Mediterranean type biogeographers not rarely mean the contemporary landscape of Spain, Sicily, and Palestine. As a matter of fact, as in the west so in the east parts of Mediterranean alongside with xerophylic landscapes of garigue, phrygana and mountain steppes, there are relict landscapes of Tertiary coniferous and deciduous forests, mesophytic meadows of alpine and sub-alpine types.

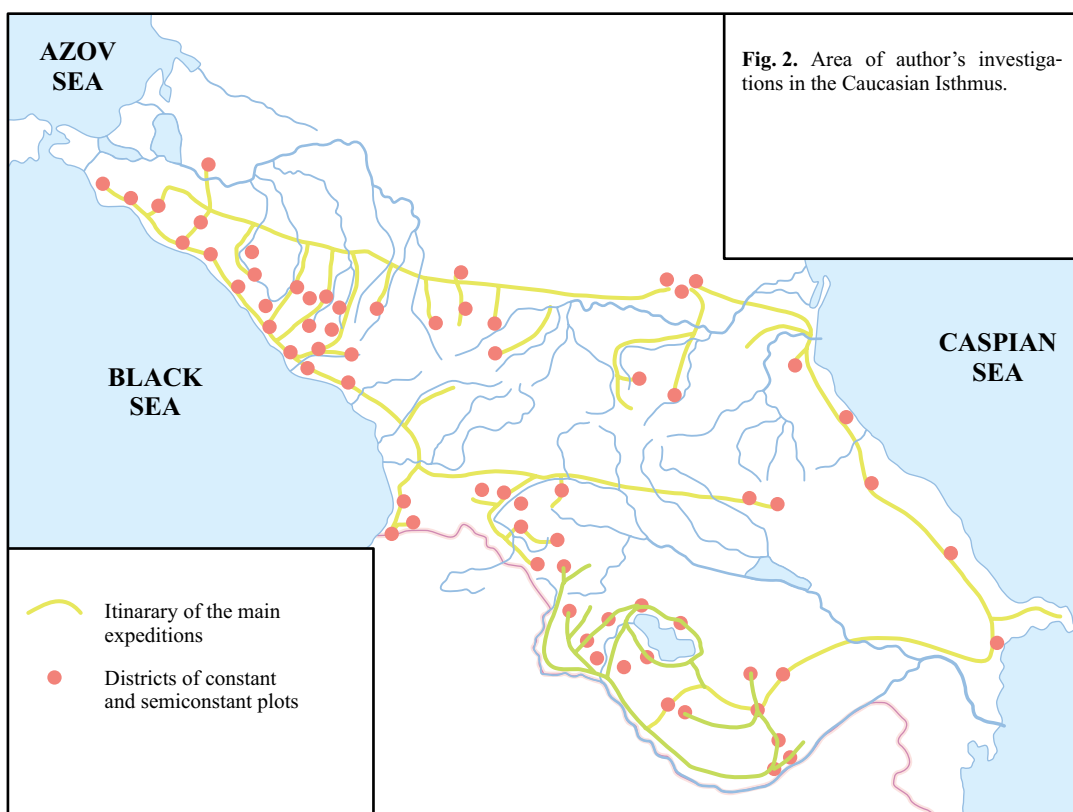
Szczerbak (1984) indicated both xerophylous and mesophylous species of amphibian and reptiles for the different centers of speciation in the limits of Mediterranean, what in our viewpoint is the reflection of many belts in the structure of Mediterranean fauna. For the Caucasian center 12 endemic species with 22 forms of *Lacerta saxicola*-complex, also *Mertensiella caucasica*, *Pelodytes causicus*, and *Vipera kaznakovi* are indicated. No doubt, Caucasus, having several centers of speciation, refers as a whole to the Mediterranean: beside the mentioned above 22 forms of *Lacerta saxicola*-complex, 5 forms of *L. derjugini*, 5 forms of *L. agilis* and many other Lacertidae: *Triturus vulgaris lantzi* (?), *Bufo verrucosissimus*, *Rana macrocnemis pseudodalmatina*, *Lacerta chlorogaster*, and *Elaphe persica*. Along with these mesophylic centers on Caucasus there are autochthonous xerophylic centers of speciation, connected mainly with the mountain-steppe landscapes of Lesser and Great Caucasus. Above the listed autochthonous for the Caucasus groups of species (Colchis, Hyrkanian, Lesser Caucasian, and East-Caucasian) representatives of European, Turanian, Asia Minor, and properly Mediterranean groups are meeting here. We shall concern the xerophylic part of the Mediter-

anean group, common for all or the greatest part of the East Mediterranean. The latter group in dependence on the character of species distribution not rarely is divided on the Mediterranean and East Mediterranean (Darevsky, 1957a). The understanding of the volume of Mediterranean group varies in different authors (Sobolevsky, 1929; Bodenheimer, 1944; Darevsky, 1957a; Anderson, 1968; Alekperov, 1978; Kireev, 1987; et al.). Alongside with it, the great majority of authors include in the number of Mediterranean faunistic elements the next species, distributed on the Caucasus: *Triturus cristatus karelinii*, *Rana ridibunda*, *Mauremys caspica*, *Testudo graeca*, *Ophisops elegans*, *Pseudopus apodus*, *Typhlops vermicularis*, *Eryx jaculus*, *Natrix natrix persa*, *N. tessellata*, *Coluber najadum*, *Telescopus fallax iberus*, and *Malpolon monspessulanus*.

Earlier, considering the herpetofauna of the West Transcaucasia (Tuniyev, 1990) we included in the East-Mediterranean group *Triturus cristatus karelinii*, *Testudo graeca*, *Lacerta media*, *L. strigata*, *L. praticola pontica*, *Pseudopus apodus*, *Natrix tessellata*, and *Coluber najadum*. Moreover, in our viewpoint *Pelobates syriacus*, *Mauremys caspica*, *Ophisops elegans*, *Ablepharus chernovi*, *Cyrtopodion kotschy colchicus*, *Typhlops vermicularis*, *Eryx jaculus*, *Natrix natrix persa*, *Elaphe hohenackeri*, *E. quatuorlineata*, *Coluber caspius*, *Eirenis modestus*, *Telescopus fallax*, *Malpolon monspessulanus*, *Vipera lebetina*, and *V. ammodytes* should be referred to the number of Mediterranean species.

Despite the rather wide Pontic-Caspian distribution of *Coluber caspius* and *Elaphe quatuorlineata* from one hand, and inclination of the range centers to the Middle East in *E. hohenackeri* and *V. lebetina* we consider the inclusion of these species into the Mediterranean group to be not less grounded than *Pseudopus apodus*, *Natrix tessellata* or *Lacerta strigata*. The base for this (as well as for all other species) served the character of recent distribution on the Caucasus and biotope dissemination in the first turn with an account of phytolandscapes. To the Mediterranean group on the Caucasus could be referred *Elaphe situata*, as it seems, up to recent time was met in the relict populations near Tbilisi, Kislovodsk, and Groznyy (Lyaister, 1909; Bannikov et al., 1977).

While regarding the general chorology of Mediterranean species of amphibians and reptiles, the investigators marked their distribution along the territory, adjusting to the coast of Mediterranean sea, Balkan peninsula, South Crimea, and separate, mainly

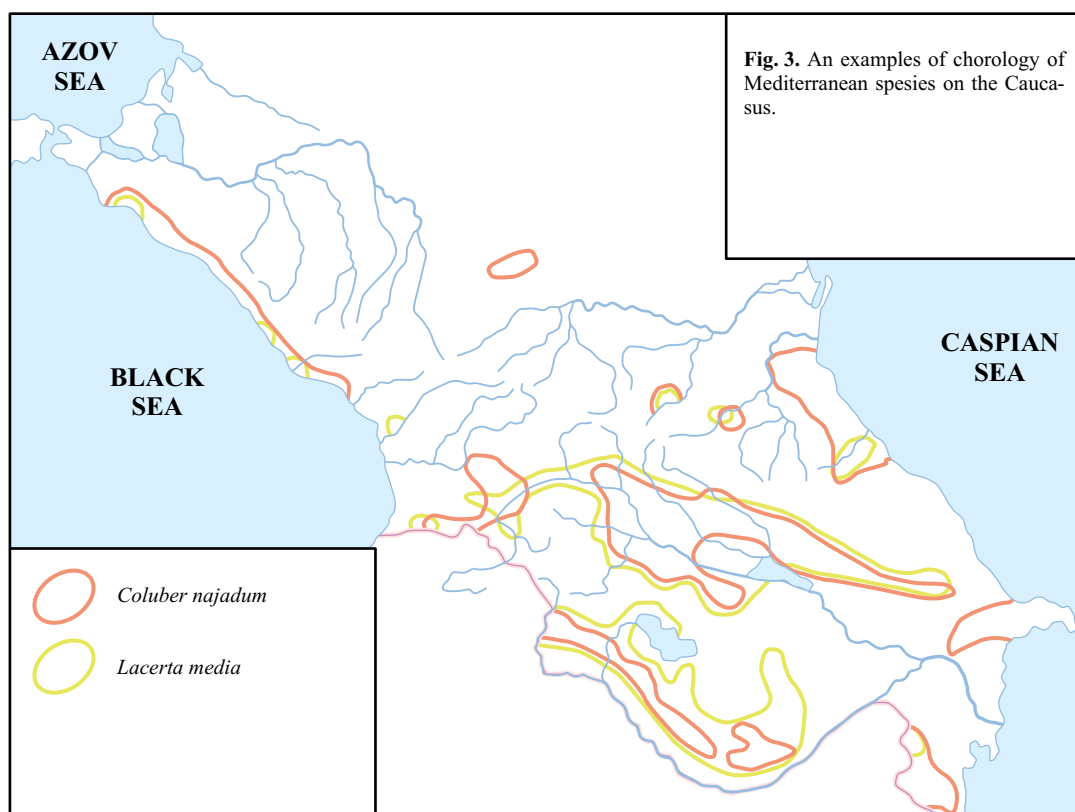


xerophytic regions of Caucasus. Let us regard more attentively the distribution of the species listed above on the Caucasian Isthmus.

