

**B.S. Tuniyev, N.L. Orlov,
N.B. Ananjeva, A.L. Aghasyan**

SNAKES OF THE CAUCASUS:

taxonomic diversity, distribution, conservation

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This book summarizes the results of snake research in the Caucasus and for the first time presents a checklist of snakes living in the Caucasus Ecoregion. It contains comprehensive information about the taxonomic and conservation status, type territories, distribution, and ecological patterns of 44 species of snakes. The monograph “Snakes of the Caucasus” represents a compilation of modern views on geographical and altitudinal distribution, habitat use, taxonomic and conservation status. The results of long-term research efforts undertaken by the authors in 1970–2018 during field works throughout the Caucasus are generalized with a special emphasis on assessment and conservation of this unique and diverse fauna. Present monograph accepts the geographical boundaries of the Caucasus Ecoregion as encompassing the territories of Armenia, Azerbaijan, Georgia, North Caucasus part of the Russian Federation, north-eastern Turkey and north-western Iran, as defined by Critical Ecosystem Partnership Fund (CEPF, www.panda.org/caucasus/cepf and www.cepf.net). The book is richly illustrated.

Б.С. Туниев, Н.Л. Орлов, Н.Б. Ананьева и А.Л. Агасян. Змеи Кавказа: таксономическое разнообразие, распространение, охрана. СПб.-М.: Товарищество научных изданий КМК, 2019. 276 с., 201 илл. + 47 карт.

Книга обобщает результаты исследований змей Кавказа, впервые приводится аннотированный список этих пресмыкающихся Кавказского экорегиона. В нем содержится детальная информация о типовых территориях, географическом распространении и экологических особенностях 44 видов змей. Монография «Змеи Кавказа» суммирует современные представления о географическом, высотном и биотопическом распространении, таксономическом и природоохранном статусе. Обобщены результаты оригинальных многолетних исследований авторов, собранные в 1970–2018 гг. во время полевых работ на всей территории Кавказа, акцентируется необходимость правильной оценки ресурсного и природоохранного значения этой уникальной и разнообразной фауны. В настоящей монографии географические границы Кавказского экорегиона приняты в соответствии с определениями CEPF (www.panda.org/caucasus/cepf) и охватывают территории Армении, Азербайджана, Грузии, северокавказскую часть Российской Федерации, северо-восток Турции и северо-запад Ирана. Книга богато иллюстрирована.

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Introduction

The Caucasus has always been one of the most alluring places for herpetologists. In spite of a long-term history of snake research in this Isthmus, many issues remain unclear ranging from taxonomic diversity of ophidiofauna, different views on taxonomic position and intraspecific structure of species to poorly studied biology of snakes living in the Caucasus.

Due to its geographical location, properties of landscapes and climates, and history of faunistic formation the Caucasus Isthmus has been acknowledged for an exceptional diversity of its flora and fauna.

Recognition of this fact and a clear understanding of biodiversity loss have driven the Critical Ecosystem Partnership Fund (CEPF), an organization dedicated to promotion of global conservation in biodiversity-rich areas, to designate the Caucasus Ecoregion in 2004. According to World Wide Fund for Nature (WWF), this region is among the world's 200 ecoregions containing biodiversity of global importance.

As to CEPF (www.panda.org/caucasus/cepf), the Caucasus belongs to 25 biodiversity hotspots which are biologically most diverse, but also most vulnerable to environmental degradation (Zazanashvili et al., 2004). These 25 hotspots are selected on a basis of species diversity per unit of area: covering only 1.4% of the Earth's land, they accommodate about 44% of all species of vascular plants and 35% of all species in four terrestrial groups (Meyers et al., 2000). Hence, the Caucasus has been globally perceived as a problem ecoregion with unique flora and fauna which is inhabited by rare, relict and endemic species and which has a global importance for preservation of our planet's biological diversity.

The Caucasus Ecoregion, historically considered as the isthmus between the Black Sea and the Caspian Sea, covers an area of 580,000 km² and comprises Azerbaijan, Armenia, Georgia, North Caucasus part of the Russian Federation, north-eastern Turkey and north-western Iran (Map 1). To reflect the fullness of biodiversity, five priority areas (corridors) are identified which contain the majority of threatened species and their relatively preserved distribution areas (Map 2). These are the corridors of the Greater Caucasus Ridge, western and eastern corridors of the Lesser Caucasus, Caspian and Hyrcanian corridors. The governments of

all countries of the Caucasus Ecoregion have joined important international conventions to reinforce their efforts in biodiversity conservation.

Investigations and correct formulation of conservation priorities in the Caucasus are in need of contemporary knowledge of taxonomic and ecological diversity of animal species and of understanding of trends in range structure of these species.

Snakes, order Serpentes Linnaeus (1758), is a unique group of terrestrial vertebrates. It is a big and diverse group of squamate reptiles, which is widely represented in the Caucasus. In the past decade, phylogenetic relationships within the families of typhlopidae, colubrid and viperid snakes were substantially reconsidered (Lee, 2005; Vidal et al., 2007; Vidal, Hedges, 2002, 2005; Pyron et al., 2010, 2013; Kelly et al., 2003, 2011; Hedges et al., 2014; Pyron, Wallach, 2014; Kornilios, 2017; Alenkar et al., 2016, 2017; Salvi et al., 2018). Over the decades that have elapsed since the regional monographs were published (Sobolevsky, 1929; Chernov, 1939; Bodenheimer, 1944; Muskhelishvili, 1970; Alekperov, 1978; Baran, 1976, 2005; Başoğlu, Baran, 1980; Latifi, 1991; Baran, Atatür, 1998; Demirsoi, 1996), many changes have occurred in interpretation of snake fauna, phylogenetic relationships between the species within a genus and at higher taxonomic levels, and the taxonomic status of many forms. In 1984–2018, a number of new species and subspecies of colubrids and viperids were described in the Caucasus (*Natrix megalcephala* Orlov et Tuniyev, 1987; *Coluber najadum albitemporalis* Darevsky et Orlov, 1994 (= *Platyceps najadum*); *Vipera wagneri* Nilson, Andren, 1984 (= *Montivipera wagneri*); *Vipera albicornuta* Nilson et Andren, 1985 (= *Montivipera albicornuta*); *Vipera darevskii* Vedmederja, Orlov et Tuniyev, 1986 (= *Pelias darevskii*); *Vipera raddei kurdistanica* Nilson, Andren, 1986 (= *Montivipera raddei kurdistanica*); *Vipera pontica* Billing, Nilson, Sattler, 1990 (= *Pelias pontica*); *Vipera lotievi* Nilson, Tuniyev, Orlov, Höggren et Andren, 1995 (= *Pelias lotievi*); *Vipera magnifica* Tuniyev et Ostrovskikh, 2001 (= *Pelias magnifica*); *Vipera orlovi* Tuniyev et Ostrovskikh, 2001 (= *Pelias orlovi*), *Pelias shemakhensis* Tuniyev, Orlov, Tuniyev et Kidov, 2013, *Pelias olguni* Tuniyev et al., 2013 and *Pelias sakoi* Tuniyev, Avcı, Ilgaz, Olgun, Petrova, Bodrov, Geniez

et Teynié, 2018. The new records of vipers and further studies were the basis for revision of interspecies structure of these species with description of new subspecies *Pelias shemakhensis kakhetiensis* Tuniyev, Iremashvili, Petrova et Kravchenko, 2018, *Pelias darevskii uzumorum* Tuniyev, Avci, Ilgaz, Olgun Petrova, Bodrov, Geniez et Teynié, 2018 and *Pelias darevskii kumlutasi* Tuniyev, Avci, Ilgaz, Olgun Petrova, Bodrov, Geniez et Teynié, 2018. New interesting records of colubrids and viperids were documented (Avci et al., 2004; Geniez, Teynie, 2005; Ilgaz et al., 2005; Tosonoğlu et al., 2007; Göçmen et al., 2007, 2011, 2014; Tuniyev et al., 2013, 2014, 2018; Çakmak et al., 2017, Iskenderov et al., 2017 and many others). This and other information, particularly that compiled by the authors, should be further analysed and understood as it was also highlighted in the resolution of the Workshop on Transboundary Cooperation in Research and Conservation of Herpetofauna of the Caucasus Ecoregion (St. Petersburg, 28–30 April 2005).

The new English-language edition monograph “Snakes of the Caucasus” compiles modern views on geographical and altitudinal distribution, habitat use, taxonomic and conservation status as well as new records of snakes within the Caucasus. It provides a full checklist of snakes living in the Caucasus summarizes the results of long-term original studies conducted by the authors in 1970–2018 throughout the Caucasus and puts a special emphasis on accurate assessment and conservation of this unique and diverse fauna. In this monograph, geographical boundaries of the Caucasus Ecoregion are accepted as defined by CEPF (www.panda.org/caucasus/cepf) (Map 1) with the regions of conservation priority and their corridors in the Caucasus Ecoregion (Map 2).

An amazingly rich diversity of venomous snakes in the Caucasus requires particular attention. Notably, viper diversity is represented by the key species of the Caucasus Ecoregion which live in its priority natural areas and thus manifest themselves as flagship and top-ranked species in international collaborative programs dedicated to conservation of critical ecosystems.

The monograph describes the characteristics of families and genera, delineates the distribution of genera, species and subspecies and, for the first time, indicates the status in compliance with the IUCN Red List of Threatened Species, Red Data Books of the countries of the Caucasus Ecoregion and the appendices of the Washington and Bern conventions. This book can be used as a reference guide about snakes of the Caucasus.

Information provided in it served the basic input for GPA-Global Reptiles Assessment database. The most comprehensive information on these species is presented in species accounts in <http://www.iucnredlist.org/> The region described in this monograph has been inhabited by 44 species of the order Ophidia belonging to 19 genera and 5 families.

Apart from their own materials and observations in the wild, the authors examined collections at Zoological Institute RAS, St. Petersburg (ZISP), Zoological Museum of Moscow State University (MGU), Sochi National Park (SNP), Zoological Museum of B. Khmelitsky National Museum of Science and Natural History, National Academy of Sciences of Ukraine (Ukraine, Kiev), Zoological museums in Berlin, Bonn and Hamburg, Germany (ZMB, ZMFK, ZMH), Natural History Museum, London, UK (BMNH), Muséum National d’Histoire Naturelle, Paris, France (MNHN), Zoological Museum of Göteborg University, Sweden (GUS), Swedish Museum of Natural History, Stockholm, Sweden (NHRM), Field Museum of Natural History, Chicago, USA (FMNH), Smithsonian National Museum of Natural History, Washington DC, USA (USNM), California Academy of Sciences, San Francisco CA, USA (CAS), Museum of Vertebrate Zoology at Berkeley, Berkeley CA, USA (MVZ), Royal Ontario Museum, Toronto, Canada (ROM), Institute of Biology CAS, Chengdu, China (CIB), the State Museum of Georgia (The Simon Janashia State Museum of Georgia), Tbilisi, Georgia (ZMT or NMG in Van Wallach et al., 2014), Adnan Menderes University Aydin, Turkey and Dokuz Eylül University, İzmir, Turkey (ZDEU); Scientific Center of Zoology and Hydroecology of National Academy of Sciences of Republic Armenia, Yerevan, Armenia (ZIRA); in the Museum National d’Histoire Naturelle of Paris, in the “Alcide d’Orbigny” collection (MNHN), and in the Centre d’Ecologie Fonctionnelle et Evolutive, in Montpellier, France (BEV); Philippe Geniez’s iconographical collection (PGe), Montpellier

Conservation status of species and territories were discussed and confirmed at the CEPF Workshop on Transboundary Cooperation in Research and Conservation of Herpetofauna of the Caucasus Ecoregion (St. Petersburg, 28–30 April 2005) and at the IUCN Global Reptile and Amphibian Assessment Workshop (Antalya, Turkey, 22–26 September 2008).

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The authors dedicate this book to the blessed memory of the great explorer of the Caucasus, our older colleague Ilya S. Darevsky.

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Chapter 1. PHYSIOGRAPHICAL OVERVIEW OF THE CAUCASIAN ISTHMUS

The Caucasus has been geographically considered as the isthmus between the Black Sea and the Caspian Sea which covers an area of 580,000 km² and gives

home to the nations of Armenia, Azerbaijan, Georgia, North Caucasus part of the Russian Federation, north-eastern Turkey and north-western Iran (Map 1).



Map 1. The map of the Caucasus Ecoregion.

It is a vast and physiographically complicated region represented by the mountain ridges of the Greater Caucasus and the Lesser Caucasus and by the marginal parts of the highlands of Asia Minor. Created by the opposite shifts of the East European (Russian) and Asia Minor plates, it is located in the eastern part of the Mediterranean Basin. A great foothill plain is spread to the north of the Greater Caucasus Ridge where it is bounded by the southern edge of the Russian Plain through the Kuma-Manych Depression. To the south, the Suram Ridge provides a linkage between the Greater Caucasus and the Lesser Caucasus. The latter then extends to the highlands of Asia Minor and northwestern Iran (Vereschagin, 1958).

The Greater Caucasus Ridge stretching over 1,500 km provisionally splits the Caucasus into the Ciscaucasus (or North Caucasus) and Transcaucasus (or South Caucasus).

The Caucasus has been a great alpine structure where the alpine belt extends from the Epi-Paleozoic Scythian Plate, a European brink of the Tethys Ocean, in the north to the Gondwanan relicts in the south. Structurally, it is divided into four zones, of which three [Ciscaucasian frontal tectonic troughs, meganticlinorium of the Greater Caucasus, Mesozoic-Kainozoic structures of the Transcaucasian massif (intermontane depressions and Adjara-Trialeti zone)] belong to the Crimean-Caucasian segment of the belt, and the fourth one (block-folded structures of the Lesser Caucasus) are a part of the Asia Minor and Iranian segment (Scherba, 1993).

The plains of the Ciscaucasus are spread from the Kuma-Manych Depression in the north to the Greater Caucasus in the south. The main orographic units are the Stavropol Upland (Mt. Strizhament, 831 m a.s.l.), laccoliths of Mineralnye Vody (18 isolated peaks, the highest is the Mt. Beshtau, 1,402 m) and the Tersko-Sunzhensky Upland (up to 926 m).

The system of the mountains of the Greater Caucasus consists of pivotal, front and transverse ridges and their branches. Its length is about 1,100 km and the largest width (ca. 180 km) is near the Mt. Elbrus (Milkov, Gvozdetsky, 1976). The Greater Caucasus has often been divided lengthways into the western, central and eastern parts whose boundaries go through the lines transecting the peaks of Elbrus and Kazbek.

The Central Caucasus is the highest and most glaciated, with the peaks over 5,000 m: Elbrus (5,642 m), Dykhtau (5,203 m), Koshtantau, Shkhara (5,068 m),

Kazbek (5,033 m) and others. The Vodorazdelnyi (Watershed) or Glavnyi (Main) and the Bokovoy (Lateral) mountain ridges are formed in the Central Caucasus by hard crystalline rocks.

The Western Caucasus is lower than the Central Caucasus (the highest peak is the Mt. Dombai-Ulgen, 4,046 m). The Vodorazdelnyi Ridge is crystalline, but the Bokovoy Ridge is mostly composed of Paleozoic sediments (Milkov, Gvozdetsky, 1976).

The Eastern Caucasus is lower than the Central Caucasus, but is higher than the Western Caucasus. Its summits are over 4,000 m: Tebulosmta (4,493 m) and Bazarduzu (4,466 m). The ridges are formed mainly by Jurassic shales.

The pivotal ridges of the Greater Caucasus are fringed to the north by generally lower front ridges and ranges. The highest is the Skalistyi (Rocky) Ridge (up to 3,646 m). In the Eastern Caucasus, the Glavnyi Ridge and the high massifs of the Bokovoy Ridge are separated by the rough area called Vnutrenniy (Inner) Dagestan which is underlain by the broad strata of hard limestones. The southern slopes of the Greater Caucasus, especially their western part, also encompass a number of front ridges and ranges: Gagarskiy, Aibga-Atsetuksky, Bzyb, Kodor, Svaneti, Lechkhumi, Rachin and, as a watershed between the Black Sea and the Caspian Sea, Suram (Likh). The highest of these ridges is the Svaneti Ridge with the summit of the Mt. Laila (4,010 m). The Kartli, Kakheti (Gombor) and other ridges branch off from the Suram (Likh) Ridge eastwards to the Alazani River (Gabrielyan, 1986).

At least four types of landscape altitudinal zonation have been recognized in the mountains of the Greater Caucasus. The West Caucasian type (west of the northern slope) is characterized by broadleaf forests with some Colchic species which are substituted at higher elevations by coniferous forests, mountain meadows and the low-lying nival belt. In the West Caucasian or Colchic type, the lower subtropical zone is represented by relict Colchic forests with lush evergreen understory and shrubs. The transition of altitudinal and landscape belts is similar to that in the northern slope of the Western Caucasus, but occurs at higher elevations. The East Caucasian type (east of the northern slope) contrasts by the appearance of dry mountain grasslands (semi-deserts in foothills), sibiljak and xerophytes, sharp shrinkage of forest belts, almost complete disappearance of coniferous forests (with only some pine stands present), expansion of mountain meadows and higher position of

the nival belt. In the East Caucasian type (east of the southern slope), lower elevations are covered by semi-deserts in the extreme east, arid sparse forest and secondary grasslands in the west. Over heights, broadleaf forests with Colchic and Hyrcanian relict plant species have been replaced by subalpine and alpine meadows and, on top elevations, by the nival belt.

The Transcaucasian Depression separated by the Dzirul massif (Likh Ridge) consists of the Colchic (Rioni) Lowland in the west and the Kuro-Arax Lowland in the east. This depression isolates the Lesser Caucasus and the Armenian Highland from the Greater Caucasus.

The Lesser Caucasus is represented by the marginal ridges of the Transcaucasian (Armenian) Highland fringing its inner part from the north and north-east (Milkov, Gvozdetsky, 1976). These ridges are the Meskheta (Adjara-Imereti or Adjara-Akhaltzikhe), Trialeti, Arsiani, Shavsheti, Erusheti, Somkheta, Bazum (Bzovdag), Pambak, Murguz (Miapor), Shakh-dag, Mrovdag, Karabakh and, partly, Zangezur. Many ridges are higher than 3,000 m, with the main peaks of Gyamysh (3,724 m), Arsian (3,165 m), Tezhler (3,101 m) and Khalab (3,016 m).

The western part of the Lesser Caucasus is formed by the Meskheta Ridge and the Trialeti Ridge of total length 259 km (Gabrielyan, 1986) which belong to the Crimean-Caucasian segment of the alpine belt and are shaped by sedimentary flysch and volcanic rocks (Scherba, 1993). The highest peaks are the Mt. Mepitskaro (2,850 m) in the Meskheta Ridge, Mt. Shaviklde (2,850 m) and Mt. Ardjevan (2,759 m) in the Trialeti Ridge. Altitudinal zonality of this part of the Lesser Caucasus is similar to that of the Colchic region, but it is not affected by limestone substrates and does not have the nival belt. According to Milkov and Gvozdetsky (1976), it is the Adjarian sub-type of the Colchic type of altitudinal zonality. The central and eastern parts of the Lesser Caucasus are geologically dominated by Mesozoic sediments with a significant contribution of volcanogenic facies and numerous intrusive bodies (Milkov, Gvozdetsky, 1976). Foothills are covered mainly by sibiljak and arid forests. In the middle elevations, there are broadleaf forests on the northern slopes and sibiljak with mountain grasslands on the southern slopes which merge with mountain grasslands of the Armenian Highland. The subalpine and alpine belts are patchily distributed in the highest parts of the ridges and experience aridization towards the east.

The central part of the Lesser Caucasus is represented by a complex of curtain-like ridges serving as a

watershed between the Kura and Arax basins, of total length 310 km (Gabrielyan, 1986). Different parts of this watershed ridge are named, from west to east, as Shirak, Pambak, Areguni-Sevan (Shakhdag), Mrovdag. The highest peak of this area is the Mt. Gyamysh (3,724 m). The Bazum, Khalab, Ijevan and Miapor (Murguz) ridges reaching the height of 3,000 m (Mts. Urasar, Murguz) run parallel to these ridges.

The eastern part of the Lesser Caucasus comprises the Karabakh Ridge with the highest Mt. Beyuk-Kirs (2,725 m).

The Armenian (Javakheti-Armenian or Transcaucasian) Highland represents a 1,500–2,000 m high lava plateau and plains overhung by ridges of different orientations. It extends from the volcanic Javakheti Plateau in the west to the Karabakh Highland in the south-east. To the south, the Armenian Highland extends down to Mesopotamia. In the Caucasus Ecoregion, the highest peaks are the isolated Mt. Aragats (4,090 m) and the summit of the Zangezur Ridge, Mt. Kaputjikh (3,904 m). The Agridag Ridge and two magnificent extinct volcanoes (Mt. Greater Ararat or Masis, 5,165 m and Mt. Lesser Ararat or Sis, 3,914 m) are located to the south of the Arax River and mark the southern boundary of the ecoregion. Among the other numerous volcanoes, the most well-known are the Great Abul (Didi Abuli, 3,301 m), Arailer (2,577 m) and Ishkhanasar (Ishikhli, 3,552 m). Volcanic forms play a significant role in the relief of the highland. It has highly continental climate, so is marked by the Asia Minor type of landscape altitudinal zonality: semi-deserts of the lower belt are replaced by arid grasslands and phrygana, then by mountain grasslands and the subalpine belt. The nival belt is poorly developed, except for the Mt. Greater Ararat. The forest belt is either absent or fragmentary.

Some geographers distinguish the Arax blockfolded ridges or Near-Arax Lesser Caucasus. These ridges include the Eranos, Urts (Saray-Bulag), Vayk (Daralagez), Zangezur, Bargushat and Meghri. In Iran, the Zangezur Ridge extends into the Karadag Mts.

The Talysh Mts. consist of three longitudinal ridges with transverse branches. The main Alasher-Burovar Ridge reaches the height of the Mt. Kemurkey (2,477 m). The two other ridges, Peshtasar and Burovar, form the front ranges. This is the north-western part of the Alborz system whose direct linkage with the folded structures of the Lesser Caucasus was cut off in the beginning of the Upper Pleistocene because of formation of the tectonic trough of the Lower Arax (Gadjiev, 1986). These

mountains are formed by flysch and volcanogenic paleogenic strata and by intrusions of basic rocks. The Talysh Mts. differ from all the Transcaucasus by unusual altitudinal distribution of precipitation: it is most abundant in the lower and middle belts (1,500–1,700 mm) and above the heights of 1,500–2,000 m the amounts of precipitation sharply decrease to 300–400 mm (Gadjiev, 1986). For this reason, elevations below 500 m are covered by relict Hyrcanian forests which are then substituted by common Caucasian oak and beach-hornbeam forests spreading up to 1,800 m. Elevations from 1,900 m and higher are occupied by mountain xerophyte vegetation.