## MATERIAL

Materials on the chorology and biotope distribution of Mediterranean species of amphibians and reptiles were gathered in the expeditions and during the stationary works in the different regions of Caucasian Isthmus from 1977 up to 1992 (Fig. 2). Additional material was taken from the numerous literature sources, where the distribution of the species interesting for us are regarded. Materials on the chorology of distinguished by us group of amphibians and reptiles are indicated for the Caucasus as a whole in the works of Nikolsky (1913), Morits (1916), Terentjev and Chernov (1949), Bishoff and Engelmann (1976), Bannikov et al. (1977), Orlova (1978), Tuniyev (1985a), and Rudik (1989). In addition, the vast regional material on Armenia (Chernov, 1939; Dal', 1954; Darevsky, 1957; Melkumyan, 1973; Egiazyryan, 1981; Agasyan, 1986); Georgia (Muskhelishvi-

li, 1970; Pitskhelauri and Bakradze, 1973; Bakradze, 1977; Pitskhelauri, 1990); Azerbaijan (Schmidt, 1909; Dombrovsky, 1913; Sobolevsky, 1929; Alekperov, 1954; 1973; 1978; Aliev, 1973, 1977, 1985, 1989; Alekperov et al., 1978; Chegodaev, 1973; Ananjeva and Nikitin, 1977; Aliguseinov, 1981; Dzhafarova, 1981; Kuzmin, 1981; Gadzhiev et al., 1985; Akhmedov, 1989a, 1989b; Daghestan (Shibanov, 1935; Krasovsky, 1929, 1932; Khonyakina, 1964; Alkhasov, 1981; Leont'eva, 1986); Chechen-Ingush republic (Lyaister, 1909; Chernov, 1929; Karnaukhov, 1977, 1985, 1987; Tochiev, 1987; and Lotiev, 1987); North Ossetia (Naniev, 1978; Kuryatnikov and Udovkin, 1987); Kabardino-Balkar Republic (Neemchenko and Tembotov, 1959; Shebzukhova, 1967, 1973); Karachai-Cherkess Autonomous and Stavropol' region of Russia (Fedorov, 1956; Tertyshnikov and Vysotin, 1987; Tertyshnikov, 1992); Adygei Autonomous and Krasnodar region of Russia (Rossikov, 1890; Brauner, 1905; Orlova, 1973; Tuniyev, 1983, 1985b, 1987a; Galichenko and Pereshkolnik, 1985; Shebzukhova, 1989); Abkhazia (Rostombekov, 1939; Milyanovskii, 1957; Rudik, 1986; Tu-



niyev, 1987b); Adzharistan (Deryugin, 1899; Nesterov, 1911; Vedmederya, 1977) were analyzed.

Materials from the territories adjusting to Caucasus were taken in account: from the north – Kalmytskaya Republic (Kireev, 1973, 1987); Rostov Region of Russia (Gus'kov et al., 1983), from the south-boundary districts of Turkey and Iran (Deryugin, 1899; Nesterov, 1911; Bodenheimer, 1944; Clark et al., 1966; Anderson, 1968; Clark and Clark, 1973; Nilson and Andr n, 1986; Nilson et al., 1988).

## DISCUSSION

After composing the spot ranges for each of the species with the use of lines the chorology of Mediterranean amphibians and reptiles on the Caucasian Isthmus was schematized, for instance, as it is shown for the *Coluber najadum* and *Lacerta media* (Fig. 3). The map of superposition shows the density of distribution of Mediterranean species (Fig. 4). They are completely absent in the highlands of axial part of the Main Ridge (higher than 2000 m above the sea level) and in the most elevated parts of the Lesser Caucasus,

poorly represented in the West Transcaucasia, Colchis lowlands, and in the upper belts of the mountains of Great and Lesser Caucasus, alongside, several plots with the high representation of Mediterranean species are distinguishing (Fig. 5). The largest of it embraces the foothill and middle mountain regions of the East Transcaucasia, located semicircular around the Kuro-Araksian lowland with the plots stretching to the foothills of Talysh (including Zuvand) and to the south slope of Lesser Caucasus and Armenian Highland along the left bank of Araks, excluding Ararat valley properly and other plots along the river Araks. The second plot is distinguishing on the Caspian coast of the Daghestan foothills. The series of plots on the north slope of the East Caucasus represent the contrast pattern to the greatest part of the territory with the complete or almost complete absence of the Mediterranean species – these are the semiarid depressions between the Main and Rocky ridges (Gunibskaya, Itumkalinskaya, Targimskaya, Sadono-Unalskaya, etc.). Analogous on the West Caucasus the narrow band of Black Sea coast from Anapa to Sukhumi is distinguishing. The representation of

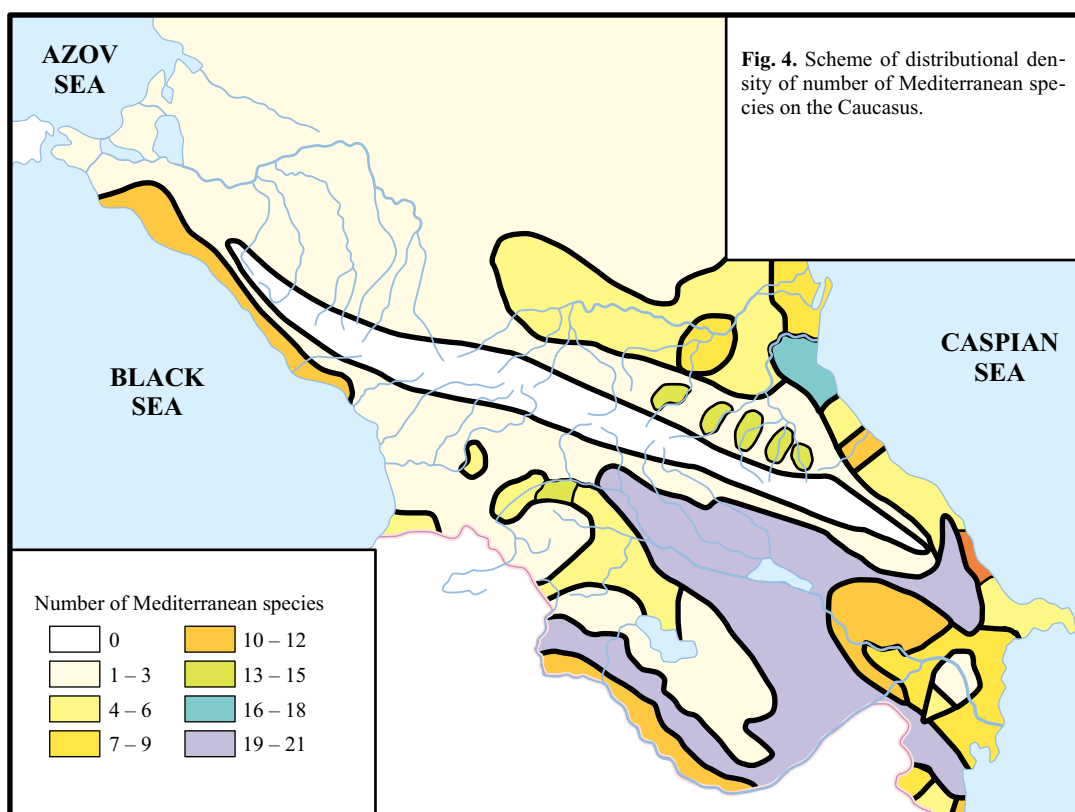


Fig. 4. Scheme of distributional density of number of Mediterranean species on the Caucasus.

Mediterranean species in the canyon of the upper streams of the Kura River is also high. One more plot of the West Transcaucasia out of the limits of the former USSR deserve attention. It is located in the lower streams of the river Chorokh (Artvinskaya depression).

Before the consideration of amphibians and reptiles fauna of the plots, listed above, it is appropriate to analyze their contemporary phytolandscape conditions, so far as it is known, that prochoroz is accomplished not by the separate species but by the communities as a whole (Chkhikvadze, 1989b).

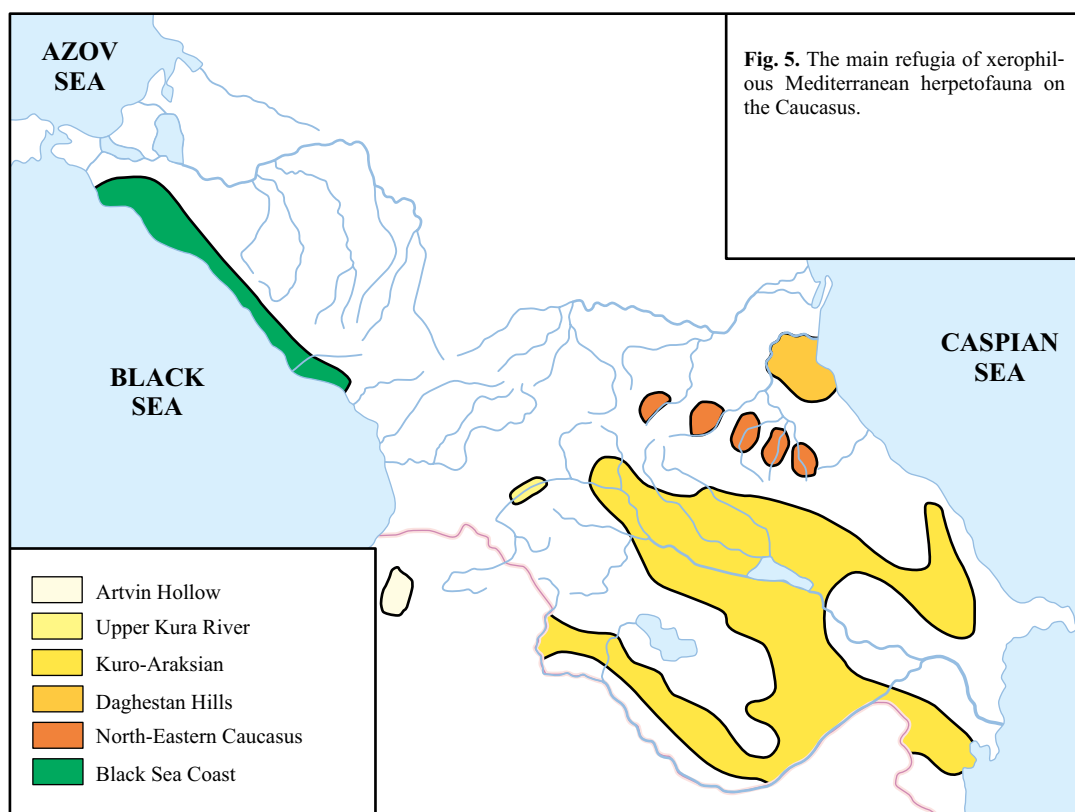
The vast foothills and midhills of the Great and Lesser Caucasus setting the lowest part of the Kuro-Araksian lowlands and Ararat's valley are covered with arid open woodland with *Pistachio* light forests, *Juniper* light forests, *Pistachio* – *Juniper* light forests different variants of shibliak (*Paliurus spina-christy*, *Pyrus salicifolia*, *Amygdalus fenzliana*, and *Rhamnus pallasii*) along the river valleys of the southern part of refugium sycamore groves remained (*Platanus orientalis*), sparsely along the river valleys — groves of *Pterocaria pterocarpa* and near the springs and close

location of the soil waters — brushwood of *Ficus carica*. On the lowest altitude limit these open woodlands transform into the subtropic *Bothriochloa ischaemum* steppe, and on the upper limit are changed by phrygana and tomillares. As a whole the vegetation of this refugia bears the East-Mediterranean — Middle Eastern appearance.