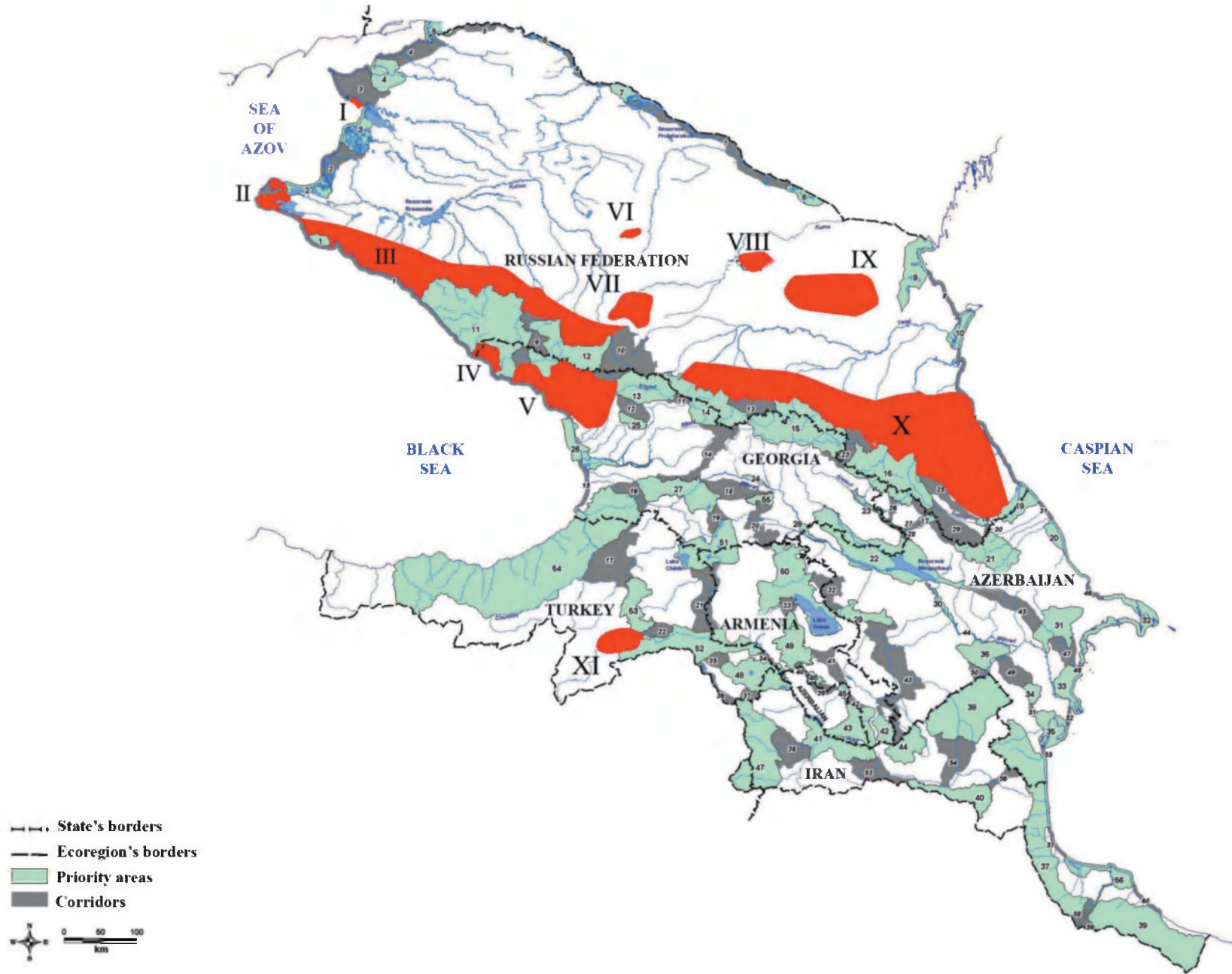
The Pontic Ridge in Turkey and the western part of the Alborz Mts. in Iran represent the marginal southwestern and south-eastern parts of the Caucasus Ecoregion. The western part of the Alborz Mts. is bounded by the rivers of Kyzyluzgen and Sefirud separating it from the central and eastern parts of the Alborz which extend to the left bank of the Atrek River. The highest peak of the western Alborz is the volcano Sebelan (4,821 m). The Talysh, northern slopes of the western Alborz and the South Caspian Lowland are covered by Hyrcanian landscapes. The coastline South Caspian Lowland stretches along the foothills as a 2–6 km wide strip, expanding up to 30–40 km in river deltas. Its coasts are straight, uniform and comprising the 200–400 m wide hardly accessible swamps along the strip of shoreline

sand dunes and beaches. Lagoons and swamps alternate with alder-wing nut and oak forests, fields and orchards.

The Pontic (Lazistan) Ridge extends between the mouths of the rivers of Ieshil Irmak and Çoruh. The Caucasus Ecoregion covers the eastern part of this ridge from the mouth of the Deirmen-Dere River near Trabzon to the Çoruh River. The highest peak is the Mt. Kaçkar (3,937 m). The most common landscape here is the Adjaro-Lazistan sub-type of the Colchic type of landscape altitudinal zonality.

So, the pattern of the Caucasus Ecoregion is very diverse. It encompasses a number of splendid mountain peaks, foothill plains and lowlands. Researchers of the Caucasus noted a unique neighbourhood of all altitudinal belts in a relatively small area. Vereschagin (1958) wrote that in a single day one can travel through all landscapes, from hot Caspian deserts at 28 m below sea level across the grasslands, lowland and montane forests, highland meadows up to the snowfields and glaciers at 4,000–5,000 m (Alisov, 1969). Such a diversity of landscapes and climates underlies the richness of biological diversity in general and of faunistic diversity in particular.

In this book, we consider the Caucasus within the boundaries delineated in the most recent guidelines of CEPF (www.cepf.net, map 1), including the priority conservation areas and corridors between them (Map 2).



Map 2. The regions of conservation priority and their corridors in the Caucasus Ecoregion (with our modifications highlighted in red).

Chapter 2.

A BRIEF HISTORY OF HERPETOLOGICAL RESEARCH IN THE CAUCASUS

The history of snake research in the Caucasus is closely linked with the general history of zoological and herpetological investigations in this region. In the early periods of regional studies, information about these vertebrates was not separated from strictly ophiological works. Therefore, we consider it reasonable to provide a synopsis of basic stages of herpetological research in the Caucasus.

The period of amphibian and reptilian studies in the Caucasus lasts over two centuries, beginning from the seminal works by J.A. GÜldenstädt and S.G. Gmelin, the Russian Academicians and travelers of the 18th century. In 1770–1773, J.A. GÜldenstädt explored the Ciscaucasus and a significant part of Georgia (GÜldenstädt, 1787) where he recorded 6 species of reptiles. In the same period (1769–1773), S.G. Gmelin undertook a great expedition to northern Iran and visited the Ciscaucasus, southern slopes of the East Caucasus and the Lenkoran Lowland. The collections of S.G. Gmelin (1785) also contained some species which were new to science: *Testudo caspica* (= *Mauremys caspica*), *Lacerta guttata* (= *Phrynocephalus guttatus*), *Lacerta deserti* (= *Eremias arguta deserti*). The great academic expeditions endeavoured in 1768–1774 by P.S. Pallas, I.I. Lepekhin, S.G. Gmelin, J.A. GÜldenstädt and J.G. Georgi, who surveyed a vast territory from the Black Sea coast to the Lake Baikal, had made a substantial contribution to investigations of the northern part of the Caucasus. The input made by P.S. Pallas was particularly outstanding, as in his monumental work “Zoo-graphia Rosso-Asiatica” (Pallas, 1811) he described 151 species of mammals, 425 birds, 11 amphibians, 41 reptiles and 241 fishes, many of them were described as new species. Apart from giving information about the distribution of a number of Caucasian reptiles, he also described the new species *Testudo ibera* (= *Testudo graeca ibera*), *Lacerta sanguinolenta* (= *Trapelus sanguinolentus*), *Coluber persa* (= *Natrix natrix persa*), *Rana verrucosissima* (= *Bufo verrucosissimus*) and others. In 1793, the explorer himself traveled along the

Caucasian fortified borderline from the delta of Volga to the Ciscaucasus where he visited Mineralnye Vody (Mineral Waters), then called the Wells of Alexander (Sytin, 1997).

In 1825–1826, a well-known Russian naturalist E.I. Eichwald surveyed the Ciscaucasus and the Transcaucasus where he made extensive collections, including those described later (Eichwald, 1831) as new species, such as *Gymnodactylus caspius* (= *Cyrtopodion caspius*), *Stellio caucasius* (= *Paralaudakia caucasia*), *Lacerta strigata*, *Trigonophis iberus* (= *Telescopus fallax iberus*), *Coluber najadum* (= *Platyceps najadum*), *Bufo colchicus* (= *Bufo verrucosissimus*).

Professor of Moscow State University I.A. Dvigubsky (1832) described 3 species of tortoises, 6 lizards and 12 snakes for the Caucasus (Fig. 1). He also suggested to name the Caucasian toad as *Bufo verrucosissima* as it was originally described by Pallas and had also provided the descriptions, thereafter forgotten, of *Coluber nigricollis* (= *Eirenis modestus* (Martin, 1838)), *Coluber rubriventer* (= *Elaphe hohenackeri* (Strauch, 1873) and *Coluber obtusus* (now *Macrovipera lebetina obtusa*). In 1830, a zoologist from St. Petersburg E. Ménétries was charged by the Academy of Sciences to undertake a big journey to Azerbaijan. He visited the Lenkoran district to explore the mountainous areas, deserts of Zuvand, forests of the Talysh Mts., coastal lowlands and the southern parts of the Mugan. The Salyan Steppe, Apsheron Peninsula (mostly around Baku) and, partly, northeastern area of Azerbaijan were investigated. The total list of amphibians and reptiles living in Azerbaijan composed by E. Ménétries included 33 species (Alekperov, 1978). His herpetological collections also contained some new species (Ménétries, 1832) still retaining their taxonomic identity: *Scincus bivittatus* (= *Ablepharus bivittatus*), *Ophisops elegans*, *Coluber ravergieri* (= *Hemorrhoids ravergieri*), *Coluber collaris* (= *Eirenis collaris*).

E.F. Eversmann (1834) had published an overview of lizard species known in Russia and described the

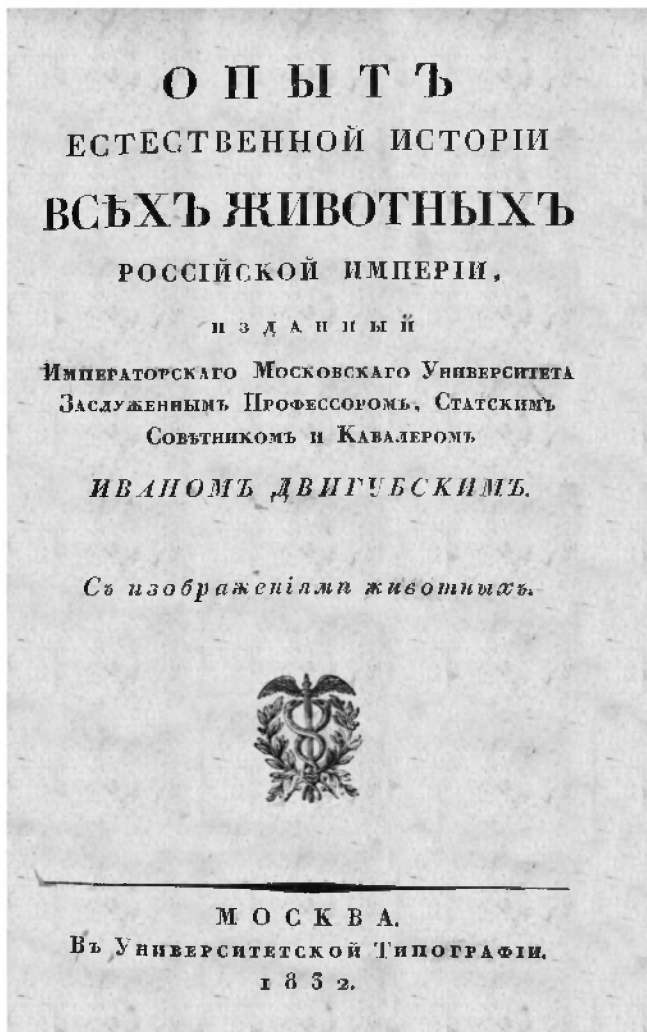


Fig. 1. Cover page of the book “Natural history of all animals of the Russian Empire. Reptiles” by I. Dvigubsky (1832).

new species, *Lacerta saxicola* and *Lacerta praticola*, from the Ciscaucasus. The description of the former species should be regarded as a starting point of the greatest zoological discovery of parthenogenesis in higher vertebrates in the group of the Caucasian lizards (Darevsky, 1967). Now, these lizards have been united into the genus *Darevskia* Arribas, 1997 (Ananjeva et al., 2006; Arribas et al., 2017). In the same period, a botanist R.F. Hohenacker explored the areas of Karabakh, Shirvan, Elizavetpol district and the Talysh Mts. and in 1834–1835 had made an extensive zoological collection which also included a number of previously unknown reptiles (Hohenacker, 1837). The materials of E. Ménétries and R.F. Hohenacker, as well as V. Mochulsky’s entomological collections from Nakhichevan, were later used by E.I. Eichwald

(1841) for his well-known monograph “Fauna Caspio-Caucasica” (Fig. 2).

A. Nordmann (1840) took a cruise to the Chernomorskaya (Black Sea) Province and gave descriptions of some Colchic reptiles, including *Otophis eryx* var. *colchica* (= *Anguis fragilis colchicus*), *Tropidonotus natrix* var. *colchica* (= *Natrix natrix persa*) and *Tropidonotus natrix* var. *nigra* (= *Natrix natrix scutata*).

In the late 1840s, some herpetological collections made by M. Wagner in the Arax riverside were processed by A. Berthold (Berthold, Wagner, 1850) and in Azerbaijan reptiles were collected by F. Buchse and A. Friche. The latter of these naturalists had made an interesting record of *Vipera ammodytes transcaucasiana* in the vicinity of Elizavetpol (Gyanja).

In 1862, an Italian explorer F. De Filippi took a voyage to northwestern Persia and also visited en route Georgia, Armenia and Azerbaijan (Nakhichevan), then entered Persia via Julfa. On a way back, from Persia to Russia F. De Filippi came into Astara, Lenkoran and Baku. The results of this trip included the two newly

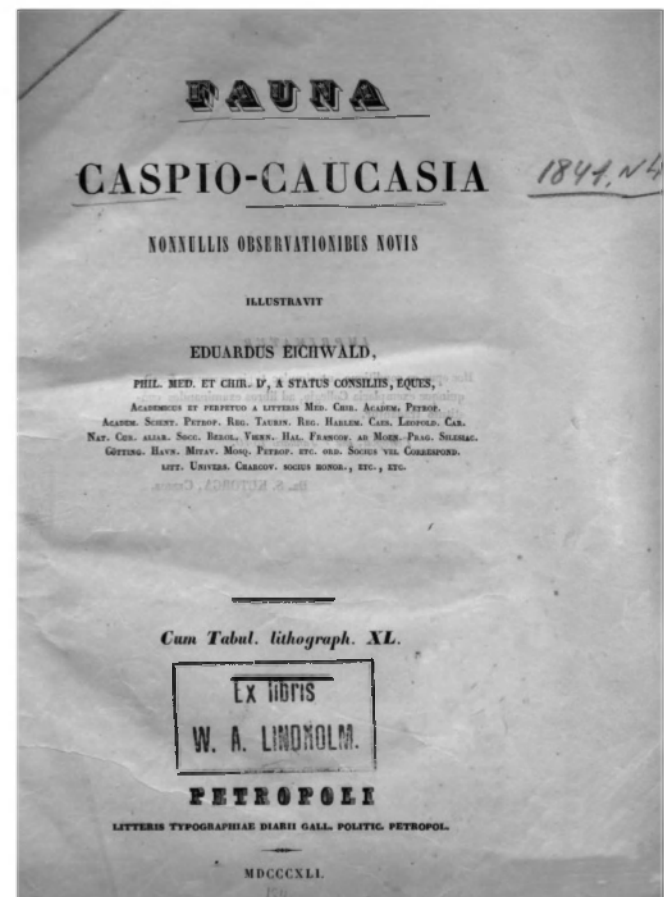


Fig. 2. Cover page of the book “Fauna Caspio-Caucasica nonnullis observationibus novis” by E. Eichwald (1841).



Fig. 3. Cover page of the book “Collections of the Caucasian Museum. Vol. 1. Zoology” by G. Radde (1899).

described lizards – *Lacerta brandti* and *Phrynocephalus persicus* (De Filippi, 1863).

An exceptionally important role in faunistic research in the Caucasus was played by the Caucasian Museum (now S. Janashia National Museum of Georgia, Tbilisi, Georgia) with its first director G.F.R. Radde who set it up in 1865 in Tiflis (now Tbilisi). In 1866 and 1870, G.F.R. Radde took two trips to the eastern and southeastern parts of Azerbaijan, and a year later together with G. Sievers had traveled into Armenia and Nakhichevan. In 1875, G.F.R. Radde visited southern Georgia and western Armenia. Herpetological collections made during these expeditions were delivered to the Zoological Museum of the Academy of Sciences and the Caucasian Museum, and then were partly examined by O. Schneider (1878). Detailed information about herpetological collections of the Caucasian Museum was published in 1899 in the volume “Collections of the Caucasian Museum” (Radde, 1899) (Fig. 3).

Limited knowledge about snakes of the Russian Empire and the Caucasus in particular was significantly systematized owing to the monograph “Die Schlan-

gen des Russischen Reichs” published by Academician A.A. Strauch (1873) (Fig. 4) who founded the St. Petersburg scientific school of herpetology and worked as director of the Zoological Museum, Imperial Academy of Sciences in 1879–1893. L.Ya. Borkin (2003) in his essay about the development of herpetology in Russia, associated the name of this distinguished scientist with the shaping of herpetology as an independent scientific discipline. He divided this period into two stages, the first of which was called after A.A. Strauch (Fig. 5). A.A. Strauch indicated 21 species of snakes living in the Caucasus, including a new rat snake species *Coluber hohenackeri* (= *Zamenis hohenackeri*). He also wrote the first overview of viperids (Strauch, 1869) (Fig. 6). A similar fundamental role for Caucasian lacertids was played by the monograph of a famous Russian herpetologist Ya.V. Bedriaga (1886) which was published a decade later with descriptions of the new species *Lacerta paradoxa* (= *Lacerta agilis grusinicus* Peters, 1960) and *Lacerta depressa rudis* (= *Darevskia rudis*).

“A systematic list of reptiles and amphibians of the Caucasus region” written by a renowned Russian zoologist K.F. Kessler (1878) is a reputed work in herpetological lit-

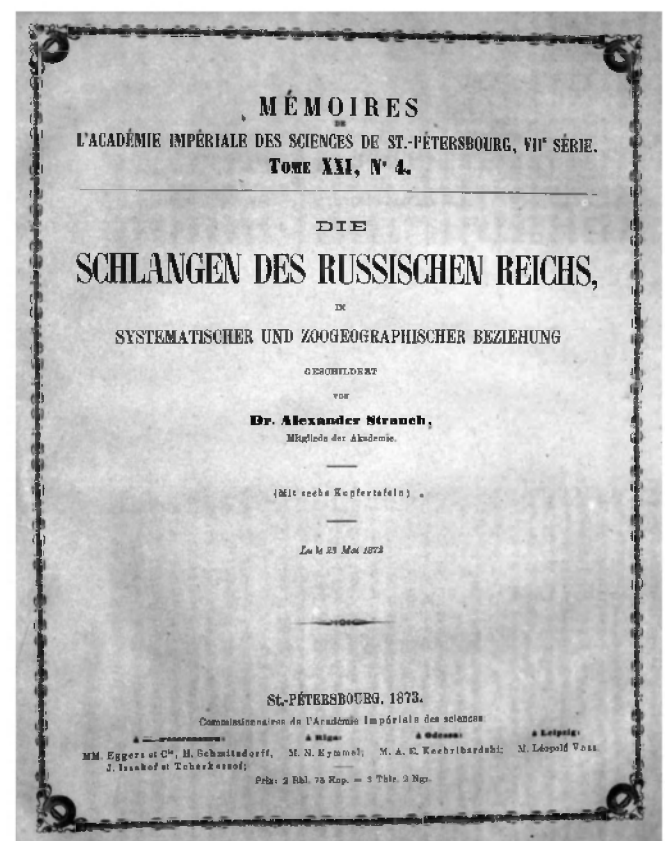


Fig. 4. Cover page of the book “Die Schlangen des Russischen Reiches” by A. Strauch (1873).



Fig. 5. Portrait of Academician A. A. Strauch.

erature about the Caucasus. This list was incorporated to his “A journey to the Transcaucasus for zoological purposes” as a separate chapter. In spite of relatively small amounts of his own collections, K.F. Kessler had made a substantial input by processing and generalizing information provided by O.A. Grimm, I.A. Porchinsky, M.N. Bogdanov and P.K. Stefanovich which was collected from different parts of the Caucasus Isthmus and stored at St. Petersburg State University. A new species *Lacerta portschinskii* (= *Darevskia portschinskii*) was described in this work.

In the 1870–1880s, reptiles of the Caucasus isthmus had been collected by A. Brandt, I. Polyakov, S. Zelinsky, N. Nasonov, K.M. Baer, P.R. Freiberg and N.A. Zarudnyi. A part of these materials delivered to the Zoological Museum of the Academy of Sciences was later identified by A.A. Strauch (Bogdanov, 1888) and the collections sent to the Zoological Museum of Moscow State University were mentioned by N.M. Kulagin (1888) in his “Lists and descriptions of the collections of reptiles and amphibians of the museum”. During the same peri-

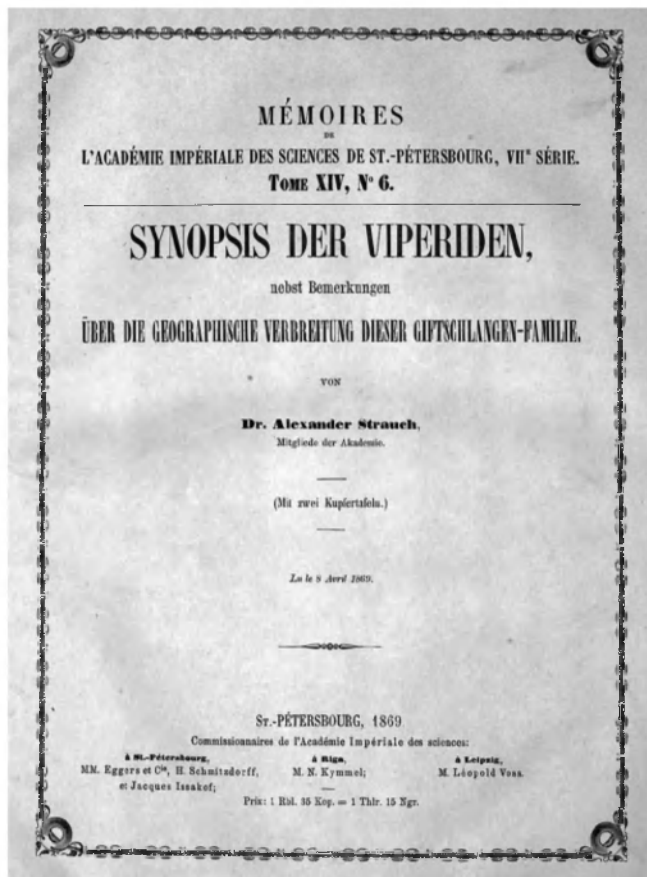


Fig. 6. Cover page of the book “Synopsis der Viperiden, nebst Bemerkungen über die geographische Verbreitung diese Giftschlangen Familie“ by A. Strauch (1869).