It is notable, that located lower the proper Kuro-Araksian lowland also as a valley of the river Araks is covered with semidesert and desert vegetation, mainly halophyte, more close to the Iran – Turanian desert vegetation, then to the vegetation of all other parts of Caucasus.

It is interesting to note, that Grossgeim (1936) in his famous work “The flora of Caucasus” referred the desert of Kuro-Araksian plate to the Turanian province together with the East Precaucasia and Apsheron peninsula. Later on Lavrenko (1965) included these deserts (without the East Precaucasia) in the particular Kuro-Araksian province of Iran – Turanian subregion of Afro-Asian (Sahara-Gobi) desert region.

The Caspian coast of Daghestan, composed by the slopes of East Caucasus, is covered by the pri-



mary and secondary shibliaks, groups of *Quercus petraea* and *Quercus pubescens*, altering with the *Juniper* light forests, thorn forests, and xerophyllous bushes. In the mouth of the river Samur the liana forests within the participation of *Pterocaria pterocarpa*, *Hedera pastuchovii*, *Periploca graeca*, etc., is developed, what makes this plot similar in appearance with the forests of Talysh and representing the derivate of the forest of the Hyrkan type.

East-Caucasian refugium of oreoxerophytes, including shibliaks and phrygana, are located along the Jurassic slate depression of northern slope of the Great Caucasus between the Main and Rocky ridges. It is the series of semiarid depressions, stretching from the internal Daghestan (Gunib Plateau) up to the upper waters of the river Kuban. In the plant communities participate *Juniperus*, *Paliurus spina-christy*, *Cerasus incana*, *Colutea orientalis*, *Berberis*, *Astragalus*, and many others. The age of vegetation is interpreted differently. The majority of authors are keeping the Pliocene origin of the vegetation (Krasnov, 1894; Grossgeim, 1948; et al.). According to the opinion of Galushko (1974), semiarid depressions

of Chechen-Ingushetia are younger then located on the west and east depressions of Kabardino-Balkaria and Daghestan, and, apparently, not older than Holocene. The remains of xerophyllous flora on the ridges, dividing the depressions, spoke for the existence of single vast Mediterranean refugium from the Pre-El'brus to Daghestan, broken later on the number of microrefugia in the Pleistocene and in a different degree of preservation having remained up to now.

It should be underlined, that the tracks of xerothermic period are discovered and on the West Caucasus in the district of Yatyrgvarta and Magisho mountains (Altukhov, 1967), here, however, the xerophyllous vegetation never was widely developed due to the climatic peculiarities and powerful influence of Colchis, which is observed also now.

The Black Sea refugium, embracing the extreme western edge of the Great Caucasus in the district of Anapa – Gelendzhik – Dzhubga and the series of enclaves from Tuapse to Sukhumi represent particular Crimea – Novorossiisk province of Mediterranean. On the west of the refugium remained *Pistachio* and *Juniper* light forests, the plots of tomillares and



*Quercus pubescens* droves, on the east — *Cytisus monspessulanus*, *Punica granatum*, *Arbutus andrachne*, *Erica arborea*, and *Laurus nobilis*. Along the whole refugium *Pinus pityusa*, *Cistus tauricus*, *Paliurus spina-christy*, *Rhus coriaria*, *Cotinus coggygia*, and *Colutea cilicicus* are common.

The valley of the river Chorokh in the district of Artvin represent itself the dry and hot depression surrounded by the circle of high ridges (Pontic, Shavshetsky, and Arsiansky), with the 500 – 600 mm of year precipitation, in a form of short summer rains (Menitsky, 1984). Voronov (1908) describing the changes of vegetation from the lower streams of Chorokh to the Artvin, indicated that already beyond Borchkha the dry slopes are covered with “rare forests from the crooked *Quercus iberica* with *Carpinus orientalis*, pine groves, woodlike juniper, thickets of xerophylic bushes... In the most dry sites of the district, as for example, in Ordzhokh, Ardanuch, sometimes in the Imerkhev canyon the woodlands are practically absent, the bare rocks are covered with rare, scarce *Punica granatum*, *Rhamnus palasii*, junipers, etc., or covered with thorn *Astragalus*” (p. 3). It is rather notable, that there are collections of typical Mediterranean oak *Quercus infectoria* ssp. *infectoria* from this region (Menitsky, 1984), and groves of typical Mediterranean pine *Pinus pinea* are meeting (Nasimovich, 1979).

It should be noted, that on the Caucasus different in age and origin relict types of vegetation and their refugia are often located near by on the confined territory. This rule, repeating in all regions of Caucasus reflect the result of repeated translocations of the vertical vegetation belting, having place already in the Pliocene, and in the Pleistocene-Holocene particularly. Only for the Holocene there have been marked 11 such translocations (Kvavadze and Rukhadze, 1989). That is why although the general scheme of distribution of Mediterranean vegetation in Fig. 6 reflects the picture as a whole, is yet in many aspects conditional. On the place we are discovering on mosaic distribution of plant communities, especially on the Black Sea coast of Caucasus, in the semiarid depressions of the East Caucasus, in the district of Karabakh, upper streams of Kura river and in the vicinity of Artvin. So, on the Black Sea coast of Caucasus the solid distribution of the East-Mediterranean vegetation is taken place only on the extreme north-west from Anapa to Gelendzhik. Further on, in direction to the south-east this vegetation is represented by the series of enclaves, located on the steep sea hills, with

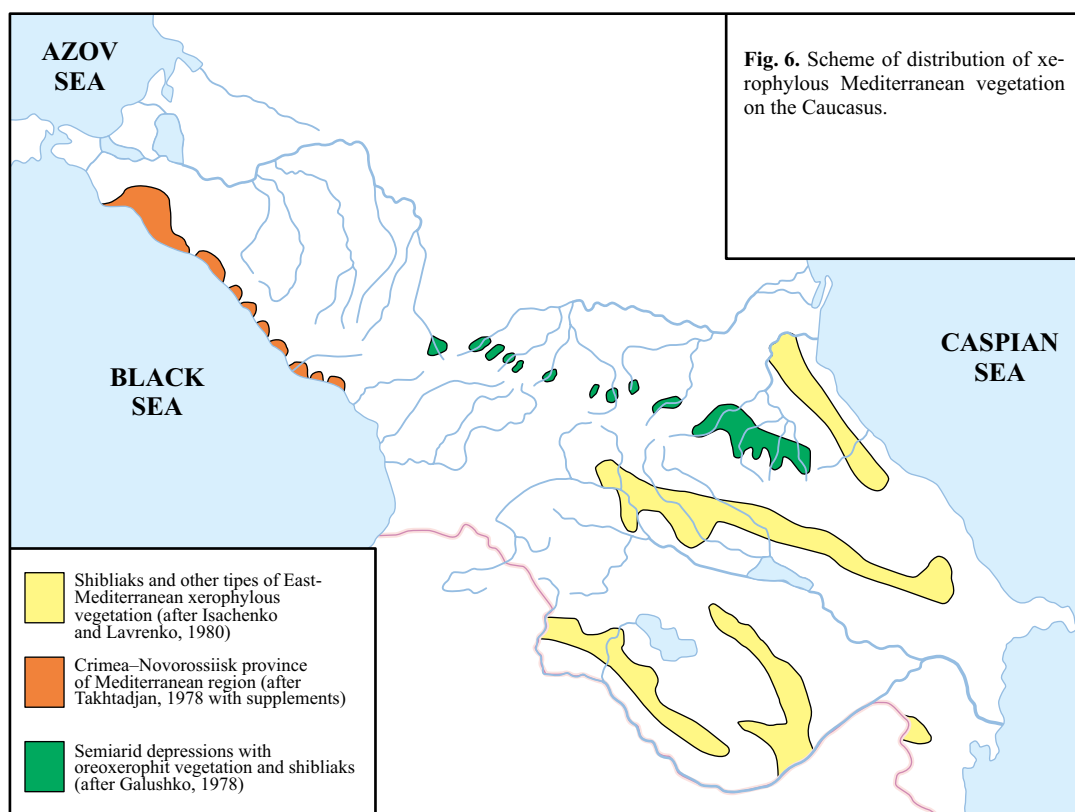
the slopes of the south and east exposition, distributed among the Colchis vegetation. The marine Mediterranean vegetation remains only along littorial (Kolakovsky, 1974b). In the semiarid depressions of the East Caucasus oreoxerophytic vegetation is growing on the steep slopes of east exposition, whereas the slopes of the western exposition are covered with mesophylic forests, therewith, for instance, for the Itum-Kalinskaya depression (Chechen-Ingushetia) the existence of four group local disjunctions in one refugium has been marked: 1) steppe species; 2) oreoxerophytes; 3) shibliaks; and 4) deciduous forests (Galushko, 1974) (Fig. 7). In the region of Nagornyi Karabakh the relicts of the Mediterranean shibliaks and arid light forests (*Pistacia mutica*, *Cerasus mahaleb*, *Pyrus salicifolia*, *Cotinus coggygia*, *Punica granatum*, *Paliurus spina-christy*, *Rhus coriaria*, etc.) are growing near by with the Colchis-Hyrkan relicts (*Zelkova carpinifolia*, *Castanea sativa*, *Taxus baccata*, etc.) (Arushanyan, 1973). In the upper streams of the Kura River already in the limits of Borzhom canyon the transition of vegetation from Colchis type in the Baniskhevi and Likani canyon through the intermediate variants (in Chitakhevi and Kvabiskhevi) to the Mediterranean in Zoreti canyon is observing. Along the river Chorokh the direct closeness from the dry Artvin depression in the side canyons and in the mediate mountain belt a rich Colchis-Lazistan vegetation with such forest founders as *Quercus petrae dshorochensis*, *Picea orientalis*, *Carpinus betulus* and many others is represented (Menitsky, 1984).

In correspondence with the variegate vegetation the herpetocomplexes of the different regions of Caucasus are complex. Nevertheless, the core of the fauna always could be determined, independently from the regarded xerophylic or mesophylic group of the animal world.