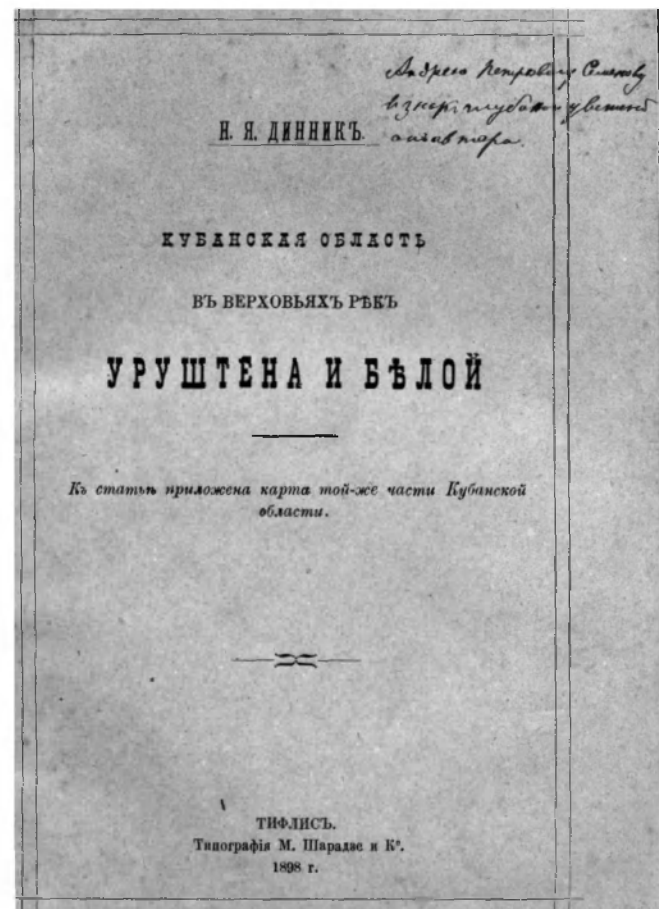


Fig. 7. Cover page of the book “Kuban Region in the upper Urushten and Belaya rivers“ by N.Ya. Dinnik (1898).

od, after the Caucasian war in 1864 herpetological studies began in the northwestern parts of the Ciscaucasus, the only *terra incognita* in the region. The first collectors were N.Ya. Dinnik (1898) (Fig. 7), K.N. Rossikov (1890), A. Bryansky, A.M. Zavadsky, G.Kh. Shaposhnikov, E. Utner, I. Bezukh, V. Konstantinov, D. Volnukhin, P. Vinogradov-Nikitin, S.F. Tzarevsky (1915a,b,c; 1916) and others. Their collections have been stored at the Zoological Museum of the Russian Academy of Sciences, Zoological Museum of Moscow State University and S. Janashia Museum of Georgia.

In 1888, the Council of the Imperial Russian Geographical Society had commissioned its member K.N. Rossikov (1890) to carry out zoogeographical research in the western part of the Ciscaucasus and in the headwaters of the Bolshaya (Greater) Laba River. This explorer had described a number of interesting records of amphibians and reptiles, including the species which had later gone extinct due to landscape changes (Fig. 8).

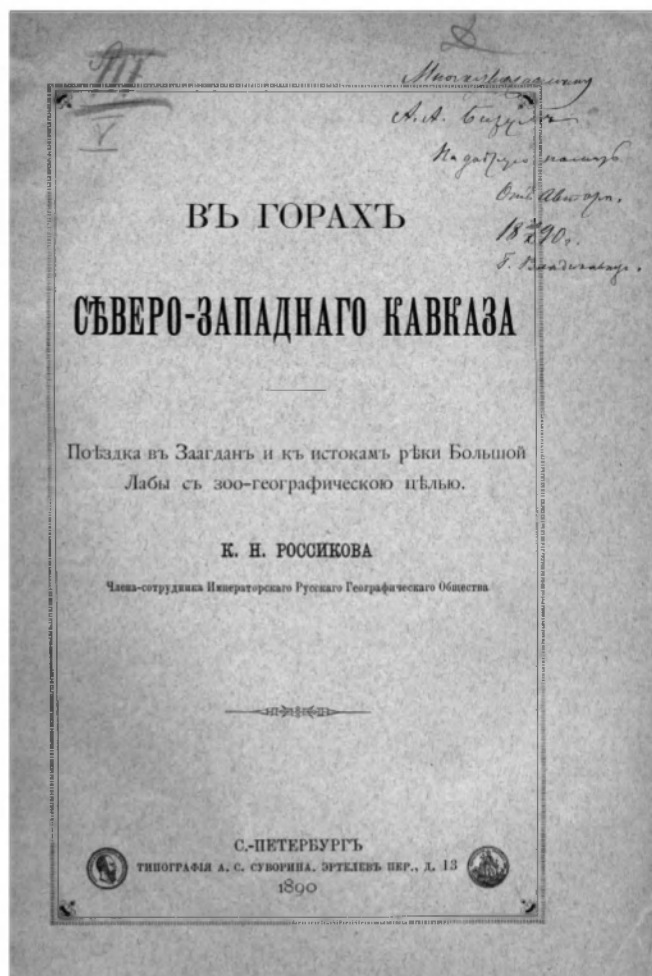


Fig. 8. Cover page of the paper “In the mountains of the north-western Caucasus” by K.N. Rossikov (1890).

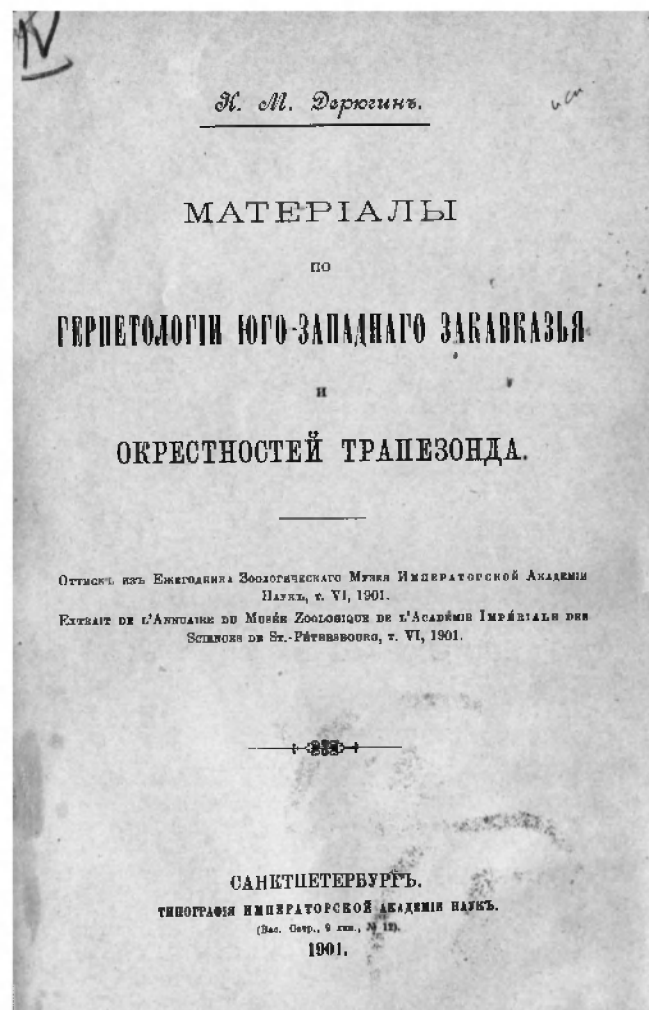


Fig. 9. Cover page of the paper “Materials on the herpetology of southwestern Transcaucasia and the vicinity of Trapezond” by K.M. Deryugin (1901).

Among the expeditions undertaken in the late 19th century, one of the most important was a zoological trip ventured by K.M. Deryugin to the Çoruh area of the southwestern Transcaucasus which is now a part of Turkey. K.M. Deryugin (1899, 1901) (Fig. 9) had supplied some new data about species distribution and indicated 3 tortoises, 23 lizards [including a new *Lacerta derjugini* Nikolsky, 1898 (= *Darevskia derjugini*)] described from his collections] and 23 snakes in his “A systematic list of amphibians and reptiles occurring in the Caucasus and Transcaucasus”.

Some herpetological collections made by a Crimean zoologist O. Retovsky on the Black Sea coast of the Caucasus and Turkey were later processed by O. Boettger who also studied G.F.R. Radde’s and G. Leder’s collections of 1880 from Lenkoran (Boettger, 1886) and G.F.R. Radde’s and I. Valentin’s materials of 1890

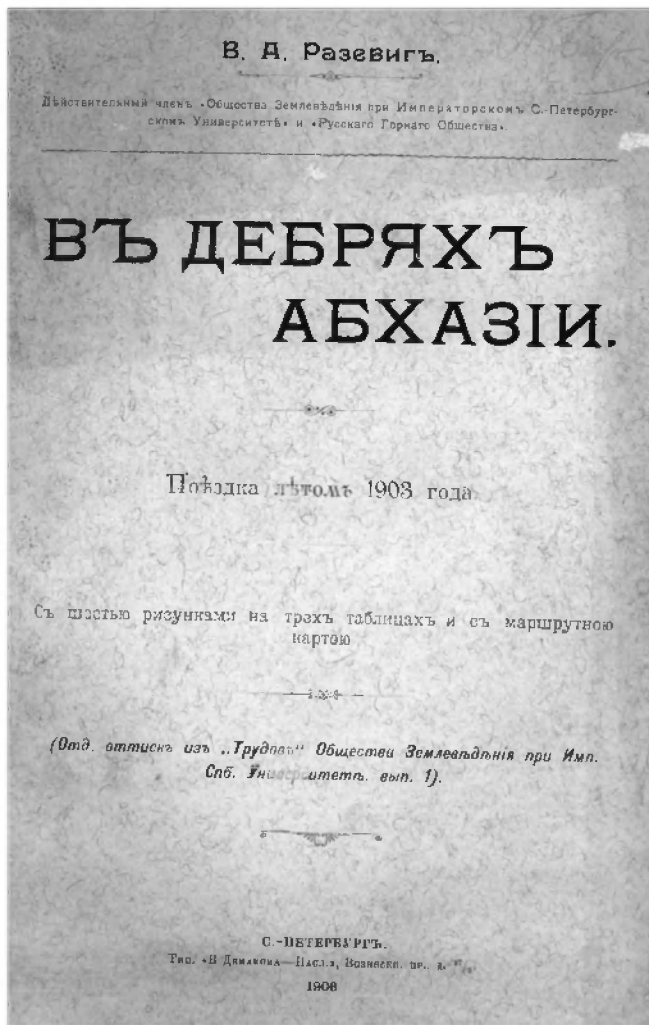


Fig. 10. Cover page of the paper “In the deep forests of Abkhazia. A trip of summer 1903” by V.A. Rasewig (1906).

from Karabakh, Nakhichevan and Armenia (Boettger, 1892). All these collections have been maintained at the Senckenberg Museum of Frankfurt am Main (Boettger, 1893, 1898). O. Boettger described a number of new species, particularly *Cyclophis modestus* var. *punctatolineata* (= *Eirenis punctatolineatus*) and *Lacerta muralis* var. *valentini* (= *Darevskia valentini*). Collections of that period which were provided to the Zoological Museum of the Academy of Sciences were made in the eastern Transcaucasus by I. Porchinsky, A. Becker, N. Zarudnyi, A. Kaznakov and others.

A notable input to the studies of reptiles of the Caucasus was made in the 1880–1890s by a ranger of the Lagodekhi Reserve L.F. Mlokosiewicz and the well-known Caucasian zoologists A.B. Shelkovnikov and K.A. Satunin. The most productive were K.A. Satunin’s trips to the Arax riverside in 1893 and 1894 when he found the

species new to the Caucasus: *Mabuia aurata* (= *Trachylepis septemtaeniata transcaucasica*) and *Contia satunini* (= *Rhynchocalamus melanocephalus satunini* Nikolsky, 1899). Collections made by these researchers partly entered the Zoological Museum of the Imperial Academy of Sciences and partly were delivered to the Caucasian Museum in Tiflis. Huge herpetological collections stocked by the end of the 19th century were processed by O. Boettger and published by G.F.R. Radde (1899) in the first volume of “Collections of the Caucasian Museum”. In 1903, a trip was undertaken by V.A. Rasewig (1906) to study the flora and fauna of Abkhazia (Fig. 10). From 1892 to 1906, A.B. Shelkovnikov studied the behavior of reptiles and amphibians in the Geoktepe, Aresh district (Shelkovnikov, 1910) (Fig. 15) and in the summer of 1911 he took a trip to Svaneti (Shelkovnikov, 1913). The works by L. Mehely (1894), V.O. Elpatjevsky (1902) (Fig. 11), Sabanejew



Fig. 11. Cover page of the paper “On relationships between the species *Contia modesta* Mart. and *Contia collaris* Mén” by V. Elpatievsky (1902).

(Elpatjevsky, Sabanejew, 1906) (Fig.13), Zugmayer (1906) and A.F. Laister (1908a,b, 1909, 1912) (Fig. 12) appeared in almost the same period and described different issues of the herpetofauna of the Transcaucasus. L. Mehely described a new subspecies *Phrynocephalus helioscopus horvathi* Mehely (= *Phrynocephalus persicus*) from the collections made by G. Horvath in southern Armenia a year earlier. Expeditions of A.B. Shelkovnikov which began in the late 1890s in Azerbaijan continued in 1905 when he together with R. Schmidt and A. Kaznakov took a voyage over the northern parts of Armenia and the adjacent areas of western Azerbaijan. Later, in 1906 he visited the Zuvand region. Collections, including a species *Lacerta parva* Boulenger from the shoreline of the Lake Sevan which was new to the Caucasus, were delivered to the Caucasian Museum and identified later by A.M. Nikolsky (1909a). In almost the same period, A.A. Silantiev (1903) and A.A. Brauner (1903, 1905) (Fig. 13)

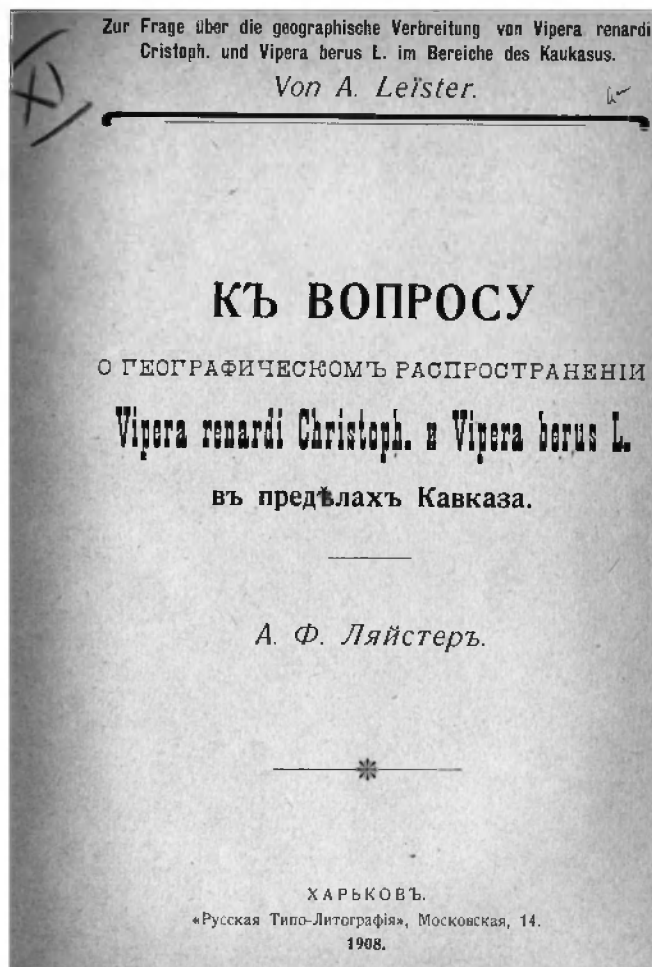


Fig. 12. Cover page of the paper “On the geographical distribution of *Vipera renardi* Christoph and *Vipera berus* L. in the Caucasus” by A.F. Leister (1908a).

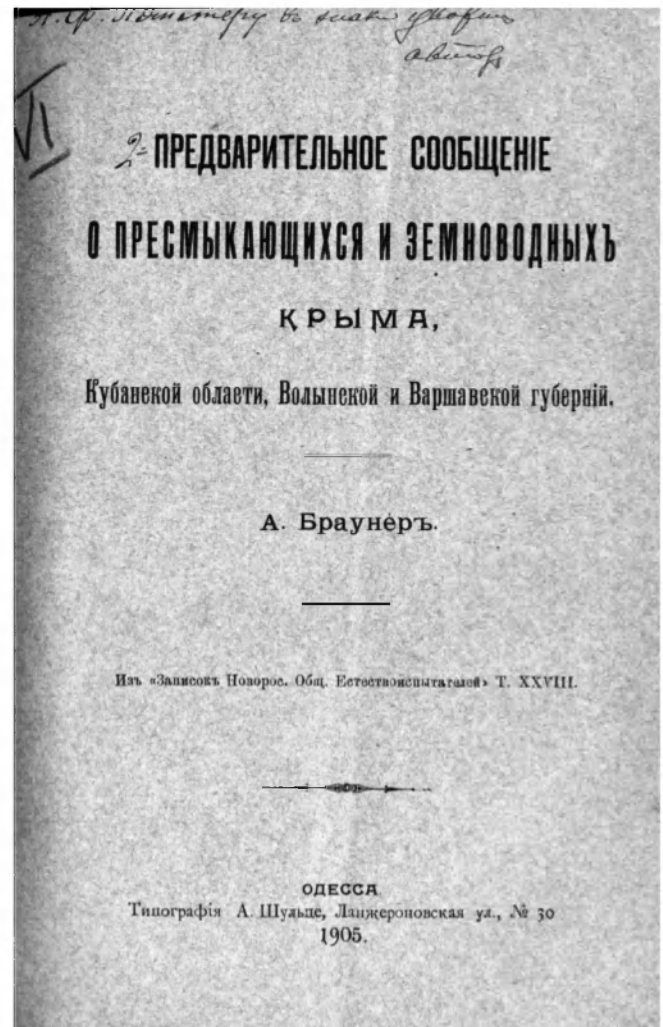


Fig. 13. Cover page of the paper “A preliminary communication on the reptiles and amphibians of the Crimea, Kuban Region, Volhynian and Warsaw Governorates” by A.A. Brauner (1905).

had published their materials about the herpetofauna of the Black Sea coast of the Caucasus and the Kuban Region.

In 1905, A.M. Nikolsky published his first compilation “Reptiles and amphibians of the Russian Empire” which summarized all information available by that time on the herpetofauna of the Caucasus.

A review of A.M. Nikolsky’s work was made by K.A. Satunin (1906) in his article “On herpetological fauna of the Caucasus region” who, in general, assessed this monograph positively but indicated some inaccuracies related to the description of the Caucasus.

In 1909, a Hungarian herpetologist L. Mehely (1909) had published a monograph dedicated to the large group of Eurasian wall lizards previously unified under the name *Lacerta muralis*. The most important result of this revision was the rehabilitation of the spe-

cies status of *Lacerta saxicola* Eversmann (= *Darevskia saxicola*) described by E.F. Eversmann back in 1834 and the description of a number of new species and subspecies, such as *Lacerta caucasica* (= *D. caucasica*), *Lacerta mixta* (= *D. mixta*), *Lacerta saxicola gracilis* (= *D. daghestanica* Darevsky, 1967), *Lacerta saxicola* var. *brauneri* (= *D. brauneri*) and others (Mehely, 1909).

This work had spurred A.M. Nikolsky (1910a) to reconsider the system of Caucasian rock lizards. He also reviewed the Caucasian representatives of the genus *Eryx* (Nikolsky, 1910b) (Fig. 14) and described a new viper species *Vipera kaznakovi* (= *Pelias kaznakovi*) from the western Transcaucasus (Nikolsky, 1909b, 1910c), a new species of the genus *Contia* (= *Eirenis*) and a Caucasian subspecies of the viviparous lizard *Lacerta vivipara stenolepis* (Nikolsky, 1911) which is now considered as a synonym of *Lacerta* (= *Darevskia*) *praticola* (Mertens, Wermuth, 1960; Orlova, 1978a).

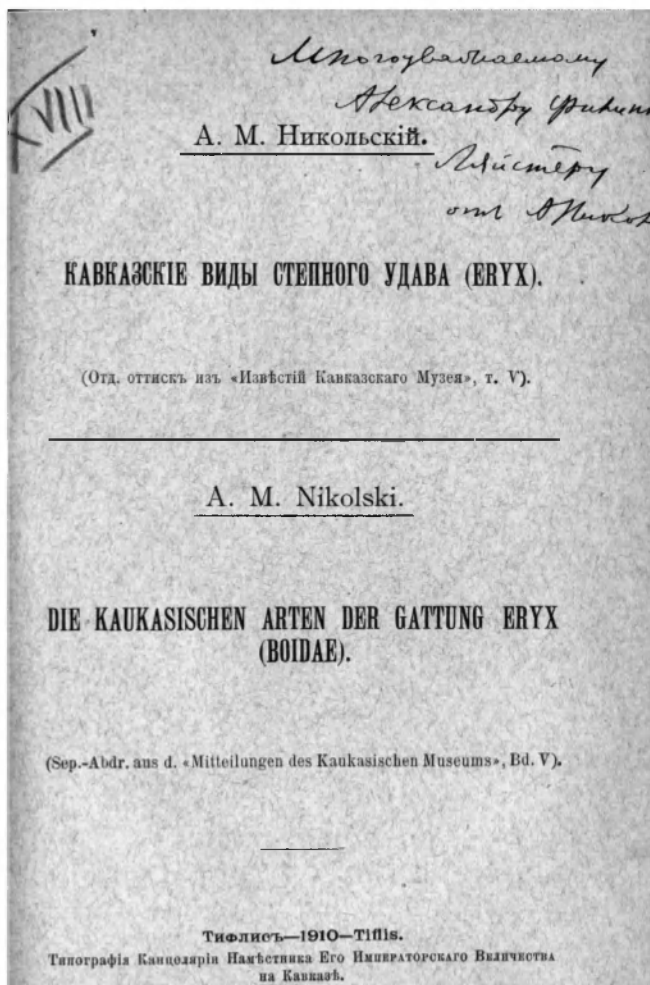


Fig. 14. Cover page of the paper “Die Kaukasischen Arten der Gattung *Eryx* (Boidae)” by A.M. Nikolsky (1910b).

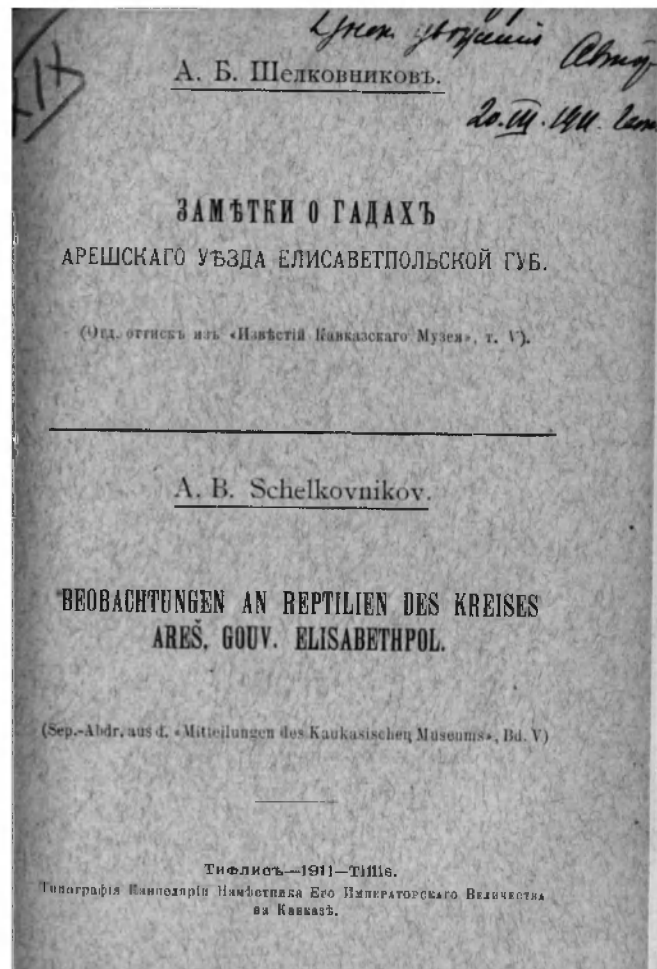


Fig. 15. Cover page of the paper “Beobachtungen an Reptilien des Kreises Areš, Gouv. Elisabethpol” by A.B. Shelkovnikov (1910).