### Kuro-Araksian Refugium

Among the widely distributed along the whole territory of the refugium (Table 1) species should be indicated *Pelobates syriacus*, *Testudo graeca*, *Mauromys caspica*, *Lacerta media*, *L. strigata*, *Pseudopus apodus*, *Ophisops elegans*, *Natrix tessellata*, *N. natrix persa*, *Coluber najadum*, *C. caspius schmidtii*, *Typhlops vermularis*, *Eryx jaculus*, *Elaphe hohenaekeri*, *E. quatuorlineata*, *Telescopus fallax*, *Eirenis modestus*, *Malpolon monspessulanus*, and *Vipera lebetina*. If on the north of the refugium (in the south





foothills of the Great Caucasus and in the valley of the Kura River) these species inhabit rather low altitudes — up to 600–700 m above the sea level, in Araksian part, on the south of the refugium, these species occupy already more high belts of the mountains, sometimes achieving 2000 m above the sea level. In the most low plots of Kura-Araksian plate, over the limits of the distinguished refugium, the species of Turanian origin — *Eremias velox*, *E. arguta*, *Cyrtopodion caspius*, and *Ablepharus pannonicus* are meeting. In the valley of Araks to these species *Psammophis lineolatum* and species the formation of which is connected with the semidesert and desert regions of Armenian and western part of Iranian highlands: *Eremias strauchi*, *E. pleskey*, *Mabuya aurata*, *Eirenis punctatolineatus*, *Rhynchocalamus melanocephalus satunini*, *Coluber nummifer*, *Ablepharus bivittatus*, and *Pseudocyclophis persicus* are added. No doubt, it would be incorrect to consider all these species on the Caucasus as a Late Pleistocene migrants. Middle Eastern xerophylic complex of flora and fauna, occupying more perfect step of fitness to the arid conditions, is closely connected with the Medi-

terranean one. The latter assumption evidence for the long existence on the Caucasus along with the Mediterranean cenoses elements on the Middle Eastern cenoses. Otherwise, such species as *Laudakia caucasia*, *Phrynocephalus persicus*, *Eumeces shneideri*, *Eirenis collaris*, and *Coluber ravergieri* and species of Armenian Highland could inhabit this territory already in the Pliocene.

On the upper limit of distribution the Mediterranean species are meeting together with Caucasian and Lesser Caucasian species (*Rana macrocnemis*, *R. camerani*, *Archaeolacerta*-complex, *Vipera eriwanensis*, etc.), also as with the representatives of the middle mountain belt of the Armenian Highland (*Vipera raddei* and *Lacerta parva*).

Mediterranean species, which have a limited partition the Kuro-Araksian refugium are represented by *Triturus cristatus karelinii*, (foothills of the Great Caucasus on the north and Talysh — on the south), *Cyrtopodion kotschyi colchicus* [is known (Flärdh, 1983) from the Turkey part of the Ararat valley], *Lacerta praticola* (the north part of the refugium), *Ablepharus chernovi* (Razdan canyon in Armenia), and

*Vipera ammodytes transcaucasiana* (vicinities of Gyandzha on the Azerbaijan). All listed species practically occupy the most mesophylic part in the general xerophylic spectrum of the Mediterranean species. Suppression of this species in the refugium with the existence of the great number of Turanian and Iranian (Middle Eastern) species once again underlines the peculiarity of this territory and the complexity of its formation.

### Refugium of the Daghestan Foothills

It is relatively poor refugium in species number (Table 1), though, in our opinion, the possibility of finding such species as *Elaphe hohenackeri*, *Eryx jaculus*, and, possibly, *Triturus cristatus karelinii* is not

**TABLE 1.** Distribution of the Mediterranean Herpetofauna in the Main Refugia of the Caucasian Isthmus

No	Species	Regions					
		1	2	3	4	5	6
1	<i>Triturus (cristatus) karelinii</i>	+	-	-	+	+	+
2	<i>Pelobates syriacus</i>	+	+	-	-	+	?
3	<i>Testudo graeca</i>	+	+	-	+	-	-
4	<i>Mauremys caspica</i>	+	+	-	-	-	-
5	<i>Cyrtopodion kotschyi colchicus</i>	-	-	-	-	-	+
6	<i>Lacerta media</i>	+	+	+	+	+	+
7	<i>Lacerta strigata</i>	+	+	+	+	-	+
8	<i>Lacerta praticola</i>	+	+	+	+	?	?
9	<i>Pseudopus apodus</i>	+	+	-	+	+	?
10	<i>Ophisops elegans</i>	+	+	-	-	-	-
11	<i>Ablepharus (k.) chernovi</i>	+	-	-	-	-	-
12	<i>Natrix tessellata</i>	+	+	+	+	+	+
13	<i>Natrix natrix persa</i>	+	+	+	+	+	+
14	<i>Coluber najadum</i>	+	+	+	+	+	+
15	<i>Coluber caspius/schmidti</i>	+	+	-	+	-	+
16	<i>Elaphe hohenackeri</i>	+	-	+	-	+	+
17	<i>Elaphe quatuorlineata</i>	+	+	-	+	-	-
18	<i>Telescopus fallax</i>	+	+	-	-	+	?
19	<i>Malpolon monspessulanus</i>	+	-	-	-	-	-
20	<i>Eirenis modestus</i>	+	+	+	-	+	+
21	<i>Eryx jaculus</i>	+	-	-	-	-	+
22	<i>Typhlops vermicularis</i>	+	+	-	-	-	-
23	<i>Vipera ammodytes/transcaucasiana</i>	+	-	-	-	+	+
24	<i>Vipera lebetina obtusa</i>	+	+	-	-	-	+
<b>Total:</b>		23	17	8	11	11	14

**Note.** 1) Kuro-Araxian; 2) Daghestan Hills; 3) North-East Caucasian; 4) Black Sea Coast; 5) Upper Kura River; 6) Artvin Hollow.

excluded. It is notable that here in the significant volume Iranian complex of species is represented (*Laudakia caucasia*, *Eumeces shneideri*, *Coluber ravergieri*, and *Eirenis collaris*), but there are no representatives of the Armenian Highland, so typical for Araksian part of the Kuro-Araksian refugium. Near the northern border of the refugium the sandy dune Sarykum with such typical Turanian species as *Phrynocephalus mystaceus* is located.

### Refugium of the North-Eastern Caucasus

The most poor among the considered regions. Along with it the species composition is so specific, and accompanying fauna and flora is typical of more south latitudes, that this district deserves to be distinguished and described as the derivate of Mediterranean cenoses. Mediterranean species are represented in different depressions in different combinations: so, *Eirenis modestus* and *Lacerta strigata* are known from the eastern part of the refugium, whereas the rest species are meeting in the majority of the semi-arid depressions. From the Iranian species on the east of the refugium remained *Coluber ravergieri*. The fact of the presence of species identical or very closed to Lesser Caucasus among them, and *Rana camerani* and *Vipera lotievi* almost in all depressions is notable.

Along the upper limit of each of the refugium of this combined refugium Caucasian species (*Vipera dinniki*, *Rana macrocnemis*, *Lacerta daghestanica*, *L. caucasica*) are meeting. Caucasian species of the forest belt (*Lacerta agilis boemica*, *Rana macrocnemis*) together with the European species (*Coronella austriaca* and *Anguis fragilis*) are typical of the Western expositions of these depressions (see Fig. 7) where they are joined by the Colchis species *Lacerta rudis*. It is interesting that in the shibliaks, phryganas and stepped meadows among the shibliaks of Itumkalin depression the Mediterranean species are joined only by *Coronella austriaca* symbiotic here to the *Elaphe hohenackeri*. All the rest species are meeting by ecotones of Mediterranean and Caucasian mountain-forest and mountain-meadow cenoses, not penetrating inside the Mediterranean phytolandscapes.

### Black Sea Refugium

The species of this refugium were described by us earlier (Tuniev, 1990). Their distribution on the Black Sea coast of Caucasus is linked to the narrow band from Anapa on the north-west to Sukhumi on the south-east. Due to the long-term transforming ac-

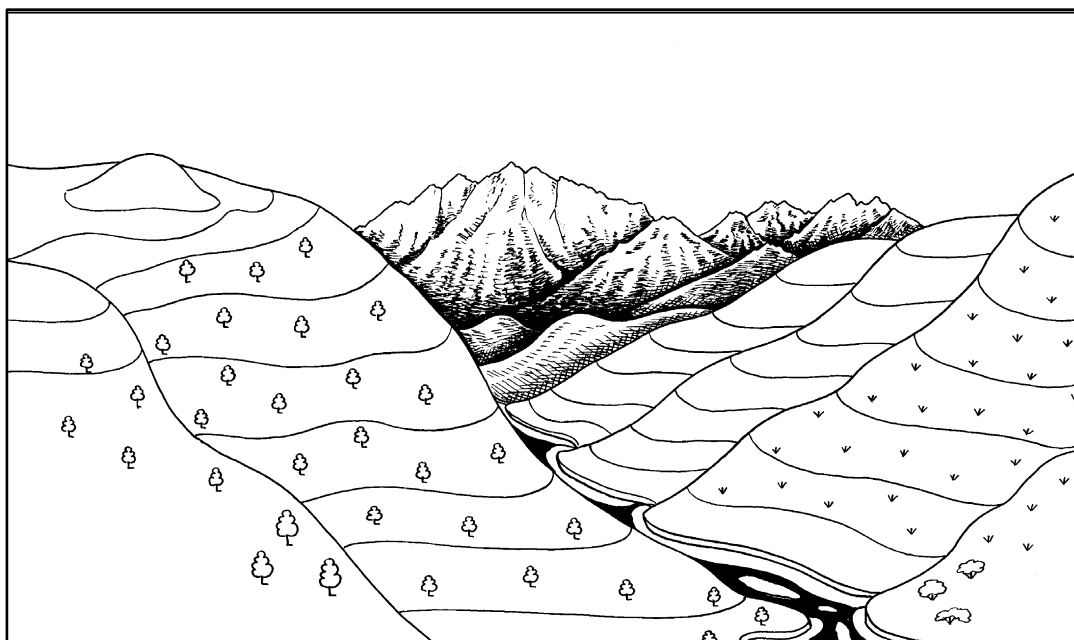


Fig. 7. Scheme of Itum-Kalinskaya semiarid depression: left side) west exposed slopes covered by broad-leav forests; right side) east exposed slopes covered by Mediterranean vegetation (habitat of Mediterranean species of herpetofauna). Below) the valley of river Argun. Far plan) The top of mountain Tebulos-Mta (4493).

tivity of the man the strict dependence in the distribution of the Mediterranean species of herpetofauna from the corresponding landscapes is not observing. These species along the forestless spaces sometimes penetrate deep into Colchis and are meeting with the typical representatives of Colchis ecological-geographical group. The most saturated in the species relation areas are observed in the well remained East-Mediterranean phytocenoses in the vicinity of Novorossiisk and Pitsunda. For this refugium the features of extinction due to the high humidity and number of precipitation preventing the modern expansion of Mediterranean species are typical. Beside the general regularity of disjunctive distribution of species on the indicated section of the coast, *Elaphe quatuorlineata* is known only from the north-western part or the refugium, *Lacerta strigata* — only from the south-east. There is an analogy with the unevenness of the recent distribution of Mediterranean species of plants, what is once again illustrated by the common tendency in development, formation and extinction of cenoses. On the north-west of the refugium such steppe species as *Bufo viridis*, *Vipera renardi* are rather common. Unique Caucasian forms *Bufo verrucosissimus circassicus* and *Lacerta saxicola szcer-*

*baki* have remained here too. In the direction towards the south these forms are disappearing or substituted by the Colchis *Bufo v. verrucosissimus*, *Lacerta saxicola darevskii*, *Vipera kaznakovi*, etc.

### Upper Kura Refugium

This not large in space plot is directly adjusted to the Borzhomi refugium of Colchis herpetofauna (Tuniyev, 1990). It represents one of those complex examples of the mutual existence of genetically different complexes of cenoses, which we have indicated with the description of vegetation of the listed refugia. In order to avoid confusion this refugium has been named Upper Kura. Here we can see, close to the Colchis influence, the remaining of the most mesophylic part of the Mediterranean species with the complete absence of other xerophytes. If such species as *Triturus cristatus karelinii*, *Lacerta media*, *Natrix tessellata*, *Natrix natrix persa*, and *Vipera ammodytes* are rather common here and even come out of the indicated territory, such species as *Pelobates syriacus*, *Coluber najadum*, *Telescopus fallax*, *Eirenis modestus*, and *Pseudopus apodus* are already rare and are meeting not along the whole territory of refugium. Turan elements are completely absent here,

and from the Middle Eastern species only *Laudakia caucasia* is meeting. In a whole, Upper Kura plot is located as in the direct closeness from the Colchis center of speciation (*Archaeolacerta* complex, *Vipera darevskii*) and Kuro-Araksian refugium of Mediterranean species, but the distribution of Mediterranean species is linked, unlike the latter, to the lower part of the Kura River canyon.

### Artvin Refugium

It is the only one of the described regions the data on which totally are taken from the literature as we have no possibility to visit this region personally. The species listed in the Table 1 confirm the remain in the Artvin valley wide spectrum of Mediterranean cenoses: from the very dry and warm, suitable for habitation of *Cyrtopodion kotschyi*, *Lacerta strigata*, *Ophisops elegans*, and *Vipera lebetina* up to xerophyllous – mesophyllous and, as it known even mesophyllous with a typical number of Colchis-Lazistan species. Vegetation diversity of the Chorokh valley from the Borchkha up to the Artvin-Ardanuch is indicated above. In correspondence with it, from one hand it is possible to suppose here the occurrence of the row of species (*Pelobates syriacus*, *Lacerta media*, *L. praticola*, *Pseudopus apodus*, *Telescopus fallax*) from the other hand — *Vipera pontica* (Billing et al., 1990) described from this region evidence for the long existence of climatic conditions, differ from Black Sea coastal Lazistan conditions in many aspects local, explaining the presence of *V. pontica* with a rather wide distribution in the seaside Adzharistan – Lazistan — *V. kaznakovi*.

### The History of Development of the Mediterranean Refugia of Caucasus

In order to understand the recent character of distribution of the Mediterranean species on the Caucasian Isthmus and pathways of remaining of the main refugia it is necessary to consider the known paleontological material. Unfortunately this material is not so large, as we would like it to be, but nevertheless it allows to judge on the general tendencies in the development of Caucasus herpetofauna. If to take in account rather complete data on fossil mammals of Caucasus (Vereshchagin, 1959) and paleobotanic data, an attempt to reconstruct the way of formation of the herpetocomplexes of the Isthmus could be made.

Premiocene history of Caucasus by the majority of the authors (Vereshchagin, 1959; Darevsky, 1967;

Alekperov, 1978; et al.) is described as the history of tropical mountain island in the Tethys with a luxurious mesophyllous flora. In any mountains, of course, arise local conditions of edaphic dryness, for instance, on the rocks or steep slopes what results in the appearance of the xerophytes. For the development of the xerophyllous vegetation, however, as the belt, significantly greater corresponding climate alteration is demanded. In this connection, it is quite possible, that before Miocene Caucasus was more humid, than the mountain land, located to the south and stretching from Afghanistan through the Central Iran, Asia Minor, Balkan up to Alps, for which the fact of continuous existence of the mountain belt of arid climate from the Cretaceous is considered to be established with the corresponding hemixerophyllous phyto-landscapes (Krishtofovich, 1954; Kolakovsky, 1974a, 1974b). The fossil herpetofauna of Premiocene Caucasus is represented by the Middle Jurassic *Stenosaurus* sp. from the Mountain Daghestan (Bakradze and Chkhikvadze, 1988), tracks of dinosaurs on the Lower Cretaceous limestones of Satapliya in the West Georgia (Gabunia, 1951), *Mosasaurus* sp. of the date Cretaceous period of Azerbaijan (Gabunia, 1958), and Oligocene-Lower Miocene records from the Benara in the South Georgia, where *Palaeochelys gabunii* (Emydidae), *Ergilemys meschethica* (Testudinidae), and *Trionyx* sp. (Trionychidae) were identified (Bakradze and Chkhikvadze, 1988). From the Middle Sarmat Caucasus became a peninsula of the Middle Eastern land (Vereshchagin, 1959; Darevsky, 1963; Menitsky, 1984) to which also were linked Anatolia and Balkans. Kolakovsky (1974a) supposes, that floristic exchange between Europe, Caucasus and East Asia was taken place up to Upper Miocene. If the Great Caucasus remained to be surrounded by sea from the three sides and remain the tropical sea climate, the basement of the Isthmus have already experience significant continental influence and gave the premises for the development of semiarid landscapes alongside with the humid ones. Supposed development of climates and landscapes could explain the presence of *Chelonia caucasia* on the Chernaya river (North Caucasus) and giant terrestrial turtle of the *Ergilemys meschethica* type beside Benar yet in the Akhaltsikh (Bakradze and Chkhikvadze, 1988).

In the Miocene the processes of “borealization” occupy practically the whole Caucasus. Thus, from the Middle Sarmat in the number of sites of the East Georgia up to the 70% of trees species already belong to the deciduous species (Palibin, 1935). Grossgeim

having compared the Upper Miocene flora of Asia Minor with this one came to the conclusion that they are very close and are characterized by the same mixture of boreal and subtropical elements. Vereshchagin (1959) considered that the fact of started process of flora "borealization" is important for the understanding of the further fauna evolution, so far, as in the Sarmat on the Caucasian Peninsula the representatives of the hipparion fauna are appearing. Particular interest for the reconstruction of Miocene landscapes and faunistic connections of Middle East with Caucasus represent the fauna of the Sekhend mountain near Maraga in Iran. Among the reptiles only the remains of terrestrial turtle are known (Bakradze and Chkhikvadze, 1988). The mammals, however, are represented by almost 40 species (*Primates*, *Carnivora*, *Tubulidentata*, *Proboscidea*, *Perissodactyla*, and *Artiodactyla*) and birds — *Struthio* sp., *Urmiornis maraghanus* (Vereshchagin, 1959). According to the opinion of Vereshchagin the clear dominance of the inhabitants of the open landscapes with the occurrence of forms, inhabiting also subtropical forests allow to speak on the mixed savanna-gilein landscapes, typical in the Miocene for the northern parts of the recent Iran Highland. In the Asia Minor the Upper Miocene mammals, discovered near the İstanbul, Upper Gediz, Mugli, and in Gelatiya and Cappadocia are of one type with the sites on Samos and on Balkans near Athens-Pikermi (Vereshchagin, 1959). Vereshchagin considered that the faunistic complex of the Maraga type was, apparently, typical for the whole Middle East, what is confirmed by the genesis of Asia Minor landscapes. More over the Upper Miocene fauna of mammals of Middle East, Caucasus, Crimea and Balkans display great similarity. It is interesting that Grossgeim (1936) considered Meotis to be the time of wide penetration on the Caucasus the south xerophyllous flora. In the East Transcaucasia many recent or close to them species of reptiles were already existing. For the Late Sarmat of the West Azerbaijan Alekperov (1978) indicate *Testudo eldarica*, in the adjoining East Georgia: in Eldari, Pantishara, and Iori — *Testudo burtschaki*, *Chelydropsis* sp., *Trionix* sp., *Emydoidea taraschuki*, and *Mauremys sarmatica* were found (Bakradze and Chkhikvadze, 1984, 1988). From the vicinity of Rustavi Zerova and Chkhikvadze (1984) indicate large *Vipera* sp. which later on was suggested to be referred to the *Vipera cf. lebetina* (Bakradze and Chkhikvadze, 1988).

In the Garedzhiiskaya steppe, between the basins of the Kura river and the river Iori, near the village

Udabno (East Georgia) *Mauremys* sp., *Ergilemys* sp., and *Testudo* sp. from Meotis were found (Bakradze and Chkhikvadze, 1988).

On the north slope of the Great Caucasus in the Miocene, alongside with hydrophyllous fauna the xerophyllous species and species typical of the recent European Mediterranean appear: from the Belomechetskaya countryside the Middle Miocene *Trionyx* sp., *Ergilemys* sp., *Protestudo* sp., and *Lacerta* sp., *Colubridae* gen. indet. have been recorded (Chkhikvadze and Lungu, 1984); Middle Sarmat amphibians and reptiles from the lake deposits on the river Belaya (Maikop) are represented by *Trionyx khosatzkyi*, *Emydidae* gen. indet., *Mioproteus caucasicus*, *Triturus* cf. *marmoratus*, *Lacerta* sp., *Ranidae* gen. indet., *Discoglossidae* gen. indet. (Estes and Darevsky, 1977; Chkhikvadze and Lungu, 1984). The fossil remains of the skulls of *Lacerta* found here were later on analyzed by Darevsky (1990) who considers that with the high degree of probability it is the representative of the subgenus *Lacerta s. str.* which could be referred to one of the recent species (*L. media*, *L. strigata*, and *L. agilis*) or to the extinct, ancestral for all of them species. To the same species according to the supposition of Darevsky, refers also *Lacerta* from the Middle Miocene of Belomechetskaya site. The mentioned records of lizards, according to the opinion of Darevsky evidence for the Asian Minor way of penetration of lacertids from the Europe to the Caucasus, so as the Asia Minor was separated by the sea channels from the Balkans only after Sarmat time. The same idea on the base of the records of *Triturus* cf. *marmoratus* and *Mioproteus caucasicus* close to the recent relict *Proteus anguineus* is suggested by Borkin (1986).

In the Lower Pliocene Caucasus still remained to be peninsula and only from the end of Pontus the sea is regressing from the Precaucasia and Caucasus transforms into Isthmus (Vereshchagin, 1959; Alekperov, 1978). Landscapes of the east and west parts of the Caucasus were already significantly different: Colchis and adjoining districts remained the belting of humid subtropics and in the Kimmerian even close to the tropics; whereas on the east the more dry Hyrkan forests in a form of continuous band stretched along the west coast of the Caspian Sea and its Kurinskii and Samurskii gulfs to the north up to Ergenei and in the internal part of the eastern part of the Isthmus arid and semiarid landscapes extended.