In 1911, A.B. Shelkovnikov (1913) endeavoured a big journey to Svaneti where he had collected a series (3 individuals) of interesting vipers. They, along with an individual collected by N.Ya. Dinnik (1902) (“headwaters of the Malaya (Lesser) Laba River”), later underlay the description by A.M. Nikolsky (1913) of a form called *Vipera berus dinniki* Nikolski, 1913 (= *Pelias dinniki*). A year earlier, A.N. Kirichenko (1910) made a small collection of reptiles in the Talysh Mts. and published his herpetological observations.

A significant contribution to better understanding of the herpetofauna of the south-western Transcaucasus and the borderline areas of Asia Minor was made by expeditions of P.V. Nesterov in 1911–1912 who had described several lizards and snakes not indicated for these areas before (Nesterov, 1911a, b, 1912) (Fig. 16). In 1910–1914, L. Lantz and O. Cyren collected lizards in different parts of the Transcaucasus and then published a

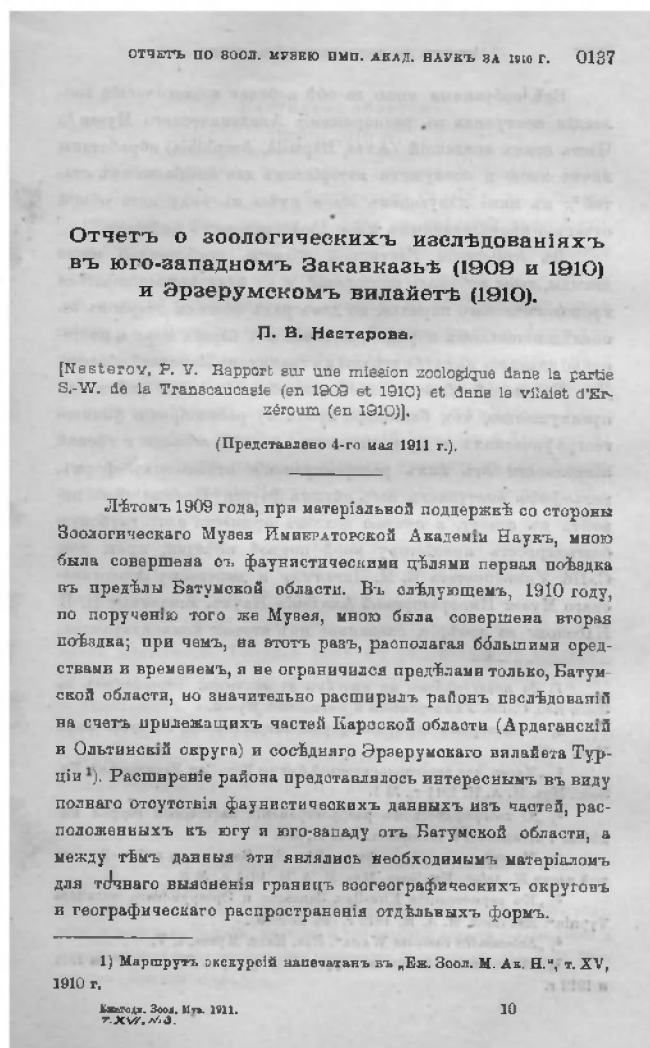


Fig. 16. Cover page of the paper “Report on zoological investigations in south-western Transcaucasus (1909 and 1910) and Erzerum Vilayet” by P.V. Nesterov (1911b).

series of special saurological works (Lantz, 1926, 1928; Lantz, Cyren, 1936, 1947). In 1914, P.V. Nesterov also traveled from the Persian Gulf along the Turkish-Iranian border and collected interesting herpetological materials in Kurdistan and Iranian Azerbaijan. P.V. Nesterov (1916) described the new species of tailed amphibians, *Rhithotriton derjugini* [(= *Neurergus microspilotus* (Nesterov, 1916)] and *Salamandra semenovi* (= *Salamandra salamandra semenovi* Nesterov, 1916). In the same year, S.N. von Vijk collected lizards in north-western Iran. His and Nesterov’s collections entered the Zoological Museum of the Academy of Sciences.

Some private studies of the herpetofauna of Georgia, Azerbaijan and Armenia were carried out in 1908–1914 by R.G. Schmidt (1909), B.A. Dombrovsky (1913), A.Sh. Shugurov (1914) (Fig. 17) and A.F. Leister (1908a, b). A.F. Leister (1912) had published

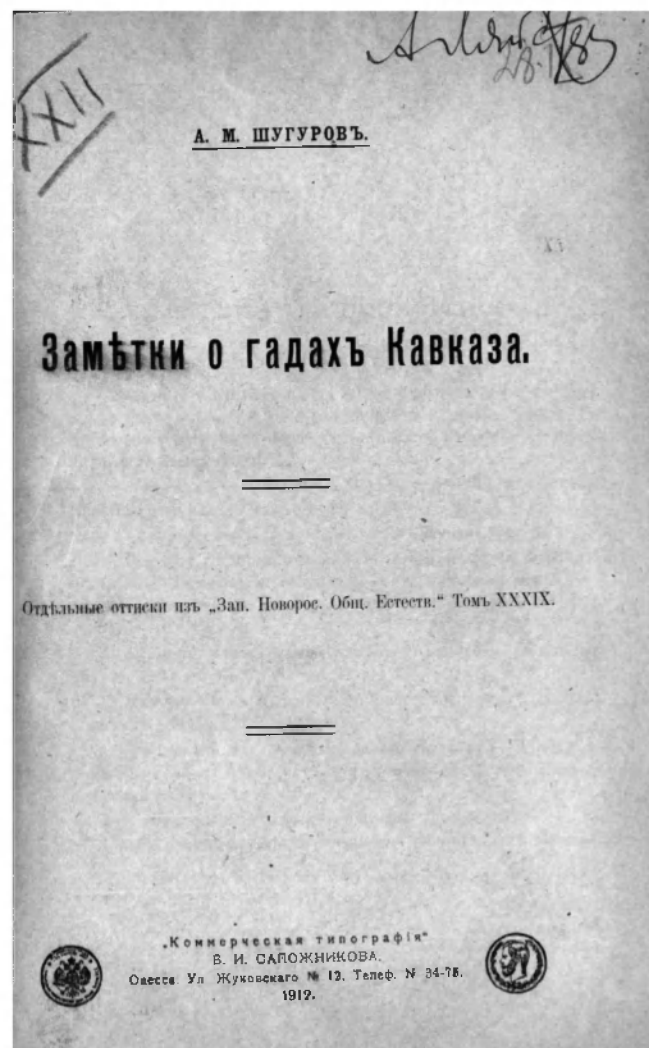


Fig. 17. Cover page of the paper “Notes on the reptiles of the Caucasus” by A.M. Shugurov (1914).

a compilation “Reptiles of the Erivan Province” based mostly on literature review.

An important event was the publication of the monograph “Reptiles and amphibians of the Caucasus” by A.M. Nikolsky (1913) which summarized the results of all herpetological research conducted in the Caucasus isthmus by that time. The author had particularly processed a rich collection of the Caucasian Museum, thus substantially expanding the list of reptiles known to live in the Caucasus and clarifying their distribution areas. As A.M. Nikolsky himself never visited the Caucasus, his monograph contained some mistakes, principally geographical ones, which were later criticized by K.A. Satunin (1916). S.F. Tsarevsky (1914, 1915a, b, 1916) worked on systematics of some Caucasian snakes and L.D. Moritz (1916a, b) wrote interesting notes on the herpetofauna of the Stavropol Region and all the Ciscaucasus.

As mentioned above, the monograph by A.M. Nikolsky (Fig. 18) was an immense contribution to herpetology of the Caucasus. The second stage of the development of herpetology as an independent science in Russia was linked with the personality of A.M. Nikolsky (Borkin, 2003 (Fig.19). In 1915–1918, he had published three volumes dedicated to reptiles and amphibians within the series “Fauna of Russia and adjacent countries” (Fig. 20). Information about the herpetofauna of the Caucasus in these volumes is almost the same as in his earlier monograph about the Caucasus.

The post-revolution changes (particularly, the establishment of republican academies of sciences and a wide network of universities) stimulated the rampant development of zoological studies which gradually enveloped all interesting parts of the Caucasus isthmus.

In the 1930–1940s, herpetological studies in the Ciscaucasus were carried out by K.V. Arnoldi, A. Bartenev, M. Reznikova, N.N. Sobolevsky, D.B. Krasovsky, Yu. Kostylev, B.V. Obraztsov,



Fig. 19. Portrait of A.M. Nikolsky. 1930.

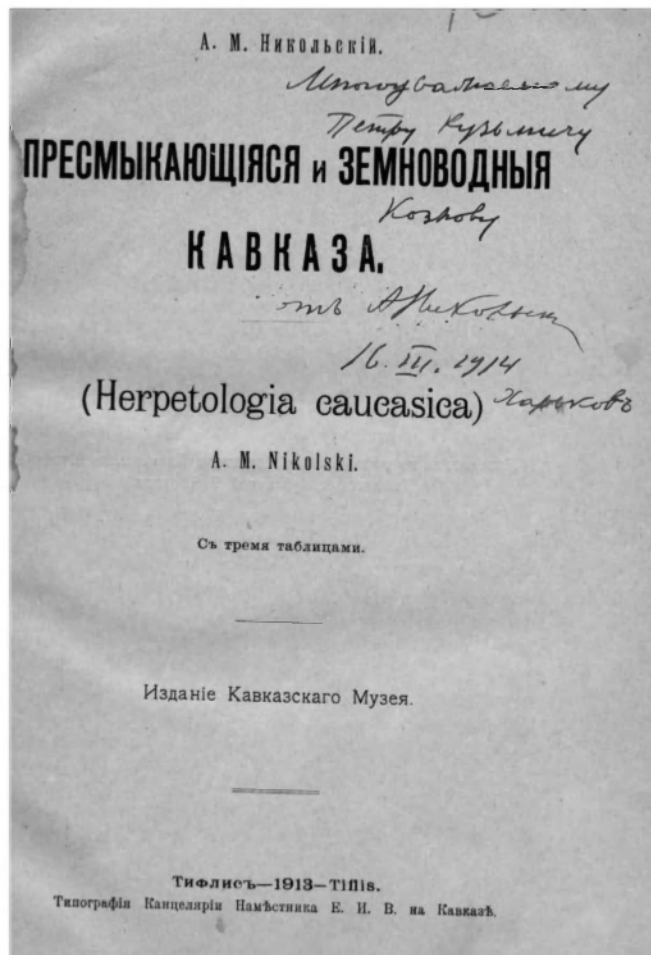


Fig. 18. Cover page of the book “The reptiles and amphibians of the Caucasus” by A.M. Nikolsky (1913).

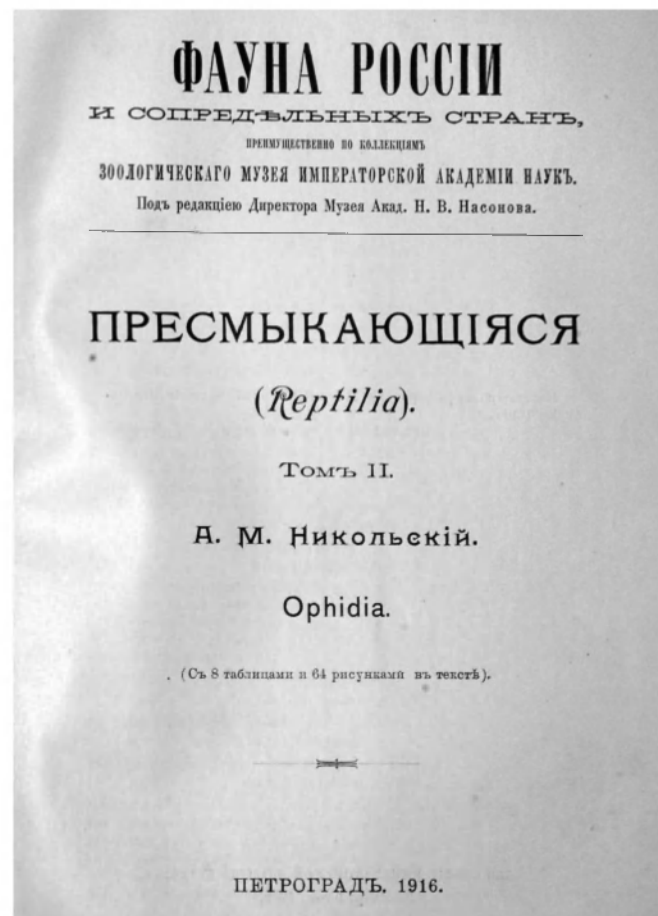


Fig. 20. Cover page of the book “The reptiles (Reptilia). Ophidia” by A.M. Nikolsky (1916).

L.I. Khozatsky, A. Gozhev, N.V. Shibanov and others. A number of eco-faunistic and biogeographical papers were published in this period (Dinnik, 1926; Terentjev, 1926; Böhme, 1928; Turov, 1928; Böhme et al., 1929 (Fig. 21); Chernov, 1929; Krasovsky, 1929, 1932, 1933; Sukhov, 1929; Leister, 1930; Bartenef, Reznikova, 1931, Bartenev, Reznikova, 1935; Shibanov, 1935 (Fig. 22); Krasavtsev, 1941, Krassawzeff, 1943). Particularly, N.Ya. Dinnik (1926) wrote an interesting review “Snakes of the Ciscaucasus”. D.B. Krasovsky (1933) described a new subspecies of the Caucasian toad *Bufo bufo turowi* (= *Bufo verrucosissimus turowi*). A. Bartenef and M. Reznikova had described a new species of the lizard *Lacerta plicata* and a new subspecies of the Artvin lizard *Lacerta derjugini silvatica* (Bartenef, Reznikova, 1931). *Lacerta plicata* later was confirmed to be a synonym of *Lacerta derjugini* (Mertens, Wermuth, 1960; Orlova, 1978b). These authors also found a local

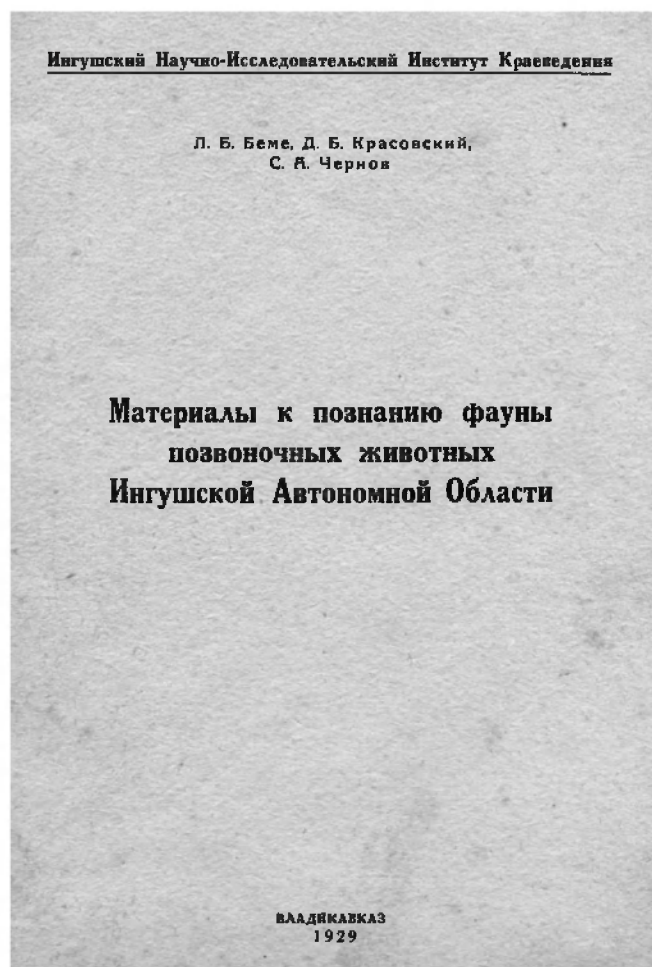


Fig. 21. Cover page of the paper “Materials on the vertebrate fauna of Ingush Autonomous Area” by L.B. Böhme, D.B. Krasovsky and S.A. Chernov (1929).

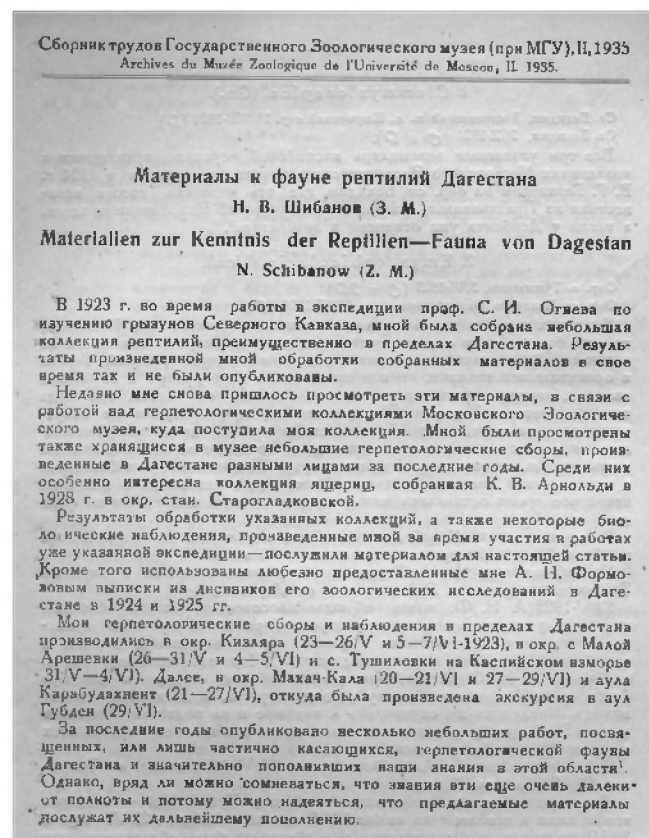


Fig. 22. Cover page of the paper “Materials on the reptilian fauna of Dagestan” by N.V. Shibanov (1935).

population of *Rana esculenta esculenta* (= *R. lessonae*) in the mouth of the Achipse River which still remains a zoological enigma as this is the only record of this taxon on the Black Sea coast and generally in the Caucasus far away from the main geographical range.

In Kavkazsky (Caucasian) Reserve, a hunting management station was established in 1934–1935 and a zoological station in 1936. Such distinguished zoologists as A.A. Nasimovich, I.V. Zharkov, S.S. Donaurov, V.K. Popov and others worked here in different times. In 1937 and 1940, their collections were delivered to the Zoological Museum of Moscow State University.

G.P. Barach (1925), V.N. Rostombekov (1930, 1939), S.A. Chernov (1926), A.V. Bogachev (1938) and P.S. Chanturishvili (1940) worked in the same period in the Transcaucasus. Of particular importance were the monographs “Herpetofauna of the Talysh and the Lenkoran Lowland” by N.I. Sobolevsky (1929) (Fig. 23) and “Herpetological fauna of Armenian SSR and Nakhichevan ASSR” by S.A. Chernov (1939) (Fig. 24). The works of these scientists had substantially expanded the existing knowledge about distribution,

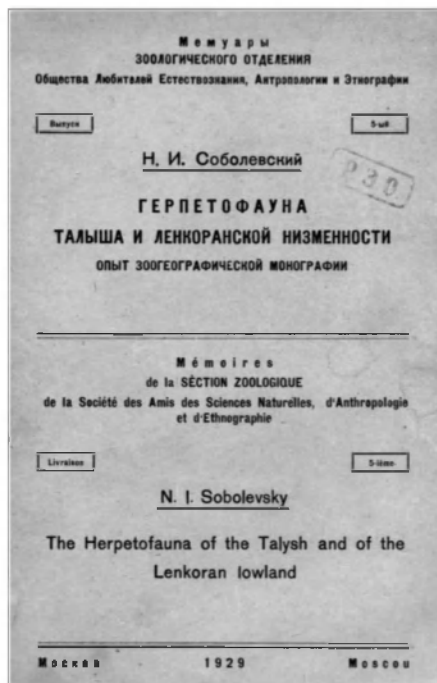


Fig. 23. Cover page of the paper “The herpetofauna of the Talysh and Lenkoran Lowlands (a zoogeographical monograph)” by N.I. Sobolevsky (1929).

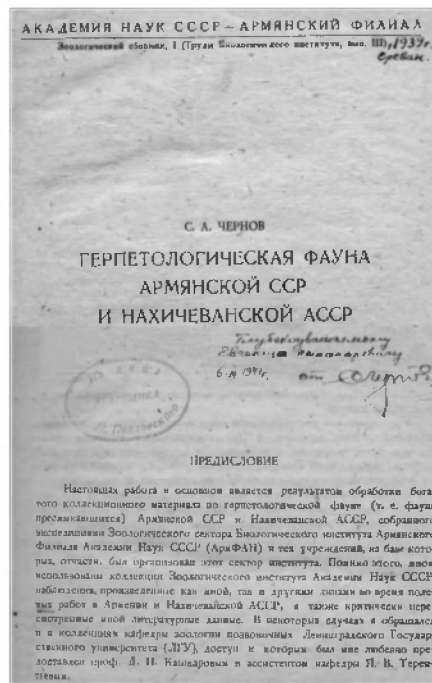


Fig. 24. Cover page of the paper “The herpetological fauna of the Armenian SSR and Nakhichevan ASSR” by S.A. Chernov (1939).

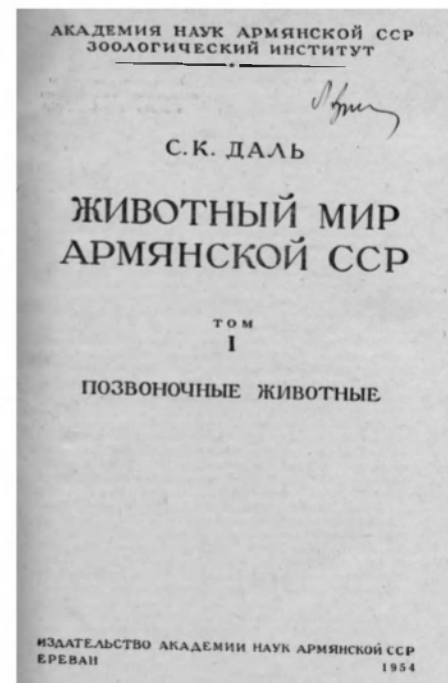


Fig. 25. Cover page of the book “The fauna of the Armenian SSR” by S.K. Dahl (1954).

systematic position and ecology of many poorly studied lizards, snakes and tortoises. The article “On the herpetology of Abkhazia” by R.P. Barach came out in 1925. Later, reptiles of this republic were described by V.N. Rostombekov (1939) and E.S. Milianovsky (1957), but as justly mentioned by T.A. Muskhelishvili (1970) none of these papers ensued from comprehensive research of the herpetofauna of Abkhazia.

Herpetological research in the Caucasus boomed in the 1940–1970s. Numerous eco-faunistic papers about reptiles of Armenia were published by S.K. Dal (1944–1953) who later summarized them in his monograph “The fauna of Armenian SSR” (1954) (Fig. 25). The volume of F.S. Bodenheimer (1944) about the herpetofauna of Turkey is still a valuable reference. W.B. Bischoff and V.E. Engelmann (1976) published some notes about their voyage across the Ciscaucasus and the Transcaucasus. The separate volume of the multivolume edition “The Animal World of the USSR, 1958” was devoted to the results of the study of the USSR mountain areas in which, in turn, in a special chapter on the Caucasus, reptiles were considered in a systematic review of animals of the Caucasian Isthmus including snakes (Vereshchagin, 1958).

In 1947–1966, ecology, systematic status and faunistic patterns of reptiles of Armenia were studied by I.S. Darevsky who, particularly, was the first to note the European lidless skink for the Caucasus (Darevsky, 1953). This skink is represented here by an endemic subspecies *Ablepharus kitaibelii chernovi* Darevsky, 1953 which is now reconsidered as a distinct species *Ablepharus chernovi* (Eremchenko, Scherbak, 1986). I.S. Darevsky also discovered *Psammophis lineolatus* in the Caucasus (Darevsky, 1959).