Particular appearance to the flora of West Transcaucasia gave the ferns, which in abundance and di-

versity have no analogous even among the known more ancient Tertiary flora and could be compared only with Cretaceous (Mchedlishvili, 1963). The floristic composition of Colchis beside the abundance of ferns is characterized by the exclusive richness of subtropical forms among the gymnosperms (*Ginkgo adiantoides*, *Podocarpus*, *Cedrus*, *Tsuga*, *Abies*, *Clyptostrobus*, *Sequoia*, *Cryptomeria*, etc.) and angiosperm plants, and the absence of edificators give it the ancient tropic appearance, somehow resembling the floras of Oligocene. In the vegetation on the base of the pollen analysis it is possible to distinguish the dark coniferous forests, deciduous forests, evergreen forests, forests of the river valleys and hydrophyllous formations (Mchedlishvili, 1963).

Tertiary relicts of the West Caucasus which have remained up to now are very diverse in their generic connections, but most clearly in the opinion of Malev (1938) they reveal the close connection of Caucasian flora with the flora of Mediterranean. The flora of Mediterranean is composed by two complexes: hemixerophyllous and mesophyllous. The first one is the modified xerophorized derivatives of the ancient subtropical flora of the Poltava type with the significant including of Middle Eastern elements, the second one is the weakly modified derivative of Angarid or Turgai flora. Grossgeim (1936) connect the formation of the widest center of xerophyllous flora in the form of recent Mediterranean with the second half of Tertiary. Despite the abundance of Mediterranean species in the Caucasus flora, however, the type of Mediterranean vegetation is almost absent on the Caucasus now, excluding makvis on the Black Sea coast and shibliak in the center and on the east of the Isthmus. The connection of the xerophyllous flora of Caucasus, however, according to Grossgeim is particularly clear with the Middle East, from where the ancient xerophytes could penetrate not only to Transcaucasia, but and on the north slope of Great Caucasus in the Daghestan. On the development of two xerophyllous centers in Armenia and Mountain Daghestan have spoke earlier also Kuznetsov (1909). It is interesting that in the opinion of Grossgeim (1936) the main way of penetration of Mediterranean elements to Caucasus passed through Manych from the north, and the main migration of Mediterranean species took place comparatively late, before the Ice age.

Differences in the flora of the West Transcaucasia and West Precaucasia were marked already in the Kimmerian: in the West Precaucasia the number of ferns, subtropical forms of gymnosperm and angio-

sperm plants significantly decreased, the number of herbaceous plants increased. The pollen spectrums reflect the existence here of forest-steppe vegetation (Mchedlishvili, 1963). It is interesting in this connection, that the Pliocene records of reptiles from the north slope of the Great Caucasus are referred to the fauna of Moldavian complex, which have the wide distribution along the whole north Black Sea area. Thus, from the site Kosyakinskii pit (North Caucasus) *Lacerta* sp., *Bufo* sp., *Rana* sp. (Vereshchagin, 1959), *Melanochelys pidoplickoi*, *Sakya riabinini*, *Testudo cernovi cernovi* (Bakradze and Chkhikvadze, 1988; Chkhikvadze, 1989a, 1989b) were recorded. And from the north Black Sea area (Ukraine and Moldova) *Andrias* sp., *Mioproteus* sp., *Latonia* cf. *sefriedii*, *Ophisaurus* sp., *Varanus* sp., *Vipera* cf. *lebetina*, *Chelydropsis nopcsai*, *Melanochelys pidoplickoi*, *Sakya riabinini*, *Testudo cernovi cernovi*, and *Emys orbicularis antiqua* (Bakradze and Chkhikvadze, 1988; Redkozubov and Shushpanov, 1985) are known. The latter species have been found and described from the Pliocene deposits near Stavropol' (North Caucasus). Beside it, the different representatives of the genus *Testudo* are known from the Pliocene sites in Ust'-Labinsk (Krasnodar region), vicinity of Groznyy in Chechen-Ingushetia (Alekerov, 1978).

For the majority of Mediterranean species, apparently the Upper Pliocene was the time of the last wide distribution in the North Black Sea area, including Precaucasia. Anyway, it was the last time of Mediterranean species and for the major part of Europe, where the forest complexes of Sarmat, similar with the contemporary Mediterranean were discovered even in Hungary (Andreánzsky, 1963) with the such species as *Quercus ilex*, *Pistacia lentiscoides*, *Rhus palaeocotinus*, *Rh. cf. coriaria*, *Acer decipiens*, *A. cf. monspessulanum*, *Phillyrea cf. latifolia*, and *Viburnum tinus*.

In the Pontic level of the river Kodor in Abkhazia Kolakovsky (1964) discovered unique type of sclerophyll oak paleoformation with the dominance of *Quercus sosnowskyi*. This evergreen species is the extinct link between the Himalayan – Chinese *Q. semicarpifolia* and Mediterranean *Q. alnifolia* and *Q. suber* (Menitsky, 1982). Despite the sclerophilly, Kolakovsky considered *Q. sosnowskyi* as the more hydrophilic species, than its recent Mediterranean descendants on the base of its participation in the communities of mesophyllous species *Carpinus cuspidens*, *C. uniserrata* and comparatively small part in

these communities the elements of the recent Mediterranean flora (*Arbutus elegans*, *Laurus nobilis* foss., *Myrtus rarinervis*, *Pistacia miochinensis*, *Celtis magnifica*, and *Cotinus coggygria-fossilis*). *Sakya riabinini* (Bakradze and Chkhikvadze, 1988) which is a typical element of Moldova faunistic complex is known from this site. This means that already from the Pliocene the presence of the Mediterranean species of animals on the Black Sea coast of Caucasus was observed.

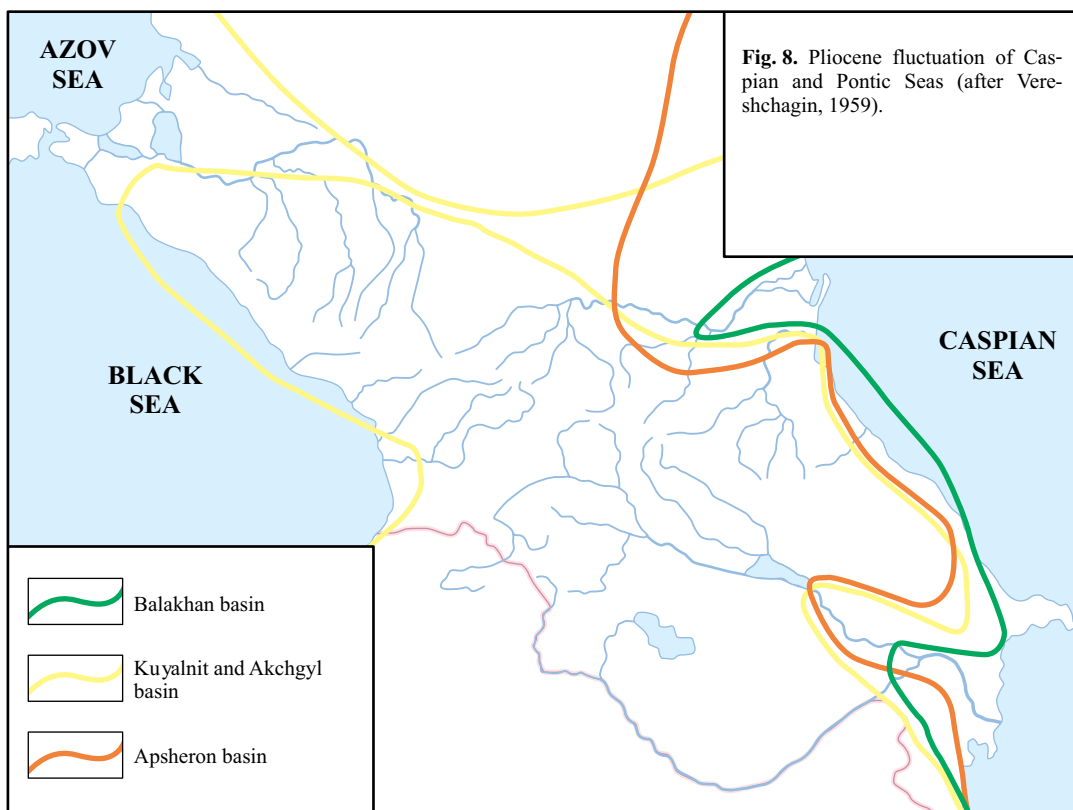
In the eastern part of Caucasus along the shores of at first Caspian sector of Pontus and then Balakhan basin was vegetation described by Baranov (1952) from Ergeni, though and deciduous but thermophylous with such species as *Corilus fossilis*, *Alnus incana*, *Quercus* sp., *Castanea* sp., and *Parrotia persica*, Araliacea. The indicator of the warm climate, as appropriately wrote Vereshchagin (1959) is *Parrotia persica*, which remained nowadays 10° S of Talysh-El'brus. Parallel with *Hyrkanian* the development of xerophylous Mediterranean and Middle Eastern vegetation was going on. The record of Upper Pliocene *Testudo* sp. from Ergeni, similar in size with the recent *Testudo graeca* (Aleksperov, 1978) is remarkable. Vereshchagin (1959) pointed on the independent Middle Eastern center of genesis of two subtypes of theriocomplexes of the Pliocene age: mountain-steppe and mountain-desert. Differentiation of the Middle Eastern complex on the mentioned subtypes is connected with the strong relief diversity of the mountain country and climatic differences. Whereas as in the broad intermountain valleys and narrow canyons the biocenoses of mountain-desert type were developing, on the near by high plateaus and ridges ecological groups of mountain steppe landscape and even meadow-steppes were forming (Vereshchagin, 1959). The impact of this south complex on the Caucasian Isthmus broke on several steps, but the most ancient in the opinion of Vereshchagin had to be considered the Miocene – Pliocene step. Apparently, in the Pliocene alongside with the Mediterranean species of herpetofauna wide distribution in the eastern part of Caucasian Isthmus had and Middle Eastern: as mountain-steppe (*Laudakia caucasia*, *Coluber ravergeri*, etc.), so mountain-desert (*Mabuya aurata* and *Coluber nummifer*). Pliocene records from the foothills of the Eastern Caucasus refer in the main to tortillas: from Kvabebi, Kumuros-Khevi (East Georgia) — *Testudo cernovi transcaucasica*, Bazaleti — *Testudo bosporica*; Enikend (Azerbaijan), Nurnus (Armenia) — *Mauremys* cf. *caspica* (Chkhikvadze,

1977; Bakradze and Chkhikvadze, 1984, 1988). From the mountain regions — Kusatibi (South Georgia) *Rana macrocnemis angeloi* (Bogachev, 1927) is known. These records evidence for the development of semiarid landscapes with warm shallow water bodies, open lands in the foothills and together with it mesophylous landscapes in mountains.