In 1949, enlarged third edition of “A Field Guide of reptiles and amphibians” was published (Fig. 26) which quite comprehensively generalized information about the taxonomy and distribution of the Caucasian species. This book produced by the classics of the Russian herpetology P.V. Terentjev and S.A. Chernov (Fig. 27) was considered by L.Ya. Borkin (2003) as a landmark between the two stages (1921–1949 and 1950–1964) of the development of herpetology in the USSR.

Research of the reptilian fauna of Georgia advanced through the studies conducted by A.G. Janashvili (1951), A.G. Janashvili and R.G. Zhordania (1977), E. Balavadze (1959), L.E. Kutubidze (1950), B.A. Negmedzianov (Negmedzianov, Bakradze, 1977),

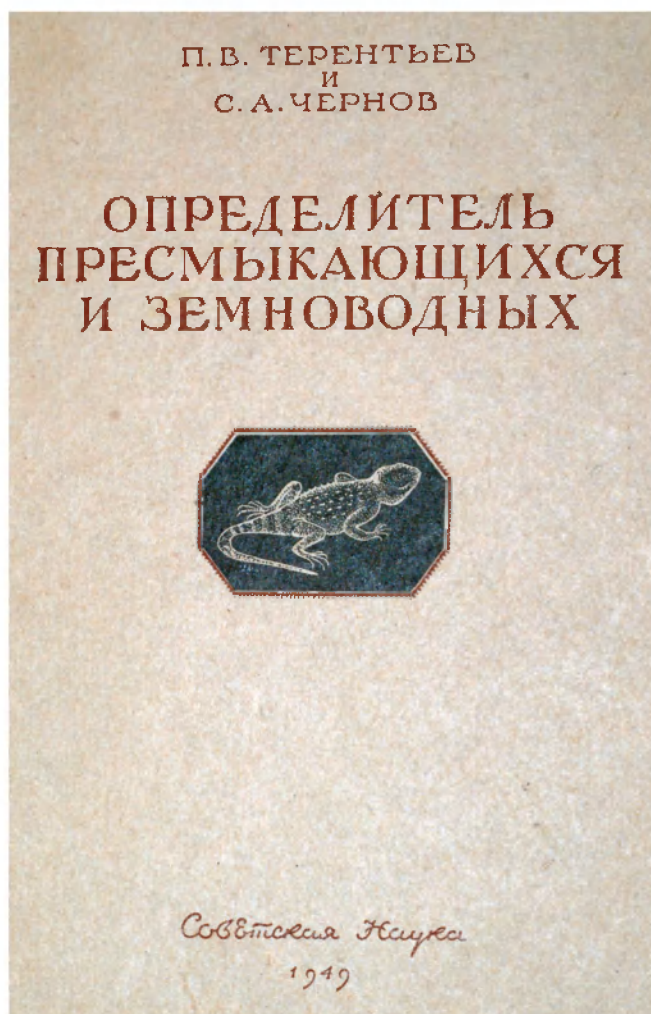


Fig. 26. Cover page of the book “A key to reptiles and amphibians” by P.V. Terentiev and S.A. Chernov (1949).

V.P. Pitshelauri (Pitshelauri, Bakradze, 1973; Pitshelauri, 1990) and other Georgian specialists. For many years the herpetofauna of this country had been studied by T.A. Muskhelishvili (1959, 1961, 1964) who published the basic results in his monograph “Reptiles of eastern Georgia” (1970) (Fig. 28). A notable input was also made by M.A. Bakradze who, particularly, discovered the Asiatic lidless skink *Ablepharus pannonicus* for the first time in the Caucasus (in Georgia) (Bakradze, Darevsky, 1973). Later this species was also found in Azerbaijan (Chegodaev, 1981). In the early 1990s, M.A. Bakradze and V.M. Chkhikvadze have compiled the checklist of amphibians and reptiles of Georgia (1992). The papers by N.M. Sirkmashvili (1967) and R.G. Zhordania (1960) apply to the same period. R.D. Jafarov wrote a paper about the herpetofauna of the Apsheron Peninsula (1948) after which he published a compilation “Reptiles of Azerbaijani SSR” (1949). The



Fig. 27. P.V. Terentiev and S.A. Chernov. Zoological Institute of the Academy of Sciences of the USSR. 1961.

long-term research of reptiles of Azerbaijan had been carried out by A.M. Alekperov whose articles published



Fig. 28. Cover page of the book “The reptiles of Eastern Georgia” by T.A. Muskhelishvili (1970).

in 1954–1976 (Aleksperov, 1958a, b, 1970, 1973, 1976) later underlay his monograph “Amphibians and reptiles of Azerbaijan” (1978) (Fig. 29). The herpetofauna of Azerbaijan is also described by Aleksperov et al. (1978, 1985), N.N. Drozdov (1964, 1966), F.G. Sharifov (1974), T.R. Aliev (1973, 1974, 1977, 1985, 1989), S.B. Akhmedov (1989), A.A. Chegodaev (1973), Yu.N. Aliguseinov (1981) and S.K. Jafarova (1981). E.V. Anisimova (1981) and G. Dusej (1989) studied geographical variation and sexual dimorphism of the smooth snake, including its Caucasian populations.

In the Ciscaucasus, in the 1960–1970s herpetological collections were made by N.P. Erofeev, I.M. Likharev, V.M. Smirin, I.S. Darevsky, M.A. Alkhasov, V.F. Orlova, V.A. Kireev, I.V. Shirokov, S. Tikhomirov, A. Kozlovsky, O.P. Bogdanov and others. Various regions of the Ciscaucasus were

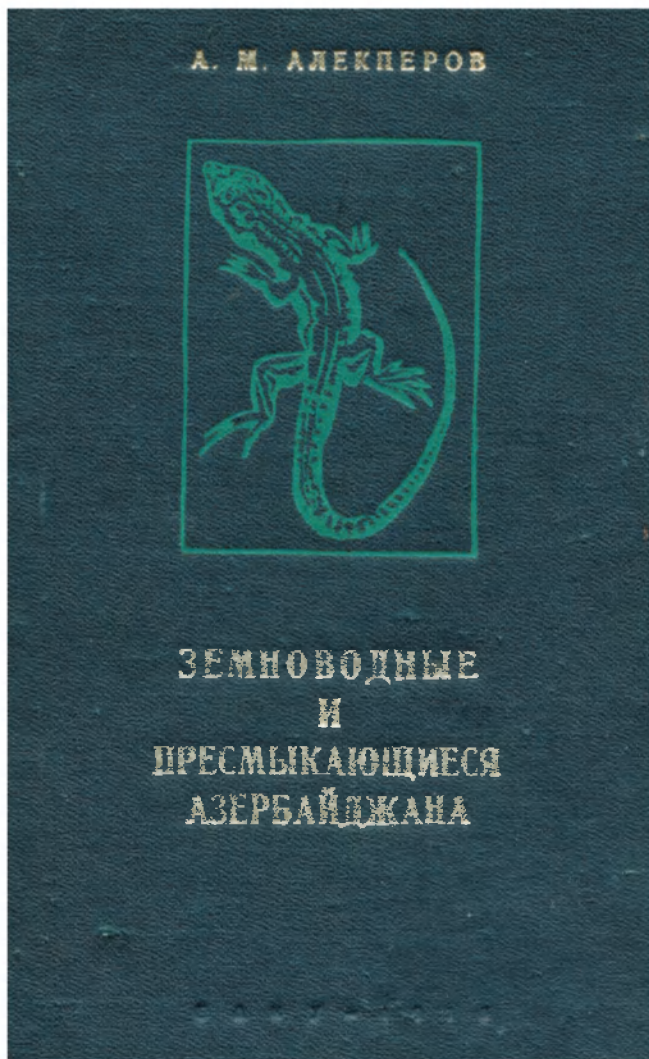


Fig. 29. Cover page of the book “The amphibians and reptiles of Azerbaijan” by A.M. Aleksperov (1978).



Fig. 30. I.S. Darevsky. 1989.

included in herpetological works of the zoologists M.A. Alkhasov (1981), Z.P. Khoniakina (1953, 1964, 1965, 1970, 1973), A.G. Bannikov (1951, 1954), V.I. Naniev (1978), N.N. Neemchenko and A.K. Tembotov (1959), S.M. Fedorov (1956), E.A. Shebzukhova (1967, 1973), M.F. Tertyshnikov and A.G. Vysotin (1987), M.F. Tertyshnikov (1992), V.F. Orlova (1973), V.A. Kireev (1973) and A.D. Karnaukhov (1977, 1985, 1987).

The long-term investigations of the Caucasian rock lizards carried out by I.S. Darevsky were finalized by the coming out of his monograph “Rock lizards of the Caucasus” (1967). In this volume, *Lacerta saxicola* traditionally perceived as a single species was split into a number of bisexual and parthenogenetic species, including the newly discovered *Lacerta caucasica alpina* (= *Darevskia alpina*), *L. saxicola nairensis* (= *D. raddei nairensis*) and others. These lizards grabbed the world’s science after the discovery of parthenogenesis, a globally important biological phenomenon, by I.S. Darevsky in the 1950s. This discovery stimulated the development of karyological, genetic and molecular studies and had made I.S. Darevsky (Fig.30) a renowned authority in this new field of science.

Furthermore, a new lizard species *Lacerta clarkorum* Darevsky et Vedmederja, 1977 (= *Darevskia clarkorum*) was discovered in the Charnali River gorge on the border between Adjara and Turkey. Later, lizards from the Charnali Gorge and the Cat Pass in Turkey were described as *Lacerta dryada* Darevsky et Tuniyev, 1997 (= *Darevskia dryada*). The habitat use patterns of *Darevskia clarkorum* were studied in the eastern part of the Lazistan (Pontic) Ridge and on the Mt. Mtirala in Adjara. In 1997, a new genus *Darevskia* Arribas, 1997

was described which unified all the Caucasian rock lizards. Independence of this genus within the subfamily Lacertinae was recently confirmed through the phylogenetic analysis and nomenclature actions (Arnold et al., 2007; Arribas et al., 2017). W.B. Bischoff and J.F. Schmidtler (2015) described the history of the Caucasian herpetological research from Pallas to Darevsky using lizards as an example.

A special research was dedicated to snakes living in the vicinities of Yerevan and in adjacent lands (Aghasyan, 1987a). In 1996, A.L. Aghasyan has published a review of snake fauna of Armenia. Karyological studies of snakes of Armenia were initiated by I.S. Stepanyan (2003). The monograph about the Herpetofauna of Armenia and Nagorno-Karabakh (Arakeyan et al., 2011) summarized the most comprehensive knowledge about composition and distribution of amphibians and reptiles. Keen debates flared up between the Swedish scientists G. Nilson and K. Andrén (Nilson, Andrén, 1985a, b, 1986a, b, 1992) and the specialists from Switzerland and Turkey (Schätti et al., 1991, 1992) about the taxonomic status of *Vipera xanthina* (= *Montivipera*) vipers within the zoological concept of the species. This discussion was preceded by vigorous research of vipers of the Caucasus and Asia Minor and the taxonomic revision of the *Vipera kaznakovi* (= *Pelias kaznakovi*) complex in the Caucasus (Vedmederja et al., 1986; Orlov, Tuniyev, 1986, 1990) and in Turkey (Başoğlu, 1947; Kretz, 1972; Billing et al., 1990), *Vipera ursinii* (= *Pelias ursinii*) complex (Nilson, Andrén, 1987, 2001; Eiselt, Baran, 1970) and the *xanthina* complex in Iran and Turkey (Mertens et al., 1967; Joger et al., 1988; Nilson et al., 1988, 1990). The descriptions of new taxa and new records appeared in herpetological literature: *Vipera darevskii* (= *Pelias darevskii*) in north-western Armenia (Vedmederja et al., 1986), *Vipera ursinii anatolica* (= *Pelias anatolica*) in south-western Turkey (Eiselt, Baran, 1970; Billing, 1985), *Vipera barani* (= *Pelias barani*) in north-western Turkey (Böhme, Joger, 1984), *Vipera bulgardaghica* (= *Montivipera bulgardagica*) in the Cilician Taurus in Turkey (Nilson, Andrén, 1985a), *Vipera wagneri* (= *Montivipera wagneri*) from the right bank of the Arax riverside in Turkey and Iran (Nilson, Andrén, 1984a), *Vipera raddei kurdistanica* (= *Montivipera raddei kurdistanica*) in the western shore of the Lake Urmia (Rezaiyeh) (Nilson, Andrén, 1986a), *Vipera albicornuta* (= *Montivipera albicornuta*) in northern Iran (Nilson, Andrén, 1985b), *Vipera albizona* (= *Montivipera albizona*) in central

Turkey (Nilson et al., 1990), *Vipera pontica* (= *Pelias pontica*) in the Artvin Depression of Turkey (Billing et al., 1990).

In the past decades, the new species *Vipera magnifica* Tuniyev et Ostrovskikh, 2001 (= *Pelias magnifica*) and *Vipera orlovi* Tuniyev et Ostrovskikh, 2001 (= *Pelias orlovi*) were described within the *Pelias kaznakovi* complex.

Taxonomic investigations of the Caucasian vipers remain to be the key issue (see *Chapter 3*) capturing attention of the world's scientific community (Nilson et al., 1995a, b, 1999b; Orlov, Tuniyev, 1986; Tuniyev, Ostrovskikh, 2001; Kalyabina-Hauf et al., 2004). For example, at the 2nd Biology of Vipers Conference held in Porto, Portugal in 24–27 September 2007, four presentations dealt with research and taxonomic revision of the Caucasian vipers (Murphy et al., 2007a; Murphy et al., 2007b; Nilson, 2007; Tuniyev, Tuniyev, 2007).

Many Caucasian species are represented by local and depressed populations or tend to experience range shrinkage and reduction of population size. Their research was spurred by the establishment of the Red Data Book of the USSR (1978, 1984) and similar editions in Russia (1987, 2001), Armenia (1987, 2010), Azerbaijan Republic (2013), Georgia (1982), South Ossetia (2017) and the North Caucasus republics and territories of the Russian Federation (1988, 1998, 1999, 2000a,b, 2002, 2004, 2007, 2009, 2012, 2013, 2014, 2017) with well-documented information about rare and threatened species. The papers dedicated entirely to threatened species (Bannikov, Makeev, 1978; Darevsky, 1979, 1987a, b; Tuniyev et al., 1988; Tuniyev, 1985a, 1989, 1991; Tuniyev, Nilson, 1995) or to individual snake species (*Zamenis longissimus* – Tuniyev, 1982; *Rhynchocalamus melanocephalus satunini* – Aghasyan, Tuniyev, 1985; *Pseudocyclophis persicus* – Aghasyan, 1987b; *Pelias dinniki* – Bozhansky, 1982, 1984, 1986; Tuniyev, Volčik, 1995) were published.

In the Soviet times, results of numerous studies of the Caucasian herpetofauna had been regularly presented at All-Union herpetological conferences held in Leningrad (1962, 1964, 1971, 1977), Ashkhabad (1981), Tashkent (1985) and Kiev (1989). Their proceedings were published in six volumes “Herpetological issues” (in Russian, *Voprosy gerpetologii*) from 1962 to 1991: <https://www.zin.ru/societies/nhs/publications.html>. Initiated by the Herpetological Committee and under its guidance, the 1st Conference on Herpetology in the Caucasus was organized in 1983 in Tbilisi and its pro-

ceedings were published in the collected paper “Herpetological research in the Caucasus” (1987) (Fig. 31).

The A.M. Nikolsky Herpetological Society (<http://www.zin.ru/societies/nhs/history.html>) has organized seven congresses (2000, 2003, 2006, 2009, 2012, 2015? 2018) and their proceedings were published in 2001, 2005, 2008, 2011, 2012, 2016 and 2019: <https://www.zin.ru/societies/nhs/publications.html>. They contain the latest information about amphibians and reptiles (including snakes) of the Caucasus.

In the last decade the new records both in the field and collections as well as observation of the Caucasian snakes in Armenia (Sanz et al., 2008; Agasyan et al., 2009; Ettling et al., 2012, 2013, 2016; Ettling, Parker, 2017), Azerbaijan (Bunyatova 2011; Bunyatova et al., 2012; Bunyatova, Djafarova, 2013; Kidov et al., 2012a,b; Kukushkin et al., 2012; Tuniyev et al., 2013; Nadjafov et al., 2013; Akhmedov et al., 2015; Dor-

onin, 2016; Iskenderov, Akhmedov, 2017; Iskenderov et al., 2017) and Georgia (Bekoshvili, Doronin, 2015; Mačát et al., 2016; Tuniyev et al., 2014, 2018) were published, also in the monograph on the herpetofauna of Armenia and Nagorno-Karabakh (Arakelyan et al., 2011) (Fig.32).

In the recent time the data on the herpetofauna of Ciscaucasus (E.S. Roitberg et al., 2000; K.Yu. Lotiev, 1987, 2007, 2015; Doronin, 2012, 2015; Kidov et al., 2013; Doronin et al., 2013, 2016) and Abkhazia (Doronin, 2011) and many others were published. The herpetofauna of Kavkazsky State Reserve was studied by B.S. Tuniyev (1983, 1987, 1989, 1994, 1999; Tuniyev, Tuniyev, 2006c) and of Sochinsky National Park by B.S. Tuniyev and S.B. Tuniyev (Tuniyev, Tuniyev, 2006a, b; S.Tuniyev, 2008). In the late 1990s, active herpetological studies in Dagestan were restarted under the leadership of L.F. Mazanaeva (Mazanaeva, Sultanova, 2001, 2012; Mazanaeva et al., 2009, 2011; Leontyeva, Mazanaeva, 2010; Mazanaeva, Askenderov, 2008; 2014; Mazanaeva, Ananjeva,

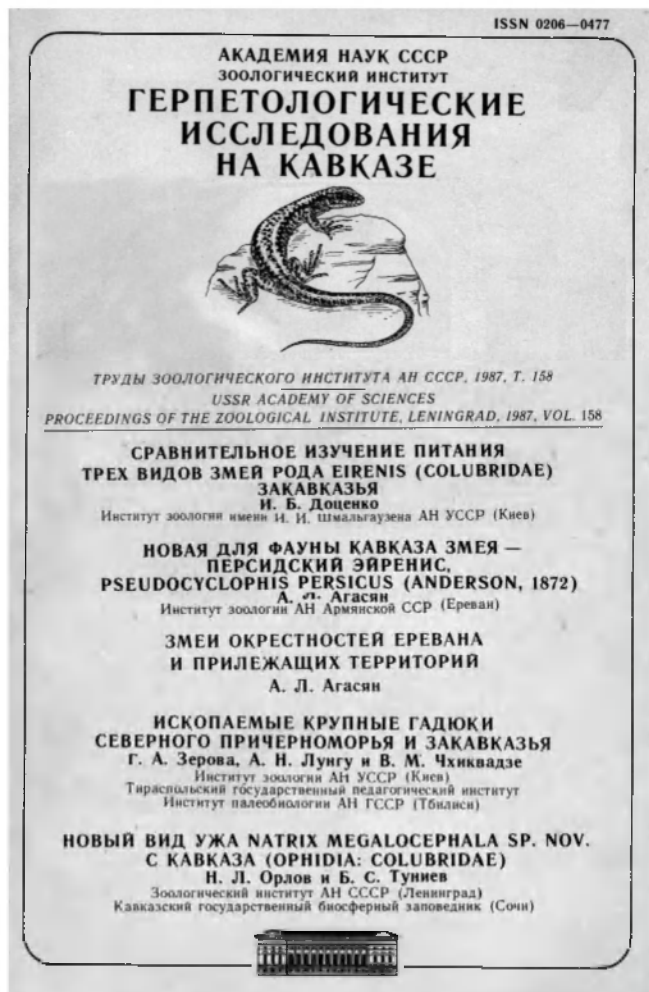


Fig. 31. Cover page of the proceedings “Herpetological studies in the Caucasus” (1987).

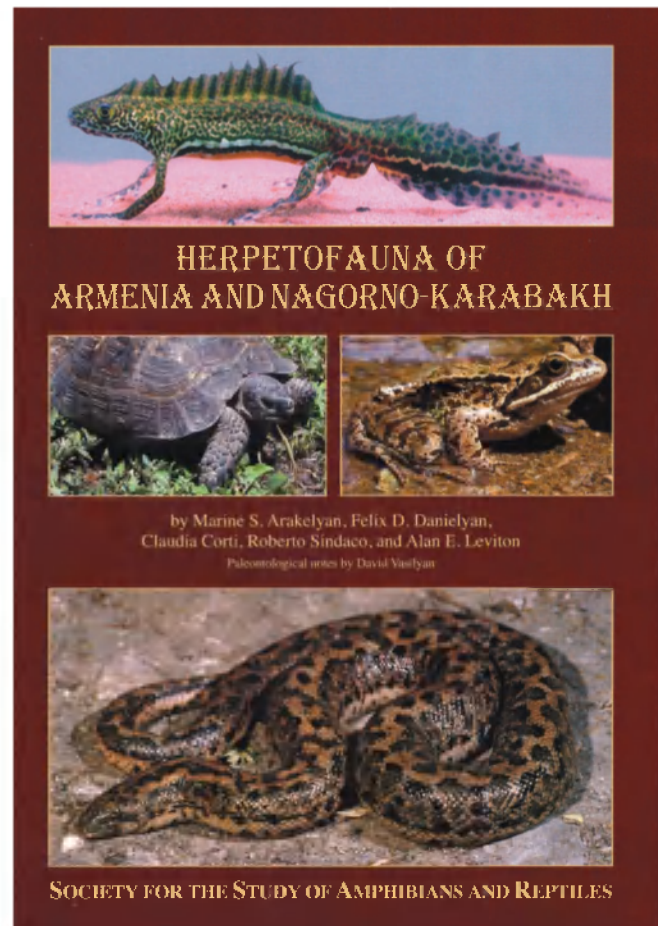


Fig. 32. Cover page of the book “The Herpetofauna of Armenia and Nagorno-Karabakh” by M. S. Arakelyan, F. D. Danielyan, C.Corti, R.Sindaco and A.E. Leviton (2011).



Fig. 33. Cover page of the book “Turkish herpetofauna (amphibians and reptiles)” by I. Baran and M.K. Ataturk (1998).



Fig. 34. Cover page of the book “Türkiye Amfibi ve Surungenleri” by I. Baran (2005).

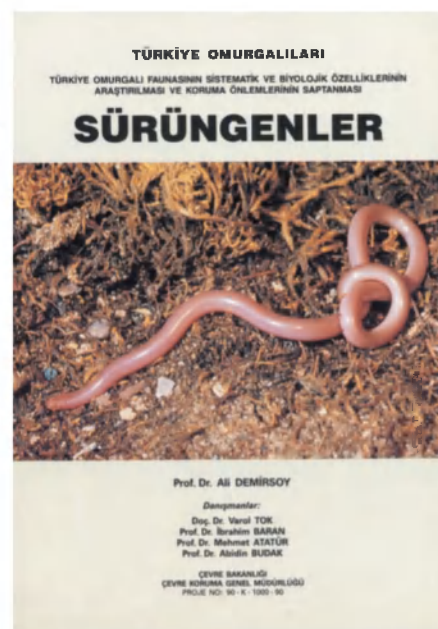


Fig. 35. Cover page of the book “Sürüngenler. Çevre Bakanlığı” by A. Demirsoy (1996).

2016; Askenderov et al., 2017 and others). Information about new records of reptiles on the Taman Peninsula was published by Tuniyev and Tuniyev (2004) and by Starkov and Orlova (2007).

Apart from these studies, particular attention should be paid to the papers and books about the adjacent parts of Asia Minor and the Near East. They include the results of herpetofauna research in Turkey (Mertens, 1952; Clark, Clark, 1973; Tok and Kumlutas, 1996; Baran, 1976, 2005; Başoğlu, Baran, 1977, 1980; Schmidler, Lanza, 1990; Baran, Ataturk, 1998; Demirsoy, 1996) and Iran (Mertens, 1957; Clark et al., 1966; Latifi, 1991; Anderson, 1999) (Figs. 33–36). Of special interest are the work by H. Zinner (1972) about the systematics and evolution of the *Coluber jugularis* complex, taxonomic consideration of the Iranian species of the *Elaphe longissima* complex (Nilson, André, 1984b) and the revision of the *Coluber ravergeri*–*C. nummifer* complex (Schätti, Agasian, 1985). The references related to the revision of complicated taxonomic complexes of snakes are provided in respective chapters of this book. Studies of snakes of Turkey and Iran in the territories of these countries belonging to the Caucasus ecoregion are developing rapidly in the 21st century, new finds of rare species have been described, detailed faunistic and taxonomic studies have

been carried out, zoogeographic hypotheses have been formulated and tested (Baran et al., 2001; Kutrup, 2001, Kutrup, Yılmaz, 2002; Geniez, Tynié, 2005; Jandzik, 2005; Olgun et al., 2007; N. Rastegar-Pouyani et al., 2008; Afsar, Afzar, 2009; Fathinia, N. Rastegar-Pouyani, 2010; Avcı et al., 2004, 2007, 2010, 2015, 2018; Tosonoğlu et al., 2010; Kian et al., 2011; Abtin et al., 2014; E. Rastegar-Pouyani et al., 2014; Kumlutaş et al., 2013; Mermer et al., 2012; Goçmen et al., 2007, 2011, 2013, 2014, 2015, 2017; Rajabizadeh et al., 2011a,b; 2012a,b, 2015; İğci et al., 2015; Šmid et al., 2015; B. Tuniyev et al., 2014, 2018a; S. Tuniyev et al., 2012; Mebert et al., 2015a,b,c, 2016; Gül, 2015; Gül et al., 2016a,b; Çakmak et al., 2017; Kaya, Özüluğ 2017; Torki, 2017; Behrooz et al., 2018, Fathinia et al., 2018 and others). Synopsis of snakes of Iran (Rajabizadeh, 2017) (Fig. 37) provides updated data about the biodiversity of snakes in Iran, consisting of 83 species, belonging to 35 genera and 7 families, and identification key for the species and genera.

The development of molecular genetic techniques and approaches has allowed to obtain important information on phylogenetic relationships and taxonomic status of colubrids of the genera *Natrix*, *Malpolon*, *Zamenis* and especially collected genera *Elaphe* and

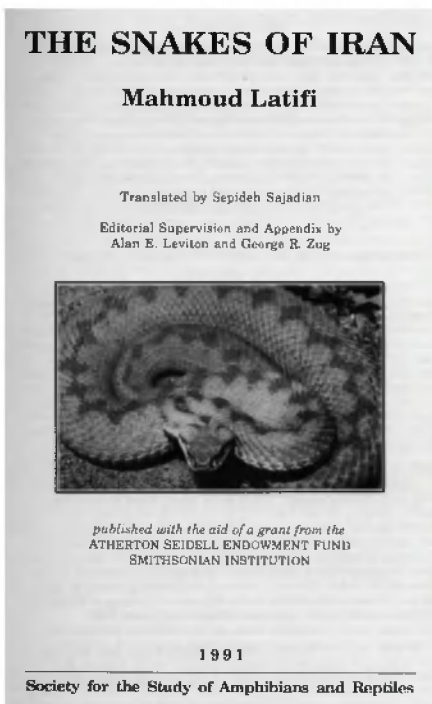


Fig. 36. Cover page of the book “The snakes of Iran” by M. Latifi (1991).



Fig. 37. Cover page of the book “Snakes of Iran” by M. Rajabizadeh (2017) [in Farsi].

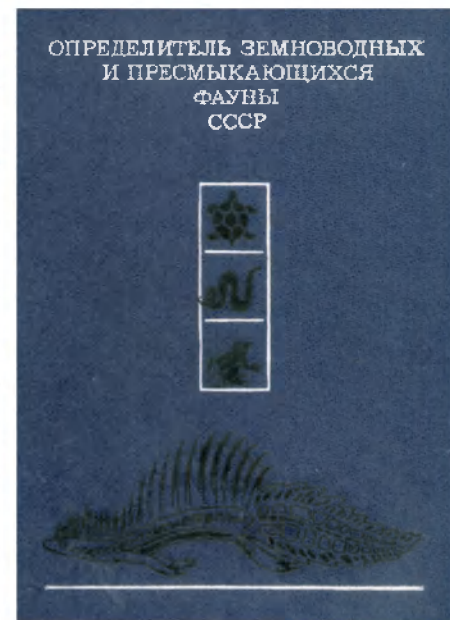


Fig. 38. Cover page of the book “A guide to the amphibians and reptiles of the fauna of the USSR” by A.G. Bannikov, I.S. Darevsky, V.G. Ischenko, A.K. Rustomov and N.N. Scherbak (1977).

Coluber (Helfenberger, 2001; Utiger et al., 2002; Nagy et al., 2003, 2004; Utiger, Schätti, 2004; Carranza et al., 2006; Guicking et al., 2006; Salvi et al., 2018). Information about snakes of the Caucasus is published in compilations of amphibian and reptilian fauna of the USSR, Eastern Palearctic, Northern Eurasia (Terentjev, Chernov, 1949; Bannikov et al., 1977 (Fig. 38); Ananjeva et al., 1998 (Fig. 39), Szczerbak, 2003; Ananjeva et al., 2006) and Russian Federation (Dunayev, Orlova, 2018) (Fig.40). Collections of the Caucasian snakes maintained at the Zoological Museum of the National Museum of Science and Natural History, National Academy of Sciences of Ukraine, Kiev ((Dotsenko, 2003) and the Museum of Nature at V. N. Karazin's Kharkiv National University (Vedmederya et al., 2007, 2009) are described in the catalogues of these museums.

The advancement of up-to-date methods in systematics, phylogeny and phylogeography has given a new impetus for collection and analysis of data on all groups of reptiles, including snakes (Garrigues et al., 2005; Ursenbacher et al. 2009; Ferchaud A.-L et al., 2012; Zinenko et al., 2015, 2016; Alencar et al., 2016; Stümpel et al., 2016; Tuniev et al., 2018a,b; Kindler et al., 2013, 2018; Kornilios, 2017; Hoffmann et al., 2018; Salvi et al., 2018).

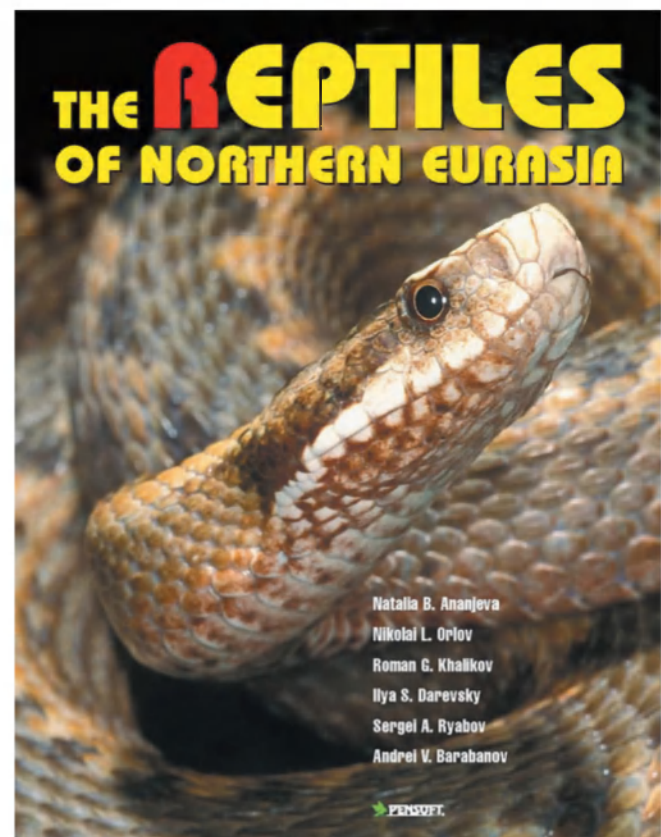


Fig. 39. Cover page of the book “The atlas of the reptiles of Northern Eurasia (taxonomic diversity, distribution and conservation status)” by N.B. Ananjeva, N.L. Orlov, R.G. Khalikov, I.S. Darevsky, S.A. Ryabov and A.V. Barabanov (2004).



Fig. 40. Cover page of the book “Snakes. Species of the fauna of Russia” by E.A. Dunaev and V.F. Orlova (2018).

The Caucasus remains one of the most important regions in this context.

Current views on snake taxonomy and phylogeny are provided below, in taxonomic parts of respective chapters. It corresponds to the modern views on the snakes fauna in the monograph of Van Wallach et al. (2014) and the current database Uetz et al., 2017 http://reptile-database.reptarium.cz/advanced_search?taxon= The modern ideas on the taxonomy and distribution of snakes of Western Palearctic were presented in the latest monograph (Sindaco et al., 2013).

Chapter 3.

TAXONOMIC COMPOSITION OF THE FAUNA OF SNAKES OF THE CAUCASUS

Order SNAKES – SERPENTES Linnaeus, 1758

The body is strongly elongated, usually cylindrical, but often laterally or dorsoventrally flattened. The tail is always shorter than the body and the head. The limbs are absent, but snakes of the suprafamilies Typhlopoidea Merrem, 1820 and Booidea Gray, 1825 retain rudimentary pelvic bones and claw-shaped rudimentary hind limbs.

The body is covered with uniform corneous scales. Snakes do not have eyelids. The eyes are externally covered with a transparent layer, which is shed along with the outer layers of the epidermis during the process of moulting. The species of the suborder Scolecophidia Cope, 1864 have the eyes hidden under the skin due to their fossorial life. The external ears and the tympanic membrane are absent in snakes, contrary to some legless lizards. A majority of recent snakes of the suborder Alethinophidia Hoffstetter, 1955 have only one right lung while their left lung is rudimentary, but the primitive groups of the infraorder Henophidia Hoffstetter, 1939 have both lungs, with the bigger right one.

The braincase is frontally ossified. The temporal arch and the bony bridges are absent. The quadrate, supratemporal, pterygoid, palatine and maxillary bones are connected with the braincase by elastic ligaments to ensure high mobility. There are no tympanic cavity and the Eustachian tubes. The mandibles are interconnected by a tensile ligament which allows a snake (along with a generally high kinesis of the skull) to swallow large prey whole. The well-developed teeth are situated on the maxillary, palatine, pterygoid and dental bones. The anlage of teeth on intermaxilla occurs in embryogenesis of all the groups of snakes. Some groups of the infraorder Henophidia Hoffstetter, 1939 (e.g., the family Pythonidae) have functional teeth on the intermaxilla throughout their ontogeny, but most of recent snakes lose these teeth (the *egg teeth*) after cutting of the egg

membranes and hatching. The snake's teeth are very sharp, bent backwards and well adapted to capture and swallow prey whole.

Swallowing prey whole is also associated with the development of venom-producing temporal salivary glands, venom-conducting canals and unique fangs located on the maxillae. In a number of colubrid snakes, these teeth are grooved, enlarged and located behind the normal teeth in the posterior part of the maxillae. For this reason, these snakes are called *opisthoglyphous* (*rear-fanged or rearward grooved*). There is no internal canal, so venom is channeled towards the puncture through an external groove. In elapids, fangs are fixed on the maxillae and completely folded around the venom channel. Vipers have the pipe-grooved and large fangs which can move when the mouth is open, injecting venom like by a syringe. The advanced elapids and viperids do not have teeth other than the fangs on the shortened maxillae. Some primitive elapids still retain normal teeth on the longer maxillae which are separated from the fangs by a diastema.

Paleontological data and modern phylogenetic studies show that the evolution of venom-producing mechanisms in snakes of the suprafamily Colubroidea Oppel, 1811 (families Colubridae Oppel, 1811 (*sensu lato*); Elapidae Boie, 1827; Hydrophiidae Fitzinger, 1843; Atractaspididae Günther, 1858 and Viperidae Laurenti, 1768) proceeded almost concurrently and independently. Along with the suprafamily Acrochordoidea Bonaparte, 1831 they belong to the infraorder Caenophidia Hoffstetter, 1939 (Kelly et al., 2003; Vidal et al., 2007; Fry et al., 2006, 2008). The newest phylogenetic investigations (Vidal et al., 2007) have demonstrated the Asian origin of the primarily nocturnal caenophids. During the evolution (ca. 100 million years), the venom-producing mechanisms and venoms themselves diversified and developed from changes in biochemical composition and specialization of venoms to advanced morphology of dentition and venom glands.

The trends in body elongation and limb reduction known in many lizards have reached their extremum in snakes. Most snakes do not have the shoulder girdle and front limbs, but in some primitive genera the rudimentary pelvic girdle and hind limbs are preserved. The vertebrae are procoelous, with characteristic supplementary arthrodial facets above the spinal canal. The number of precaudal vertebrae varies from 120 to 454. In vertebral articulation, the wedge-shaped process *zygosphene* of each vertebra fits the corresponding concavity *zygantrum* of the posterior surface of the preceding vertebra. Generally, the axial skeleton is organized to maximally fit the creeping movements on and under the ground, over the trees and rocks, as well as for swimming. Normally, the development of the serpentine body shape in squamate reptiles is associated with these adaptations.

Snakes can be oviparous and ovoviviparous, often with the development of the placenta spuria.

Snakes inhabit all continents and most islands of the continental origin, except for the Antarctic. Even large-bodied species are known to colonize distant islands on wood rafts, as it happened with the arrival of the reticulated python in the Krakatoa Island (Indonesia) devastated by volcano eruption in 1888. An overwhelming majority of species lives in tropical and subtropical regions, but some have adapted to high latitudes and even cross the Polar Circle. Many species occupy the mountains of the Old and New Worlds, reaching the boundaries of the alpine and subnival belts. An absolute record is known with a colubrid (*Thermophis baileyi*) living at 3960–4400 m asl in Tibet (Zhao, Adler, 1993; Zhao et al., 1998). In the Caucasus, a number of scute-headed vipers, the genus *Pelias*) move up to 3000 m asl.

The order Serpentes comprises 2 suborders – fossorial (Scolecophidia Cope, 1864) with 2 suprafamilies and 3 families and advanced snakes (Alethinophidia Hoffstetter, 1955) with 2 infraorders (Henophidia Hoffstetter, 1939 and Caenophidia Hoffstetter, 1939), 6 superfamilies (Acrochordoidea, Uropeltoidea, Pythonoidea, Booidea, Colubroidea and Typhlopoidea), 26 families, 450 genera and more than 3500 species (Lee, 2005; Lee et al., 2007; Vidal et al., 2007; Pyron et al., 2010, 2013; Uetz et al., 2018).

In the North Palearctic fauna, we considered 5 families of snakes, including 30 genera and 75 species (Ananjeva et al., 2006). Now, the Caucasian ophidiofauna consists of 5 families, 19 genera and 44 species.

In visual field identification of wild-living snakes, the most important external characters are body proportions, shape, size and number of corneous scales and scutes covering the body (*pholidosis*).

Most frequently, species identification is based on the characteristics of shields covering the head and forming the rows on the body and tail as well as of scales covering the belly and ventral side of the tail. Only blind snakes have uniform scales on the dorsal and ventral surfaces of the body.

The other key traits in field identification are head shape, pupil type, eye size, dentition (tooth size, number and topography), body measurements and colour patterns. The structure of the skull, vertebrae, hemipenes and some other morphological characters should be analyzed, usually in laboratory conditions, to more accurately identify the species or supra-species taxa.

FAMILY BLIND SNAKES – TYPHLOPIDAE Merrem, 1820

Small worm-like snakes with a very short and thick spinelet-tipped tail. Body structure is adjusted to fossorial underground life. The significantly reduced eyes appear from under the stiff corneous scutes as dark spots and sometimes are not visible at all. The mouth is located on the ventral side of the head. Large smooth head scutes are adapted to digging. The body is covered by smooth and round-shaped scales. The dorsal and ventral scales are equal in size.

The skull is dense, compact and less kinetic than in more advanced snakes. The mandibles and maxillae do not contact each other. The premaxillary, palatine, pterygoid bones and the mandibles are toothless. The pterygoid bones are not attached to the quadrate bone and the mandible. The maxillae have several miniature teeth in their posterior lower end. The nasal bones are widely attached to the frontal and prefrontal bones. There are no supratemporal bones. The rudiments of the pelvic girdle are present in blind snakes of all genera. Some blind snakes also retain the vestiges of the hind limbs.

The family includes about 270 species living in the Americas, South Europe, Africa, Asia Minor, Central Asia, South and Southeast Asia, Indo-Australian archipelago, Philippines, Australia and a number of tropical and subtropical islands.

Blind snakes lead a fossorial and predominantly nocturnal life. They often live in termitaries, eating termites, their larvae and eggs and laying their own eggs. Blind snakes generally feed on invertebrates and are oviparous. Parthenogenetic breeding is also known, for example in the ubiquitous and tiny *Rhamphotyphlops braminus* (Daudin, 1803) named the flowerpot snake for its ability to spread all over the world in pot soil and to quickly breed in new places (Waite, 1894).

There is one genus present in the Caucasus.

Genus Blind snakes – *Xerotyphlops* Hedges, Marion, Lipp, Merin et Vidal. 2014

Xerotyphlops Hedges, Marion, Lipp, Merin et Vidal. 2014. Hedges, Stephen B., Angela B. Marion, Kelly M. Lipp, Julie Marin & Nicolas Vidal. 2014. A taxonomic framework for typhlopoid snakes from the Caribbean and other regions (Reptilia, Squamata). *Caribbean Herpetology* (49): 1–61. Type species: *Typhlops vermicularis* Merrem 1820 is the type species of the genus Hedges et al., 2014.

Blind snakes live in soil, under stones, in burrows of invertebrates and often in termitaries. After heavy rains, they usually appear on the ground surface and in dry periods, they move deep into the wet strata of soil. These snakes feed on small invertebrates, including termites, their eggs and larvae. Oviparous, a female lays 2–10 strongly elongated eggs.

There are 5 species in this genus: *Xerotyphlops etheridgei* (Wallach, 2002), *Xerotyphlops luristanicus* Torki, 2017, *Xerotyphlops socotranus* (Boulenger, 1889), *Xerotyphlops vermicularis* (Merrem, 1820), *Xerotyphlops wilsoni* (Wall, 1908). They live in arid regions of tropical, subtropical and southern part of temperate zones of western Sahara, in eastern Mediterranean region, Front Asia to Iran in the east, Dagestan to the north and Socotra Island to the south. Description of this family and the genus *Xerotyphlops* is provided in Grillisch and Grillisch's (1993) guidebook on reptiles and amphibians of Europe dedicated to the families Typhlopidae, Boidae, Colubiridae 1: Colubrinae (Fig. 41). There is one species of this genus living in the Caucasus. It is used as a model group in biogeographic and phylogenetic studies (Kornilios et al., 2011, 2012, 2014; Kornilios, 2017).

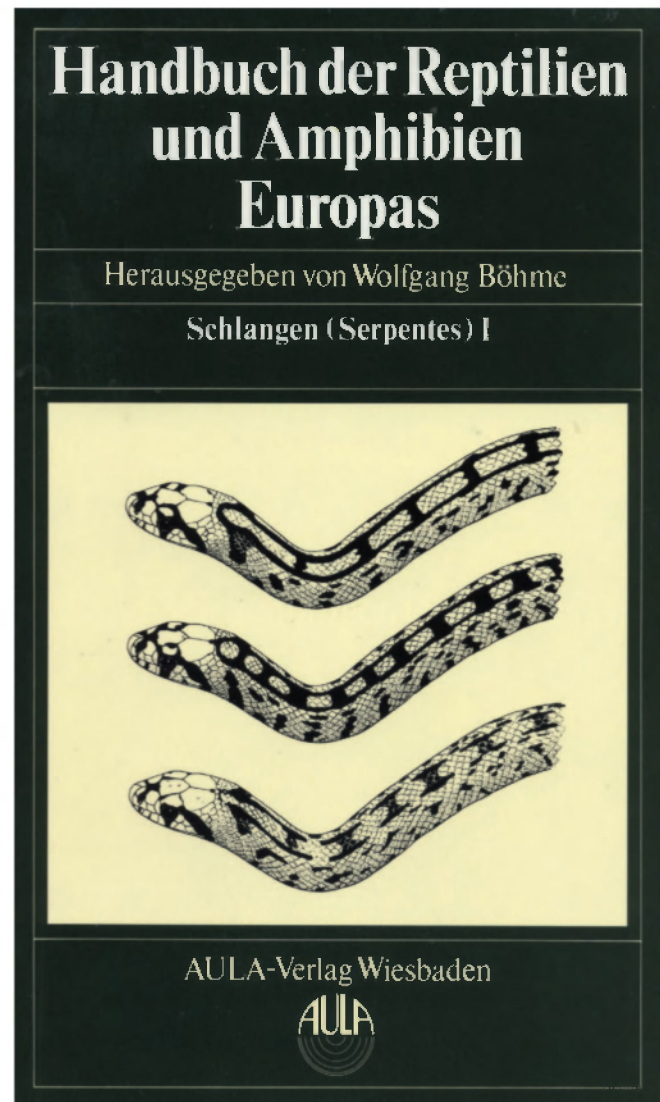


Fig. 41. Cover page of the book “Handbuch der Reptilien und Amphibien Europas”. Vol. 3/I (1993).

European blind snake – *Xerotyphlops vermicularis* (Merrem, 1820) (Fig. 42)

Typhlops vermicularis Merrem, 1820, Versuch eines Systems der Amphibien / Tentamen Systematis Amphibiorum. J.C. Krieger, Marburg: 158 (xv +191) pp., 1 pl.

Terra typica. In the original description – “Archipelago Asia”, then Mertens and Müller (1928) described it as “Griechische Islands” (Greek islands – Grillitsch, 1993; Ananjeva et al., 2006).

Type specimens. Not indicated (McDiarmid et al., 1999; Van Wallach et al., 2014).



Fig. 42. European blind snake, *Xerotyphlops vermicularis* – Kapan, Armenia.

Distribution. Balkan Peninsula, Asia Minor, Syria, East Caucasus, Central Asia (southern Turkmenistan, Uzbekistan, Tajikistan), Iran and Afghanistan (Afroosheh et al., 2012, 2013),

Distribution in the Caucasus. Armenia, Azerbaijan, eastern Georgia, southern Dagestan, north-eastern Turkey and north-western Iran (Map 3).

Habitats. Open and plain areas in arid and semi-arid foothills and mountains covered by xerophilic vegetation. Sometimes blind snakes occur in juniper sparse forests and foothill scrublands composed of *Amygdalus fenzliana*, *Rhamnus pallasii* and other plants. In Armenia, these reptiles are most common on stony slopes with thinly distributed shrubs and herbs in semi-desert and dry steppe zones. They can be found at elevations up to 2000 m asl. Some records are known in mudflow beds and mountain grasslands. Blind snakes often live in termitaries and anthills. In wormwood semi-deserts of Dagestan, they occur in habitats with *Artemisia fragrans* and some *Iris furcata* and *Geranium* sp. Snakes also inhabit the *Salsola gemmascens nodulosa* desert in Gobustan Reserve (Azerbaijan) and interchanging

rocky and gentle (<30°) hills at 600–800 m in the Aker riverside covered by *Juniperus foetidissima* and *J. excelsa polycarpus* (Lachin district).

In Armenia, this species is recorded in the V-shaped rocky canyon of the Arpa River, between Eghegnadzor and Areni, at 800–1000 m in riparian pistachio forests stretched as a 60–80 m wide narrow strip along the westerly exposed left bank. In this sparse forest with trees standing 5 or more metres apart, the dominant species are equally represented *Pistacea mutica*, *Acer ibericus*, *Crataegus orientalis*, *Celtis caucasica*, *Amygdalus fenzliana* and *Rhamnus pallasii*. The most common herbal plants are *Artemisia fragrans*, *Stachys inflata* and *S. stschegleewii*.