Peculiarities of taphonomy and species composition of the Upper Pliocene mammals of Transcaucasia, according to Vereshchagin (1959), confirm the occurrence there in the Apsheron (Upper Pliocene) moderate but not cold climate, strong volcanic activity and reflect to the certain degree arid or semiarid conditions in the eastern and south parts of Caucasus. Apparently, already in the Pliocene the primary break of hemixerophylous landscapes of the Caucasian Isthmus: on Transcaucasian and North-Caucasian, due to the continuous intensive orogenesis from one hand and successive transgressions took place in Caspian Sea — from the other. For our understanding of remain of Recent Mediterranean refugia great significance has the fact of vast flood during the period of all three Caspian transgressions Balakhan, Akchagyl and Apsheron (Fig. 8) of lowlands of the contemporary Kuro-Araksian lowland, Apsheron peninsula and lowland of the Terek River. The foothill Daghestan remained to be stable land, which apparently, was connected in the Pliocene with the recent refugia of the North Caucasus. At the same time, most probably, aridization and separation of Artvin depression from the humid Lazistan, due to the same process of orogenesis, which created conditions of “rainy shadow” in the depression, surrounded by the high Pontic, Shavshet, and Arsiyan ridges, is taking place. Similar to the Artvin, semiarid conditions could be developing in the Akhaltsikh Highland, upper the recent Upper Kura refugium. What concerns Black Sea coast of Caucasus, here, in the Pliocene still prevailed humid landscapes and only separate representatives of the xerophylous flora and fauna penetrated on the areas of steep seaside slopes with the local conditions of edaphic dryness.

Thus, in the Paleogene all families, survived up to the recent already existed (Bakradze and Chkhikvadze, 1988). On the Caucasus and in the nearest vicinities of this Isthmus the habitats have been as mesophylous, so in great diversity xerophylous species of herpetofauna, identical or close to many recent species of Caucasus. Darevsky (1963) consider that to the end of the Pliocene on the Caucasus the primary core of its recent herpetofauna with such





genera as *Agama*, *Lacerta*, *Ophisaurus*, *Anguis*, *Typhlops*, *Malpolon*, and *Vipera* have been already formed.

The Pleistocene history of Caucasus is in the first turn the impact of glaciation in the axial part of the Great Caucasus and in the most high areas of the Lesser Caucasus and Armenian Highland attended with the glacial and pluvial periods of pulsation of Black and Caspian Seas basins also the indirect impact of European sheet.

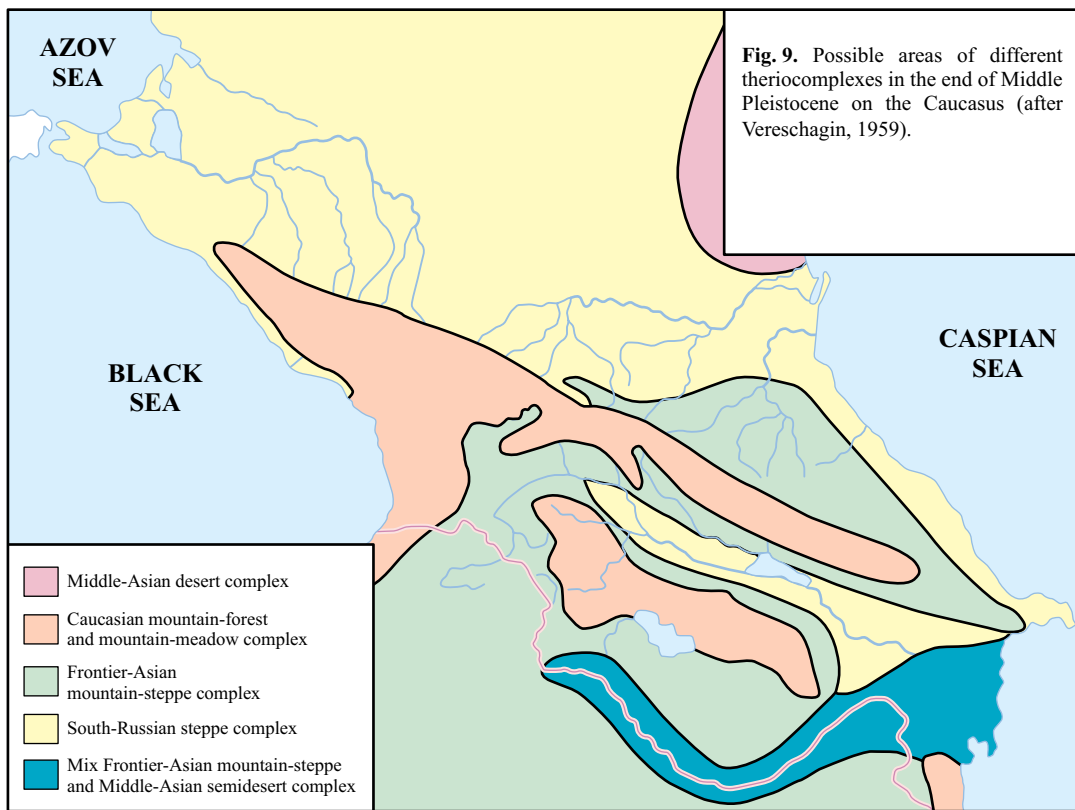
On the Great Caucasus the glaciation concerned mainly the Central and West Caucasus and significantly less was displayed on the East Caucasus. Shifts of vegetation belts connected with the phases of glaciation declined to the foothills the forest belt on the north slope of the West and Central Caucasus and on the south slope the upper boundary of the forest went down up to the altitude 1000 – 1200 m even in the most protected and warm Abkhazia (Kvavadze and Rukhadze, 1989). The data of pollen analysis have shown that the lower belts of forest practically have not been changed (excluding the extinction of the most thermophilous forms), and the main

changes occurred in the upper-forest and subalpine belts. Humid and relatively warm Colchis in the Pleistocene became the main refugium of the mesophylous flora and fauna. Several more smaller in size analogous refugia remained in the foothills of the North-West Caucasus and East Transcaucasia (Tuniyev, 1990). The Pleistocene remains of *Bufo verrucosissimus* are known from the different regions of Colchis: in Abkhazia — Kholodnyi Grot and Kep-Bagaz; in Guria — Belaya cave (Chkhikvadze, 1984). Great interest represent the remains of the frogs (*Rana* sp., *R. ridibunda*, and *R. macrocnemis*) from the cave Kudaro-I in the South Ossetia (Darevsky, 1980), late it refers to *Bufo* sp., *Rana* sp. and *Ranidae* indet. (Rocek, 1993). Xerophylous Mediterranean formations in this period on the West Caucasus were remaining only on the extreme north-west in the region of Novorossiisk, but here, apparently, they were significantly pressed back by the Colchis cenoses, which went down. It is likely, that in the Pleistocene the west end of the Great Caucasus reached such mesophylic species as *Triturus vittatus*, *Bufo verrucosissimus*, *Rana macrocnemis*, *Lacerta saxicola*,

and *Vipera kaznakovi* together with such mesophytes as *Fagus orientalis*, *Carpinus betulus*, etc., which and today are meeting here in the relict microbiotops. It is not excluded that a small plot of the Mediterranean cenoses remained in the Kavakluk Highland in Abkhazia. Further development of Black Sea refugium of Mediterranean herpetofauna is connected with Holocene, in the xerothermic period of which the Mediterranean species of plants and animals were able to occupy in Colchis the most insolated steep seaside slopes. Together with them in the Holocene along the Black Sea coast of Caucasus the movement of the European species, among them mammals (Vereshchagin, 1959) took place.

Mediterranean species on the Black Sea coast of Caucasus, as it seems, never crossed the river Inguri. In the majority they spread to the east only till the river Kodor. Though Darevsky (1963) is correct, indicating the processes of orogenesis as the reason of the disjunction of the initial ranges of a number of xerophylous species (*Lacerta media*, *Pseudopus apodus*, *Coluber najadum*, and *Testudo graeca*) on the Caucasus, what concerns the secondary extinction of these species in the West Georgia, we cannot agree with him. Xerophylous species of herpetofauna so as conditions for their existence on the greatest part of the West Georgia never occurred. Only low plateau of Imeretia according to Vereshchagin (1959) were in the Upper Pleistocene the north-west (!) limit of distribution of the arid forms of the highlands of the Middle East (Fig. 9). Just this fact explain the record of *Testudo graeca* in the Belaya cave near Tskhaltubo (Vekua et al., 1979) together with arid mammals (*Hystrix* sp.) with the dominance of forest mesophylous species (*Talpa caucasica*, *Erinaceus europaes*, *Castor fiber*, *Ursus arctos*, *Martes martes*, etc.), but not by the former solid range of *T. graeca* from the Novorossiisk to Caspian Sea, as it is indicated by Vekua and others (1979). It is typical, that and nowadays "witnesses" of the xerophylous landscapes in the hills of Imeretiya are *Elaphe hohenackeri* and *Coluber najadum*, absent in all other places of Colchis (Rioni) lowland. Specific conditions of the Black Sea refugium brought corrections in the microevolutionary processes, the result of which are melanistic specimens of *Coluber najadum* from Abkhazia (on the south-east of refugium) and neotenic specimens of *Triturus vulgaris lantzi* (Rudik, 1989) the appearance of which could be promoted by the maximums of dry periods of Holocene, when in the Mediterranean landscapes of Pitsunda this species could remain with

the condition of constant existence in the water bodies (for instance in the lakes Inkit or Zmeinoe). On the East Caucasus, also as in some screened longitudinal valleys of the Central Caucasus mainly remained dry moderately and warm plots, especially large in Daghestan. Here also the extinction of the most thermophylous species occurred, but the belt of shibliaks and oreoxerophytes not only have not disappeared but was able to develop expansion in the Holocene on those territories where it was absent in the Pleistocene (Fig. 9). Thus, Galushko (1974), recognizing the great antiquity of Daghestan and El'brus oreoxerophytes, consider that their penetration to the depressions of Chechen-Ingushetia happened only in Holocene. It should be underlined, that and nowadays protected from the cold air from the north by the Rocky ridge semiarid depressions of the East Caucasus with the high level of sun radiation have insignificant snow cover, early coming of the spring and more long summer with the significant maximums of summer temperatures. Excluding the alpine areas of Lesser Caucasus and Armenian Highland, all other parts of Transcaucasia were not subjected to glaciation. No doubt, the general shift of belting down and pressed to the Caucasus steppe lands of the south of the European plain had to produce its influence, though it was not so transforming as in the West part of Caucasian Isthmus, from where nowadays only Pleistocene record of *Emys orbicularis* from the mountain Mashuk near Pyatigorsk (Aleksperov, 1978) is known. Just in this period the elements of South-European steppe cenoses from the east rounded Caucasus and invaded into semiarid cenoses of foothills of the south slope of the East Caucasus. Just with this period of time we connect the penetration on the left bank of the Kura River basin *Vipera renardi* which have remained today in a form of relict in the Shemakha district of Azerbaijan and, possibly, adjoining East Georgia. Particular significance for us have the facts of remain during the Pleistocene Mediterranean species on the territory of Kuro-Araksian refugium. Petrov (1939) on the base of the list of the plants remains from the Binagady site insisted on the existence in the Pleistocene on the Apsheron the savanna landscape or arid open woodland. Here the numerous remains of *Testudo graeca binagadensis*, *Lacertidae*, *Ophisaurus apodus dzhafarovi* (Aleksperov, 1978) were found. From the neighbouring regions of Azerbaijan Fat'mai — Late Pleistocene *Ophisaurus apodus dzhafarovi* and *Testudo graeca ibera* (Aleksperov, 1978) were found. The latter species was found in the