Blind snakes can also be found in phrygana on the right bank of the Arpa which is rather steep (<40°), exposed to the southeast and dominated by *Rhamnus pallasii* and *Ephedra major procera*. In the Meghri district of southern Armenia, they are recorded in *Paliurus spina-christi*–*Rhamnus pallasii* sibiljak growing on terraces along the Tsiranadzor Canyon and in *Paliurus spina-christi*–*Punica granatum* sibiljak in complicated



Map 3. Distribution map of *Xerotyphlops vermicularis*.

and rocky branch gorges near the Nrnadzor village.

Conservation status. This species is common throughout the East Caucasus and is present in a number of protected areas of Armenia, Georgia and Azerbaijan (Khosrov, Shikahogh, Vashlovani, Gobustan, Zakataly and others). At the workshop on IUCN assessment of Palearctic reptiles and amphibians in Antalya, Turkey in September 2008, its status was designated as LC. It is essential to establish a protected area in the foothills of southern Dagestan to ensure the conservation of the blind snake and other Mediterranean species in the Caucasus part of Russia.

FAMILY BOAS – BOIDAE Gray, 1825

Medium-sized and large snakes of body length ranging from 450 mm to 10 m. The world's largest snakes belong to this family. The boas have powerful musculature of the body and retain the rudiments of all three pelvic bones and hind limbs. The rudimentary claw-like hind limbs are located on each side of the anus and are better developed in males to be used for mating and courtship. Both lungs are functioning, but the left lung is shorter and by 30–80% smaller in volume than the right lung. The eyes are usually well developed and have a vertical or round pupil. The maxillary, palatal and pterygoid bones are most mobile due to elastic ligaments.

The maxillary, dental, palatal and pterygoid bones have teeth. There are no teeth on the premaxillary bones, unlike the closely related family Pythonidae Fitzinger, 1826 that was formerly considered as subfamily of the boas. The ventral surface of the body is covered by the row of longitudinal and crosswise-widened scutes.

The boas comprise a wide range of ecological (fossorial, arboreal, terrestrial and semi-aquatic) forms living in tropical and subtropical regions of all the continents and on many islands, mainly of continental origin. Beyond the subtropics, the global range of this family extends to the Palearctic and West Neartic. The description of the family and genus is provided in the volume *Handbuch der Reptilien und Amphibien Europas* (Bd. 3/I., 1993) dedicated to the families Typhlopidae, Boidae, Colubridae 1: Colubrinae (Fig. 53) and in McDiarmid et al. (1999) (Fig. 55). These snakes feed on different vertebrates, preferably homoiothermic ones, while a number of species have specialized in preying on amphibians, reptiles and even fish. All boas are ovoviviparous, in contrast to oviparous pythonids. This family encompasses 7 subfamilies: Boinae (Boas), Ungaliophiinae (Dwarf Boas), Erycinae, Calabariinae, Candoiinae, Sanziniinae and Chariniinae comprising 14 genera and more 60 species. Most of taxa are listed on the Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), aside from *Acranthophis* sp., *Boa constrictor occidentalis*, *Epicrates inornatus*, *E. monensis*, *E. subflavus* and *Sanzinia madagascariensis* ssp. that are designated under the Appendix I.

There is one genus in the fauna of the Caucasus belonging to the subfamily Erycinae Bonaparte, 1831.

Subfamily Erycinae Bonaparte, 1831

Genus Sand boas – *Eryx* Daudin, 1803

Eryx Daudin, 1803, Caracteres des vingt-trois genres qui composent l'ordre des Ophidiens. Mag. Encyclop. (An. 8), 5: (437) 433–438.

Type species. *Boa turcica* Olivier, 1801 (= *Anguis jaculus* Linnaeus, 1758), later designated by Fitzinger (1843) (in Williams, Wallach, 1989). The valid name is *Eryx jaculus* (Linnaeus, 1758).

Medium-sized snakes of body length 450–1150 mm and a characteristic body shape. The head is not delimit-

ed from the neck and is covered by numerous and rather small irregularly shaped scutes above and by small uniform scales on ventral side. The internasal scutes are quite large and regularly shaped. The intermaxillary scute is large, strongly lapping onto the upper surface of the head and is clearly visible from above. The subcaudal scutes (all or most of them) are delineated in a longitudinal row. On both jaws the front teeth are longer than the rear ones. The diastema is absent. The intermaxillary bone has a dentition and is covered on top by the frontally protruded nasal bones, which contact widely with the frontal bones.

All species are ovoviviparous. The 12 species of this genus live in South-East Europe, West and South Asia from the Arabian Peninsula to India and Pakistan, and North Africa from Morocco to Egypt: *Eryx borrii* Lanza et Nistri, 2005, *Eryx colubrinus* (Linnaeus, 1758), *Eryx conicus* (Schneider, 1801), *Eryx elegans* (Gray, 1849), *Eryx jaculus* (Linnaeus, 1758), *Eryx jayakari* Boulenger, 1888, *Eryx johnii* (Russell, 1801), *Eryx miliaris* (Pallas, 1773), *Eryx muelleri* (Boulenger, 1892), *Eryx somalicus* Scorteccei, 1939, *Eryx tataricus* (Lichtenstein, 1823) and *Eryx whitakeri* Das, 1991

All species are listed on the Appendix II of the CITES. The fauna of the Caucasus comprises 2 species of the nominate subgenus (Ananjeva et al., 1997, 1998, 2006).

Javelin sand boa – *Eryx jaculus* (Linnaeus, 1758)

Anguis jaculus Linnaeus, 1758, Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Tomus I. Editio decimal, Reformata. Laurenti Salvii, Holmiae: 228(824) pp.

Terra typica. *Eryx jaculus jaculus* – in the original source as “Aegypto” (Egypt).

Type specimens. The type is lost (in Stimson, 1969; Tokar, 1991; McDiarmid et al., 1999; Van Wallach et al., 2014).

Distribution. North Africa, northern Arabian Peninsula, Asia Minor, Syria, Iraq, Palestine, East Caucasus, Balkan Peninsula. Some authors suggest the existence of 2 subspecies (Tokar, 1991): the nominate living in North Africa eastwards to the Suez Canal and *E. j. turcicus* from the rest of the range (Tokar, Obst, 1993).

We adhere to the opinion about 3 subspecies: *E. j. jaculus* (Linnaeus, 1758), *E. j. turcicus* (Olivier, 1801) and *E. j. familiaris* (Eichwald, 1831). *E. j. familiaris* lives in the Caucasus.

***Eryx jaculus familiaris* Eichwald, 1831**
(Fig. 43–45)

E. familiaris Eichwald, 1831, Zoologia specialis quam expositis animalibus tum vivis, tum fossilibus potissimum Rossiae in universon, et Poloniae in Specie in usum lectionum publicarum in Universitate Caesarea Vlnensi habendarum, Pars posterior, Vilnae, III: 176 (404 pp, 2 pl).

Terra typica. “Nargin” [“Nargin Island near Baku” (Azerbaijan), in Nikolsky (1916)].

Type specimens. Not designated (in McDiarmid et al., 1999; Van Wallach et al., 2014).

Distribution in the Caucasus. *E. jaculus familiaris* is recorded in southern Armenia, eastern Geor-

gia, Azerbaijan, northern Turkey and some areas of the North Caucasus (Map 4). Found on the Nargin Island in the Caspian Sea, near Baku. Some singular records are known in the south of the Stavropol Territory, Chechen Republic (vicinity of Grozny, village Starogladkovskaya), Dagestan (Karanogay, Malaya Areshvka), North Ossetia-Alania (Mozdok district) and Kalmykia (north – Ergeni Upland, south – Manjekiny, Jejekiny) within Russia. The only reliable record after 100-year period (Leister, 1908, Lotiev, 2007) was made in Chechen Republik near the southern piedmond of Bargun Mountain Range (43°25.292'N, 45°53.315'E") in 2011 (Lotiev, pers. comm.). In Dagestan *E. jaculus* is not so rare as in other regions of the North Caucasus and distributed in various habitats of lowland and foot-



Map 4. Distribution map of *Eryx jaculus*.



Fig. 43. Javelin sand boa, *Eryx jaculus familiaris* – Iori Plateau, Eastern Georgia.



Fig. 44. Javelin sand boa, *Eryx jaculus familiaris* – Khosrov Reserve, Armenia.

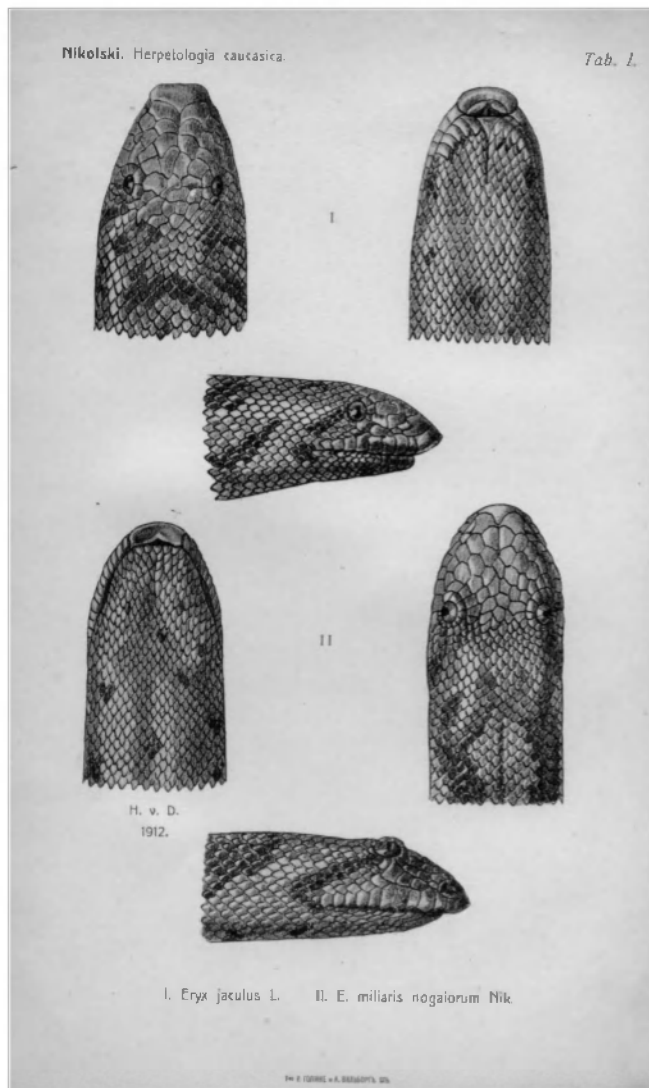


Fig. 45. A figure plate with the images of the sand boas *Eryx jaculus* and *Eryx miliaris* from the book “The reptiles and amphibians of the Caucasus” by A.M. Nikolsky (1913).

hills at the altitudes from 23 to 540 m asl. (Mazanaeva, Sultanova, 2012).

Habitats. Dry steppes, semi-deserts and arid sparse forests. Sand boas prefer to inhabit clay and stony soils, seldom live in loose sand hills, vineyards and orchards. Along the riversides they reach the altitudes 1500–1700 m asl. In the northern parts of their range (south of Russian Caucasus), boas also inhabit fescue-wormwood steppes. Habitats are always associated with arid landscapes.

In Armenia’s Arpa riverside lying between Eghegnadzor and Areni, boas were found in pistachio sparse forests growing on chestnut soils at 800–1000 m asl in the rocky canyon. The trees are sparse (5 m or more apart) with the dominant species *Pistacea muti-*

ca. The secondary species (*Acer ibericus*, *Crataegus orientalis*, *Celtis caucasica*, *Amygdalus fenzliana*, *Rhamnus pallasii*) are equally represented. The dominant herbs are *Artemisia fragrans*, *Stachys inflata* and *S. stschegleewii*. In the Aghasibeklu locality of Khosrov Forest Reserve, boas live in the ecotone of scrub semi-deserts and juniper sparse forests. In the vicinity of Abovian town, boas inhabit mountain grasslands.

Conservation status. The population is going down because of steady shrinkage of suitable habitats. At the workshop on IUCN assessment of Palearctic reptiles and amphibians in Antalya, Turkey in September 2008, its status was designated as LC. As a rare species living in the marginal parts of its global range, *E. j. familiaris* is included in the Red Data Books of the Russian Federation (2001) (category 3), Georgia (1982) (category 2), Reptiles of Georgian Red List, VU B2a, North Ossetia-Alania (1999), Dagestan (2009), Kalmykia (2013), Ingushetia (2007) and Chechen republics (2007). It lives in a number of protected areas of Russia, Armenia, Georgia and Azerbaijan (Dagestansky, Vashlovani, Khosrov Forest and others).

Desert sand boa – *Eryx miliaris* (Pallas, 1773) (Figs. 45, 46–47)

Anguis miliaris Pallas, 1773, Reise durch verschiedene Provinzen des Russischen Reichs. Kayserlichen Acad. Wissnschaften, 1771–1776. St.Petersburg, 1773, 2: 718 (369–744 pp., 30 pl., 1 map).

Terra typica. In the original description mentioned as “versus mare Caspium” (Caspian Sea coast); “the area of the Caspian Sea” (Darewskij, 1993; Ananjeva et al., 2006).

Type specimens. Not designated (in Stimson, 1969; McDiarmid et al., 1999; Van Wallach et al., 2014).

Distribution. Northern Iran, Afghanistan, Central Asia, Kazakhstan and eastern Ciscaucasus. The intraspecific variation is very complicated and many taxonomic names were suggested during the long history of species studies (Bedriaga, 1907; Tsarevsky, 1915b; Nikolsky, 1913, 1916). Here we consider two valid subspecies: nominate *E. m. miliaris* living to the east of the Volga River and *E. m. nogaiaorum* Nikolsky, 1910 in the west of the range. Individuals of the latter subspecies can often be melanistic, viz. completely black or very dark. V.A. Kireev (1974) has demonstrated that sand boas from



Fig. 46. Desert sand boa, *Eryx miliaris nogaiorum*, black morph – Nogayskaya Steppe, Dagestan, Russian Federation.



Fig. 47. Desert sand boa, *Eryx miliaris nogaiorum*, brown morph – Nogayskaya Steppe, Dagestan, Russian Federation.

the eastern Ciscaucasus are morphologically different from those living in Central Asia. Until now, the status of a number of taxa within the complex *E. miliaris-tataricus* suggested by Bedriaga (1907) and Tzarevsky (1915a) remains unclear, but they should be considered as *Eryx miliaris*. These vague taxa include *E. miliaris* var. *roborowskii* Bedriaga, 1907; *E. miliaris* var. *koslowi* Bedriaga, 1907; *E. miliaris rarus* Čarewsky, 1916; *E. miliaris tritus* Čarewsky, 1916; *E. miliaris incerta* Čarewsky, 1916; *E. tataricus bogdanovi* Čarewsky, 1916 and *E. tataricus helluo* (Pallas, 1814) Čarewsky, 1916. Tokar (1989, 1990) studied the systematics of *Eryx* and concluded that the taxa described as *E. tataricus* should be considered as *E. miliaris* [*E. miliaris miliaris* (Pallas, 1773); *E. miliaris tataricus* (Lichtenstein, 1823); *E. miliaris speciosus* (Čarewsky, 1915)], except for the distinct species *E. vittatus* (Chernov, 1959). All other names should be discarded as invalid.

The principal error of Tokar (1989, 1990) was that he initially lumped together the samples of both species (*E. miliaris* and *E. tataricus*), especially from the sympatry zones, and in allopatric populations he often used the unreliably identified specimens or approximate localizations so common in old collections. Collections of Zoological Institute of the Russian Academy of Sciences formed the basis for Tokar's works. The same error was also noted in his studies of osteological material (Ananjeva et al., 1997). The errors caused by incorrect localization and identification of museum specimens were followed by a wrong conclusion that *E. tataricus* is a junior synonym of *E. miliaris*. We consider *E. tataricus* as a valid species comprising at least 2 subspecies *E. tataricus tataricus* and *E. t. roborowskii* (Bedriaga, 1907). The species *E. miliaris* with its subspecies *E. miliaris miliaris* and *E. m. nogaiorum* Nikolsky, 1910, *E. speciosus* Čarewsky, 1915 and *E. vittatus* Chernov, 1959 have been described as distinct species. The subspecies *E. m. nogaiorum* Nikolsky, 1910 occurs in the North Caucasus, Russia.

***Eryx miliaris nogaiorum* Nikolsky, 1910** (Figs. 46–47)

E. m. nogaiorum Nikolsky, 1910. Nikolsky, 1910, *Izvestiya Kavkazskogo muzeya*. Tiflis, V, p. 6.

Terra typica. In the original description – “Karanogayskaya steppe”; Nogayskaya Steppe between the lower streams of the Terek and Kuma Rivers (Nikolsky, 1913, 1916).

Type specimens. Lectotype: MNKNU 27350 (=ZCIKU 299) (designated by Vedmederya et al., 2009). In total, A.N. Nikolsky received 6 specimens (syntypes) from the Caucasian Museum (then National Museum of Georgia, MGT) for identification and description. Possibly, the remaining 5 syntypes are stored at MGT.

Distribution in the Caucasus. The subspecies *E. m. nogaiorum* Nikolsky, 1910 occurs in the Nogayskaya Steppe on the boundary of Chechen Republik, Dagestan and Stavropol Territory, on the coastline of the Kizliarsky Bay in Dagestan and in Kalmykia (Map 5). Some records are known in “Bazhigan sands of the Achikulak Inspectorate” (Morits, 1916a, b). Nikolsky (1916) also indicated records from Astrakhan on the right bank of the Volga River. He noted that the left and right banks of the Volga are inhabited by different species *E. miliaris* (Pallas, 1773) and *E. nogaiorum* (Nikolsky, 1910), so their ranges are bisected by this river. The latter's range is limited by the Terek-Volga interfluvium (Nikolsky, 1916). Possibly, this point of view is still valid and should be tested through research of the *E. miliaris* complex.

Habitats. Sand deserts, loose and mobile sand hills, mellow soils in wormwood-saltwort and saltwort deserts and semi-deserts. Sand boas are less frequent in clay and loess deserts, takyrs with patchy vegetation, ephedra-covered sands, ravine brinks and edges of irrigated lands.

In the Nogayskaya Steppe, near the Chervlenye Buruny village, boas live in the sand desert with singular plants of *Calligonum aphyllum* scattered 20–80 m apart from each other. They also live in deserts dominated by *Calligonum aphyllum* and covered by *Rhamnus pallasii*, *Imperata cylindrica* and *Ephedra distachya*. Here, boas are sympatric with the steppe runner (*Eremias arguta*), toad-headed agamas (*Phrynocephalus mystaceus*, *Ph. guttatus*) and the steppe agama (*Trapelus sanguinolentus*). This species is also found in the Tersko-Kumsky sands (Nogayskaya Steppe) of the Shelkovsky district of Chechen Republik where it occurs in psammophilic vegetation at 100 m asl 10–12 km to the west and north-west of the Lake Budary, 5 km away from the Starogladkovskaya village. Sparse vegetation is represented by the communities of *Artemisia tschernieviana*, *Leymus racemosus* and *Isaltis subulosa*. On sand hills, boas co-exist with *Eremias velox* and rare *Phrynocephalus guttatus*. *Ph. mystaceus* is very rare and somewhere locally extinct.



Map 5. Distribution map of *Eryx miliaris*.

Conservation status. *Eryx miliaris nogaio-rum* is included in the Red Data Books of Dagestan (2009), Kalmykia (2013), Chechen Republic (2007), Stavropolsky Krai (2013) and the Astrakhan Province (2004). It is protected in Dagestansky Reserve (Kizliarsky Bay) and Chornye Zemli Nature Reserve (Black Soils) Reserve.

FAMILY COLUBERS – COLUBRIDAE Oppel, 1811

Small, medium-sized and large snakes reaching a length of more than 3.5 m. The ventral surface of the body is completely covered by one longitudinal row of crosswise strongly widened scutes and the dorsal sur-

face consists of the rows of smooth, keeled or granule-like scales. The head is covered by small unordered or large regular shaped scutes. Like in all snakes, the shape, relief and quantitative characteristics of pholidosis play a key role in colubrid identification. The eyes are located openly and their size and topography are closely related to snake life forms. Rudimentary limbs are absent. Only right lung is developed. The left lung is absent or vestigial. Most colubrids are nonvenomous and do not have the venom-producing glands and conducting canals, but some species have grooved fangs in the back of the maxillae and quite toxic saliva. The toxic property of colubrid saliva was mentioned repeatedly also in snakes of, e.g. in the genus *Hemorrhhis*. The dental, maxillary, pterygoid and palatal bones are

toothed. Dentition is heterodont which is particularly profound on the maxillary and dental bones. The maxillae are not articulated with the intermaxillary bone. Cranial ligaments are very elastic and the skull is generally highly kinetic.

This is the richest family, comprising ca. 3000 recent species and over 300 genera. Different authors in different periods of studies split it into 10–12 subfamilies (Cadle, 1988; Dowling et al., 1983; Seigel et al., 1987; Vidal, Hedges, 2002; Lawson et al., 2005; Pyron et al., 2010, 2013; Figueroa et al., 2016; Uetz et al., 2018) which are sometimes regarded as separate families.

Colubrids include various ecological forms, such as fossorial, arboreal, aquatic and semi-aquatic species which have explored all suitable environments and developed efficient strategies of feeding and breeding (Greene, 1994, 1997). Colubrids are distributed ubiquitously on all continents, except for Antarctic, and on many oceanic islands. Their range reaches the Polar Circle in the north in Eurasia and the Cape of Good Hope in the south in Africa.

In the Caucasus, colubrid's fauna consists of 2 subfamilies: Natricinae Bonaparte, 1838 with 1 genus *Natrix* and 3 species and Colubrinae Oppel, 1811 with 11 genera and 20 species. Characteristics of these genera and their species are provided in *Handbuch der Reptilien und Amphibien Europas* (Bd.3/I, 1993; Bd.3/II, 1999) (Fig. 48). Subfamily Natricinae is considered in some phylogenetic constructions as distinct family Natricidae (Pyron et al., 2013; Zheng, Wiens, 2016; Uetz et al., 2018).