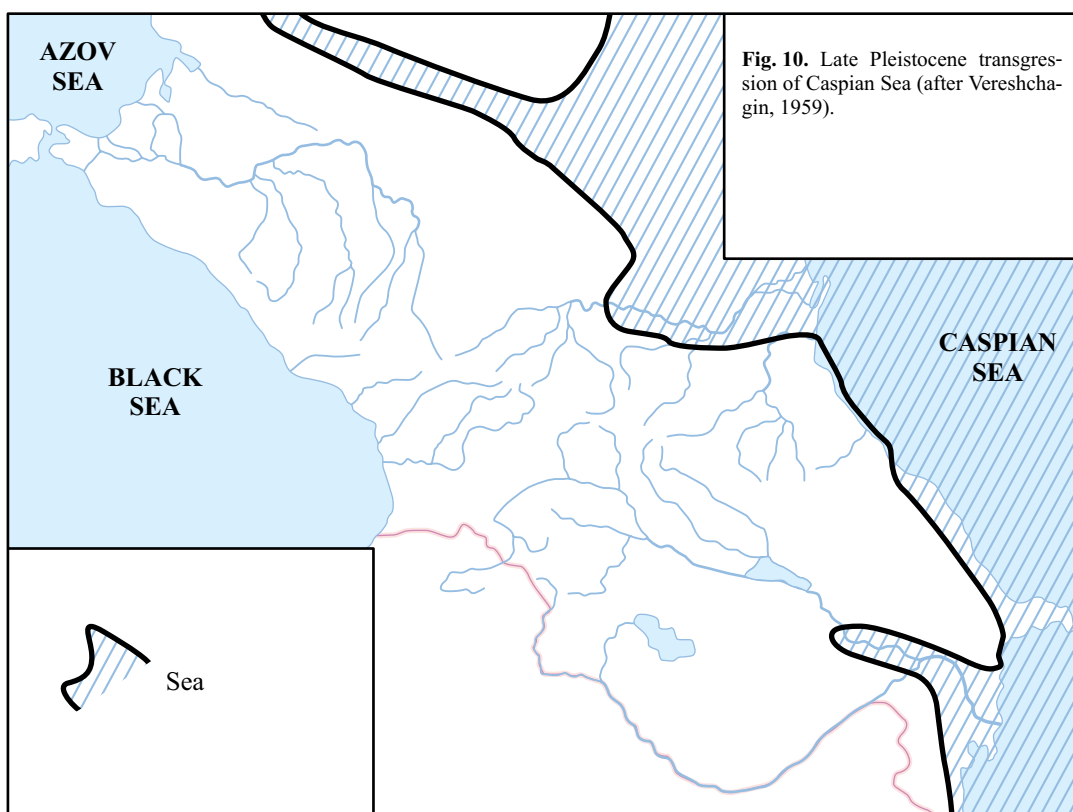


Pleistocene sites of a number of districts in the East Transcaucasus: Georgia — Mingeaur, Imeris-Gora, Tsopi, Arukho, Darkvetis Ekhi, Giena cave; Armenia — Verin Khatunorh; Azerbaijan — Damdzhila, Azykh, and Talgar (Bakradze and Chkhikvadze, 1984). The record of the Pleistocene *Pelobates syriacus* from the village Arukho in the East Georgia (Bakradze et al., 1987) is an interesting one. According to the data of Vereshchagin (1959) in the East Transcaucasus on the duration of the whole Middle Pleistocene the landscape of the dry foothills with the *Juniper – Pistachio* forests keep stable from the Pliocene and drying to the summer herbaceous cover of the steppe type. Simultaneously in the mountain regions of the East Transcaucasus the mesophylous species remained what is confirmed by the records of *Lacertidae*, *Lacerta* sp. of the type *L. agilis*, *Rana* sp., *Bufo* sp. from the cave Kudaro-I in the South Ossetia (Darevsky, 1980; Chkhikvadze, 1984; Zerova and Chkhikvadze, 1984; Roček, 1993).

Faunistic changes in the lowland districts of the East Transcaucasus were going on in the Pleistocene on the background of successive change of the three

seas — Bakinskoe, Khazarskoe, and Khvalynskoe (Fig. 10). It is supposed that the penetration of Turanian elements into the plains of the East Transcaucasus could happen three times (Alekperov, 1978). This penetration could go on as around Caspian Sea from the north and south, so and along the Apsheeron – Krasnovodsk bridge, existing in the period of maximal regression of the Caspian Sea (Darevsky, 1957a, 1957b; Rustamov, 1981). The discussion of the ranges genesis of the Turanian species of herpetofauna on the Caucasian Isthmus exceeds the frames of the current paper. We shall only mark that in our opinion in the Pleistocene from the Middle Asia to Caucasus penetrated the next species: *Ablepharus pannonicus*, *Eremias velox*, *E. arguta*, *Elaphe dione*, *Phrynocephalus mystaceus*, *Ph. guttatus*, *Cyrtopodion russowi*, *Trapelus sanguinolentus*, *Eryx miliaris*, and *Psammophis lineolatum*. The penetration of the such species as *Phrynocephalus persicus*, *Cyrtopodion caspicus* and *Agkistrodon halys* apparently occurred earlier — already in the Pliocene.

Caspian transgressions leave unflood the foothill Daghestan to the south from the Terek River. Shiffers



(1953) assume, that often meeting Mediterranean elements (meadows with *Imperata cylindrica*, brushwoods of *Paliurus spina-chrysti*, *Rhamnus pallasii*, etc., up to the oak forests with lians *Periploca graeca*) in the south part of the East Precaucasia lowland are evidence of that this territory, beginning from Tersko-Sulakskaya Lowland and farther to the south was flooded by the Caspian transgressions approximately from the time of Apsheron sea. Mediterranean species dispersed at the end of the Pliocene (Grossgeim, 1936) later on in the Pleistocene frozen on the territory of Precaucasia but remained in the most warm its south-east part (Shiffers, 1953).

Under the Caspian waters not once gone not only lowland regions of the Precaucasia, Kuro-Araksian lowland but south seaside Daghestan and Apsheron peninsula (Fig. 10). This makes understandable the poor representation of the ancient Mediterranean species on these plots and significant share of late Turanian migrants (Fig. 4).

In the Pleistocene, located to the south from the Kuro-Araksian refugium elevated plateau and mountains of the Armenian Highland were subjected to the

significant glaciation and then steppe-heath and in the lower belts-deserting. In result today the basin of Chorokh with the Artvin depression appeared to be limited from the north and west by the Euxinus (Colchis) province, in the composition of which it is included as the Subeuxinus plot (Menitsky, 1984). From the south and east Armenian – Iranian botanical-geographical province adjoins this plot the boundary of which coincides approximately with the Anatolian Diagonal of Davis (Davis, 1971).

In the Pleistocene the Upper Kura refugium decreases to the small size: beside the changes, connected with the glaciations of the Lesser Caucasus and neighbouring plots of the Armenian Highland, the volcanic activity became extremely high. According to the data of Maruashvili (1946) lava-streams covered up to 50% of the territory of Armenian Highland. Some botanists explain by this circumstance (Yaroshenko, 1941) the recent forestless of the West Armenia.

The data evidencing on the remain in the different corners of the Caucasian Isthmus Mediterranean species of herpetofauna during the most dramatic pe-

riod in the history of Palaearctic – Pleistocene glaciations represent for us particular interest. Total space of the listed refugia and species representation on the Caucasus exceed many analogous refugia of the East Mediterranean on the Balkans, islands of Aegean sea and so on. The penetration of the boreal elements on the Caucasus (as well as in the other regions of Mediterranean) according to the true note of Vereshchagin (1959) and Szczerbak (1984) have one-sided character, “Mediterraneans” themselves are more stenotope and do not come out of the limits of Mediterranean biogeographic province.

## CONCLUSION

It was noted above that biogeographic division of Caucasus is not the aim of the current work, the determination of the place of each of the distinguished refugia, however, represent not exaggerated interest. Having taken as the base the section multibelt approach in the biogeographic analysis of the mountain territories, it is impossible not to notice the shift up to the mountains from the west to the east landscapes corresponding conditions close to the Mediterranean. These processes are connected with the increasing aridisation and increase of the radiation balance in the east and south direction. Thus, describing the forests of Kopet Dag, Korovin (1934) pointed that in the composition of the main wood-bush forms they connect the rest forests of the Middle Asia with the maquis of the Mediterranean countries.

In correspondence with the said above we see that the landscapes, occupied by the Mediterranean species in the lower mountain staircase from 0 up to 600 m above the sea level on the Caucasus correspond the Black Sea and Daghestan refugia. Apparently these territories should be regarded in the limits of East-Mediterranean province in the narrow sense of this word as its exclaves. All other Mediterranean refugia of Caucasus occupy the more high mountain staircases, giving the place downstairs to the Iranian and Turanian elements. In the relation of Kuro-Araksian and Artvin refugia should be the more considered approach and differentiated estimation of the location of each of them in the Middle East, Anatolian or other biogeographic division correspondingly. Borkin (1986) pointed that the recent distribution of the herpetofauna on the Caucasus and other regions could be only the fragment of the former vast ranges.

In the conclusion it should be emphasized that the Mediterranean species on the Caucasus are character-

ized by autochthonous, antiquity and relictiness. Including of the number of refugia in the East Mediterranean *sensu stricto* and all Caucasus in the Mediterranean *sensu lato* seemed to be correct enough.

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