The assessment of taxonomic diversity of the groups *Elaphe* sensu lato and *Coluber* sensu lato is problematic and undergoing radical changes, stimulated by remarkable discoveries of new taxa. The modern system of colubrid systematics presented in this monograph hinges on the results of intensive phylogenetic and taxonomic studies, research of nomenclature and colubrid descriptions (Barabanov, 2002; Baran, Atattır, 1998; Bruno, Hotz, 1976; Böhme, 1999; Darevsky, Orlov, 1994; Darevsky, Ščerbak, 1993; Disi et al., 2001; Guicking et al., 2006; Helfenberger, 2001; Hoffmann et al., 2018; Jablonski et al., 2018; Khan, 1997, 2002; Khan, Khan, 2000; Lanza, 1963; Lenk et al., 2001a; Lenk, Wüster, 1999; Leviton, 1986; Marx, 1968; Nagy et al., 2004; Orlov, Tuniyev, 1992; Rehák, 1985, 1986; Schätti, 1985, 1986, 1987, 1988a, b, c, d; 2001a,b, 2004a,b; Schätti, Agasian, 1985; Schätti et

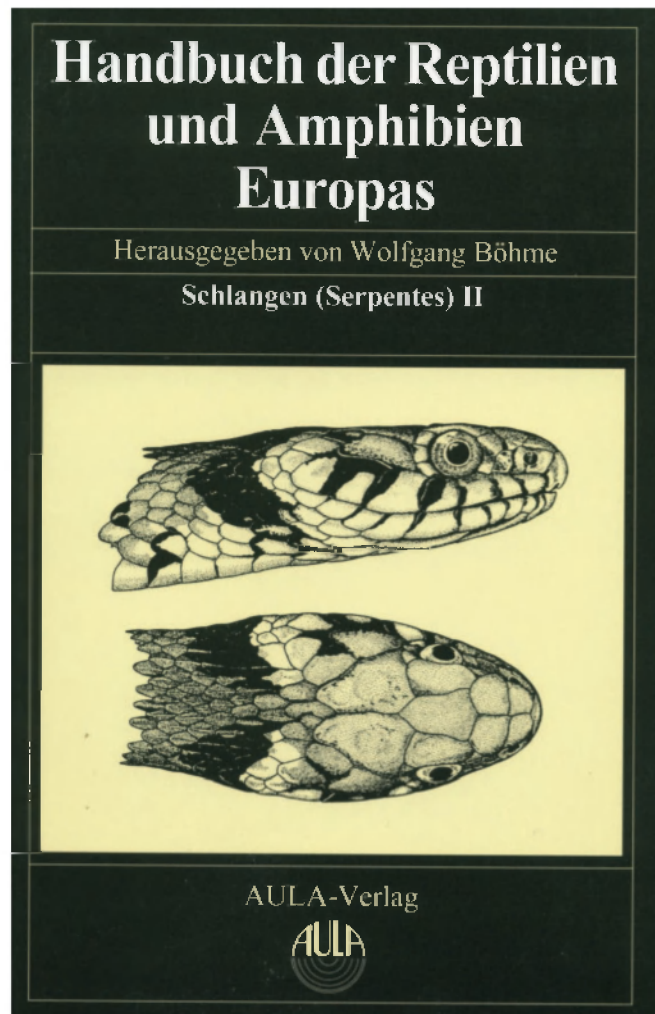


Fig. 48. Cover page of the book “Handbuch der Reptilien und Amphibien Europas”. Vol. 3/2 (1999).

al., 2001; Schätti, Desvoignes, 1999; Schätti, Charvet, 2003; Schätti, Ineich, 2004; Schätti, Lanza, 1988, 1989; Schätti, McCarthy, 2001, 2004; Schätti, Monsch, 2004; Schätti et al., 1991a,b; Schätti, Utiger, 2001; Schätti, Vanni, 1986; Schleich et al., 1996; Schulz, 1996, 2013; Tuniyev, Shammakov, 1993; Utiger et al., 2002, 2005; Utiger, Schätti, 2004; Welch, 1983, 1988; Werner, Sivan, 1991; Salvi et al., 2018).

The Palearctic species *Coluber* s.l. have been currently considered as a set of 4–5 genera: *Hemerophis* Schätti and Utiger, 2001; *Hierophis* Fitzinger, 1843; *Hemorrhoids* Boie, 1826 and *Platyiceps* Blyth, 1860. Schätti (1988d) offered to put *Coluber spinalis* (Peters, 1866) into *Hierophis*. Nagy et al. (2004) present some genetic evidence that *H. spinalis* may be associated with *Eirenis*, thus be a member of this genus. However Kharin (2011) considered this East Asian species within new monotypic genus *Orientocoluber* Kharin, 2011.

H. socotrae (Günther, 1881). is assigned to the genus *Hemerophis*. The Caucasus is inhabited by 2 genera of *Coluber* s.l.: *Hemorrhoids* and *Platyceps*.

Nagy et al. (2004) investigated the systematics of common ratsnakes *Coluber* s.l. and fossorial *Eirenis* species using the mitochondrial and nuclear DNA analysis and suggested to retain the name *Coluber* only for taxa from the Americas and to consider *Masticophis* as a junior synonym of *Coluber*. The Old World species were proposed to be assigned to *Platyceps*, *Hemorrhoids*, *Spalerosophis* and *Hierophis*. The authors note that the paraphyletic origin of the genus *Hierophis* sharing the same clade with *Eirenis* species presents a taxonomic problem. Nagy et al. (2004) demonstrate the existence of three monophyletic groups in this complex: genus *Hierophis* with all European species and the type species *Hierophis viridiflavus*; genus *Eirenis* traditionally lumping the small fossorial snakes and *H. spinalis*; genus *Dolichophis* Gistel, 1868 including the East Mediterranean species *D. jugularis*, *D. caspius*, *D. schmidti* and *D. cypriensis*.

A number of scientists (Helfenberger, 2001; Lenk et al., 2001a; Lenk, Wüster, 1999; Schulz, 1996; Utiger et al., 2002, 2005) have shown that *Elaphe* sensu lato is not monophyletic itself and comprising 12–14 genera in regard to the authors' views on systematics of Colubrinae. This issue is described in more details in a section dedicated to *Elaphe*.

Subfamily Natricinae Bonaparte, 1838

Genus Grass and water snakes – *Natrix* Laurenti, 1768

Natrix Laurenti, 1768, Specimen Medicum, Exhibens Synopsis Reptilium Emendatam cun Experimentis circa Venena et Antidota Reptilium Austriacorum, quod Autoritate et Consensu. Viennae, Joan. Thom. Trattner: 73(1–214).

Type species. *Natrix vulgaris* (= *Coluber natrix* Linnaeus, 1758). The valid name is *Natrix natrix* (Linnaeus, 1758).

Medium-sized and large snakes of body length 1200–1500 mm. Some individuals of total body length 2050 mm, including a tail, are known (Kabisch, 1999). The body is cylindrical. The cervical interception is

clear-cut. The scales are keeled, aligned in 19 rows. There are 153–193 ventral scutes and 50–86 subcaudal scutes. The anal scute is divided. The head is large, flattened and covered by symmetrical scutes. The eyes are big, with a round pupil. The maxillae have 20–25 teeth, which increase in size towards the throat. The mandibles have same-size teeth. All body vertebrae have the legible inferior processes. *Natrix* s.s. is a Palearctic genus living predominantly in the North Palearctic. True grass snakes are distributed from northwestern parts of Africa through Europe and Asia to the Persian Gulf, Afghanistan, western Pakistan, northwestern India, western China and northern Mongolia. There are 4 species in this genus: *Natrix maura* (Linnaeus, 1758); *N. megalcephala* Orlov et Tuniyev, 1987; *N. natrix* (Linnaeus, 1758) and *N. tessellata* (Laurenti, 1768).

Until recently, this genus was considered as a cosmopolitan group encompassing the North American genera *Nerodia* Baird, 1853; *Clonophis* Cope, 1888 and *Regina* Baird et Girard, 1853; Asian genera *Amphiesma* Dumeril, Bibron et Dumeril, 1854; *Rhabdophis* Fitzinger, 1843; *Sinonatrix* Rossman et Eberle, 1977; *Xenochrophis* Günther, 1864 and tropical African genus *Afronatrix* Rossman et Eberle, 1977 (Malnate, 1960; Rossman, Eberle, 1977). Phylogenetic relationships within the genus have been actively discussed using the molecular genetic techniques (see Guicking et al., 2006; Guicking, Joger, 2011).

There are three species living in the Caucasus.

Large-headed or Colchic water snake – *Natrix megalcephala* Orlov et Tuniyev, 1987 (Fig.49)

Natrix megalcephala Orlov et Tuniyev, 1987, A new species of *Natrix megalcephala* sp.nov. in the Caucasus (Ophidia: Colubridae). Trudy Zoologicheskogo instituta AN SSSR, vol. 158: 116–130, Plate 7.

Terra typica. In the original description – “Pitsunda, Abkhazia, West Caucasus”.

Type specimens. Holotype ZISP 11846, paratypes ZISP 9093, 18794, 11585, 11243, 18794, 11247, 11862, 9591, 18211, 16653, 5273.

Distribution. Endemic of the Caucasus distributed entirely within the Caucasus Ecoregion in Russian West Caucasus, Georgia, north-western Azerbaijan and north-eastern Turkey. Conspecificity of *N. megalcephala* and *N. natrix scutata* (Jandzik, 2005) could be resulted either from misidentification (melanistic *Natrix natrix scutata* (Pallas, 1771) assigned as *N. mega-*



Map 6. Distribution map of *Natrix megalcephala*.

locephala) or from morphological studies of juvenile individuals and their comparison with the originally described species. It should be noted that *N. megalcephala* is a distinctive Colchic relict with its unique morphology, chorology and ecology. Melanism, a common but not essential feature of this and other *Natrix* species, was not used in description (Orlov, Tuniyev 1987, 1992; Orlov, Tunijew, 1999). Study of mtchondrial phylogeography, contact zones and taxonomy of grass snakes (*Natrix natrix*, *N. megalcephala*) show no evidence for the distinctiveness of *N. megalcephala* (Kindler et al., 2013)

Distribution in the Caucasus. West Caucasus from the vicinity of Gelenjik (northern slope of the Markotkh Ridge, Aderba River) to the Çoruh River in

the south-west and then along the Black Sea slope of the Pontic (Lazistan) Ridge to Rize, Turkey (Map 6). From the Aderba River, the range boundary passes over the Greater Caucasus Ridge and stretches along the foothills to the junction of the Urushten and Malaya Laba Rivers. Isolated populations are found on the southern slopes of the East Caucasus near Lagodekhi and Vartashen and also on the eastern slope of the Adjara-Imereti Ridge, near Borjomi (Georgia). Recently, a new record was documented in a maritime area of northeastern Turkey, near the Kamhilem village (Ilgaz et al., 2005) and near Arhavi (Tuniyev et al., 2014).

Habitats. Colchic forests with evergreen understorey; beech, chestnut and alder forests; cherry laurel and



Fig. 49. Large-headed or Colchic water snake, *Natrix megalcephala* – Abkhazia.

azalea oakeries. In the Sochi suburbs, the range extends up to conifer-broadleaf forests (beech-fir forests on the Mt. Chugush), treeline near the Lake Khmelevskoe on the Esto Ridge (1750 m asl) and the shadow effect sites on the Aishkha Ridge (1800 m asl). Near the Lake Karakol, Maden (Turkey), the species occurs in subalpine forbs meadows and crooked tree stands at more than 1800 m asl (Mt. Trial). On the northern slope of the North-West Caucasus, water snakes do not move over 1000 m asl. This species also fares well in human-modified landscapes (after-forest glades, tea plantations, secondary hornbeam forests), but is best fit to living near rapid mountain streams.

In Turkey, a dead female was found on a tea plantation among *Alnus glutinosa*, *Castanea sativa* and *Fagus orientalis*. The species *Ommatotriton ophryticus* (Berthold, 1846), *Pelophylax ridibundus* (Pallas, 1771) and *Natrix natrix* (Linnaeus, 1758) were recorded in the same habitat. The post-mortem has shown the presence of 32 eggs (Ilgaz et al., 2005).

Conservation status. At the workshop on IUCN assessment of Palearctic reptiles and amphibians in Antalya, Turkey in September 2008, its status was designated as VU A4ce. It is also included in the Red Data

Books of the Krasnodar Territory (2007, Near Threatened, category 3) and the Republic of Adygheya (2012). Large-headed snakes do not congregate. The highest congregation of up to 3 individuals/km was recorded in riparian alder-willow forests. The highest density (5 snakes/ha) is estimated in rocky outcrops of the Psou Ridge. The limiting factors are riverside exploration, direct killing by humans, and declining of amphibian populations by introduced raccoons. Water snakes are protected in Kavkazsky Biosphere Reserve, Sochi National Park and Bolshoi Tkhach Natural Park (Russia); Pitsunda-Mussera Reserve, Pskhu-Gumista Reserve and Ritsa Relict National Park (Abkhazia); Lagodekhi Reserve and Kintrishi Reserve (Georgia); Zakataly Reserve (Azerbaijan). The Guam Gorge Natural Park including habitats on the northern macroslope of the Greater Caucasus is pending for establishment.

Grass snake – *Natrix natrix* (Linnaeus, 1758)
(Figs. 50–53)

Coluber natrix Linnaeus, 1758, Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis,

locis. Tomus I. Edtio decimal, Reformata. Laurenti Salvii, Holmiae: 216 (824) pp.

Terra typica. In the original description – “Europe”, in 1928 designated as “Sweden” (Mertens, Müller, 1828; Kabisch, 1999).

Type specimens. The type specimen has been stored in the Linnaean collection of the Zoological Museum, Uppsala University, Sweden: *Natrix natrix* – ZMUU No. 3 (= *Coluber natrix*) (Ananjeva et al., 1997).

Distribution. Europe aside from Ireland, northern Britain and northern Scandinavia (up to 67°N), north-western parts of Africa and a vast range from West Asia to north-western Mongolia, south of East Siberia, northern China and south-western Iran. High intraspecific variation led to designation of 47 scientific names and 4 (Thorpe, 1979), 9 (Bannikov et al., 1977; Ananjeva et al., 1998) and 13 (Kabish, 1999) subspecies. Contradictory conclusions partially ensue from repeating colouration patterns in different taxa. Such *homologous series* (Vavilov, 1920) of colour variations are common in many other colubrid and viperid species (Nilson et al., 1995; Tuniyev, 2000b).

Russia and adjacent countries are inhabited by three subspecies. *N. n. natrix* (Linnaeus, 1758) occurs in most of the European part of the former USSR, excluding Zavolzhie (area behind the Volga River), extreme southeastern and eastern parts of the Ciscaucasus. *N. n. scutata* (Pallas, 1771) lives in the West Caucasus, Volga basin, Ural Mts., West Siberia, Kazakhstan, Buryatia and the southern part of the East Siberia. *N. n. persa* (Pallas, 1814) is known from the eastern Ciscaucasus, eastern and southern Transcaucasus, southwestern Turkmenistan and some sites in the Crimean Peninsula. In Turkmenistan, the grass snake occurs in the Atrak riverside and the spawning canal linking the Lake Maloe Delili with the Caspian Sea (Orlov, Tuniyev, 1987).

Distribution in the Caucasus. Here we consider 3 subspecies:

1) *Natrix natrix natrix* (= *Coluber natrix* Linnaeus, 1758)

2) *Natrix natrix persa* Pallas, 1814

Coluber persa Pallas, 1814, Zoographia rossoasiatica, sistens omnium animalium extenso imperio rossico et adjacentibus maribus observatorum recensionem... t. 3, Petropoli, Acad. Scient.: 428 p.

Terra typica. In the original description – “Persien” (Persia, today’s Iran).

Type specimens. Not preserved.

3) *Natrix natrix scutata* Pallas, 1771

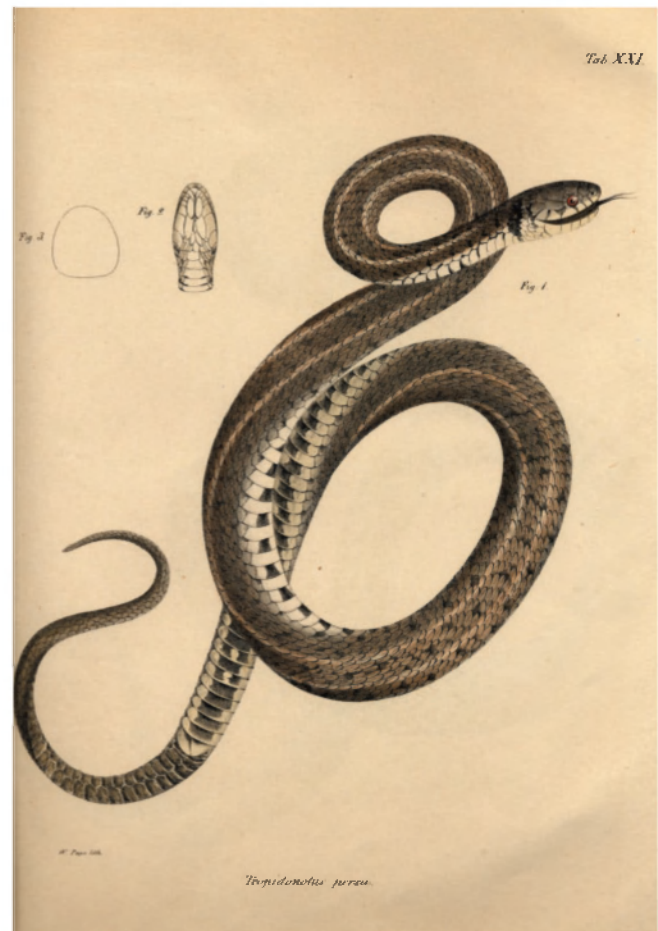


Fig. 50. A drawing of the grass snake, *Coluber natrix* (= *Natrix natrix*) from the book “Fauna Caspio-Caucasia nonnullis observationibus novis” by E.I. Eichwald (1841).

Coluber scutatus Pallas, 1771, Reise durch verschiedene Provinzen des Russischen Reichs. Kayserlichen Acad. Wissenschaften, 1771–1776, St. Petersburg, 1771, 1, 12: 3–504 pp., 25 pl.

Terra typica. In the original description – “Gurjev, N-Küste des Kaspischen Meeres” (Gurieiev, the northern coast of the Caspian Sea).

Type specimens. Not preserved.

Distribution in the Caucasus. Almost all Caucasus, except for the arid areas of the Kura-Arax Lowland, Apsheron Peninsula and Greater Caucasus highlands deprived of water (Map 7). The species is known also from northeastern Turkey and north-western Iran. The chain of isolated occurrence sites is stretched along the Black Sea coast of the Caucasus. The nominate subspecies likely exists only in the Priazovskie Plavni (Azov Sea floodplains) and the Primanychie (Manych riverside). Most of the Ciscaucasus, North Caucasus, Black Sea coast of the Caucasus and Anatolia are inhabited by *N. n. scutata*. The range of *N. n. persa* is



Fig. 51. A drawing of the grass snake *Tropidonotus persa* (= *Natrix natrix persa*) from the book “Natural history of all animals in the Russian Empire” by I.A. Dvigubsky (1832).



Fig. 52. Grass snake, *Natrix natrix persa* – Samur River, Dagestan, Russian Federation.



Map 7. Distribution map of *Natrix natrix*.

spread from southern Dagestan through all eastern and southern Transcaucasus to Iran inclusive. The last two subspecies co-exist in the Rubas and Samur riversides.

Habitats. A riparian, heliophilic, intrazonal species occurring near water flows in different habitats. It is recorded in reedbeds of the eastern Priazovie (Azov Sea area), Ciscaucasus (including the Nogayskaya Steppe), Kura-Arax Lowland, Ararat Valley, steppes and forest-steppes, broadleaf (predominantly oak) forests, riverine and lowland alder, willow and tamarisk stands, mountain grasslands and subalpine meadows of the Lesser Caucasus and the Armenian-Javakheti Highland. In Dagestan's Tabasaran district, it lives at 100–250 m asl in a rough terrain along the northern foothills of the Greater Caucasus Ridge covered by dominant poplars

Populus hybrida and sub-dominant *Quercus robur*. In riparian vegetation of the Rubas River basin with vast beds of *Phragmites communis* and *Typha angustifolia*, grass snakes are sympatric with *Natrix tessellata*, *Emys orbicularis*, *Mauremys caspica*, *Mauremys caspica*, *Pelophylax ridibundus*.

In the area of the Lake Budary (Shelkovsky district, Chechen Republik), grass snakes are common in riparian vegetation, water springs with *Phragmites communis* beds over water surface, lake marshes and recently isolated lakelets with *Holoschoenus vulgaris*, *Carex* sp. and *Lythrum salicaria*. Here, these snakes co-exist with *Natrix tessellata*, *Emys orbicularis*, *Dolichophis caspius*, *Lacerta strigata*, *Pelobates fuscus*, *Hyla orientalis* and *Pelophylax ridibundus*. In contrast,



Fig. 53. Grass snake, *Natrix natrix scutata* – Lazarevskoye, Krasnodar Territory, Russian Federation.

near the Budary water snakes are extremely rare in true sedge meadows emerging along the coastlines and covering the dryout shallow freshwater lakes. In the Itum-Kalinskaya Depression, this species is rare in the riverine Hippophae rhamnoides forest of the Chanty-Argun floodplain. The species *Hyla orientalis*, *Bufo viridis*, *Pelophylax ridibundus* and *Natrix tessellata* are common in these habitats.

In the surroundings of the Mt. Chayniza (Gobustan Reserve, Azerbaijan), grass snakes are found in *Salsola gemmascens* – *S. nodulosa* desert on a vast maritime terrace among the scattered steep hills intersected by ravines and gullies. The sympatric species are *Eremias velox*, *Ophisops elegans*, *Testudo graeca*, *Telescopus fallax*, *Xerotyphlops vermicularis*, *Eirenis collaris*, *Platyceps najadum*, *Hemorrhoids ravergieri*, *Dolichophis schmidtii* and *Macrovipera lebetina*. In Gobustan,

snakes also occur in a narrow strip of tamarisk-scrub sand desert along the ephemeral creek. The subshrubs are represented by *Caragana* sp. and *Salsola ericoides*. The other reptiles living here are *Ophisops elegans*, *Hemorrhoids ravergieri* and *Macrovipera lebetina*. In the Meghri district of southern Armenia, the species is recorded near springs surrounded by willow-blackberry thickets giving home to *Bufo viridis*, *Hyla savignyi* and *Eirenis persicus*. Grass snakes reach elevations over 2000 m asl in the southern Transcaucasus, but do not move over 1000 m in the North Caucasus. The only exceptions are the Charodinsky district and the Samur riverhead in Dagestan where snakes are recorded at 1800 m. On the Black Sea coast of the Caucasus, all records of this species are confined to the Pleistocene maritime lowlands (Imeretinskaya, Pitsunda, Colchis and others) and river mouths (Pshada, Shakhe etc.),

more seldom to the streams on maritime hills (Navagir Ridge).

Conservation status. Abundance is more or less stable; somewhere grass snakes form large congregations. At the workshop on IUCN assessment of Palearctic reptiles and amphibians in Antalya, Turkey in September 2008, its status was designated as LC. The species is protected in a number of reserves and national parks of the Caucasus.

Dice snake – *Natrix tessellata* (Laurenti, 1768)
(Figs. 54–55)

Coronella tessellata Laurenti, 1768, Specimen Medicum, Exhiben Synopsin Reptilium Emendatam cun Experimentis circa Venena et Antidota Reptilium Austriacorum, quod Autoritate et Consensu. Wien, J. Thom. Trattnem: 87(1–214), tab. V, fig.1.

Terra typica. In the original description – “in Japidia (=Lapidia), vulgo Cars (=alpine meadow)” (karst in north-western Yugoslavia) (in Gruschwitz et al., 1999); Japidia, Italy (clarified in Ananjeva et al., 2006).

Type specimens. Not designated.

Distribution. From south-western France, Rhine River valley and eastern part of North Africa through Central and South Europe, Asia Minor and Central Asia to the Persian Gulf, Afghanistan, Pakistan, north-western India and north-western China (Gruschwitz et al., 1999; Mebert, 2011). In the Middle East, it lives in Iraq, Syria, Jordan, Israel and the Nile River delta in Egypt. An isolated population is recorded in Yemen. In the former Soviet Union, the dice snake is spread on the Black Sea and Azov Sea coasts in Russia and Ukraine, in the Caucasus, Central Asia and Kazakhstan. In Tajikistan it is absent only in the eastern Pamir. In Turkmenistan, it occurs on coastlines and islands in the Caspian Sea, along the Atrek and Sumbar riversides, near small creeks and streams of the Kopetdag and Kugitangtau and in the basins of the Tedjen, Mugrab and Amu Darya Rivers. Melanistic individuals are often recorded near the top levels of altitudinal distribution (Lake Sevan) (Tuniyev et al., 2011).

Distribution in the Caucasus. Dice snakes occur throughout most of the Caucasus (Tuniyev et al., 2011) along the big and small water flows and along the Azov, Black and Caspian Sea coastlines (Map 8). Capable of living in salt water, they can occupy areas not available to other *Natrix* species.

Habitats. Dice snakes occur in different habitats. *Natrix tessellata* inhabits river valleys and canyons

covered by forest vegetation including subtropical polydominant colchic forest with dense undergrowth as well as the slow-moving lowland rivers of alluvial plains and any open stretches of river banks, seas and alpine lakes with some microstructure along their banks and shores deprived of arboreal and shrub vegetation (Tuniyev et al., 2011). Their life is strongly associated with water, but hibernacula can be located on steep slopes, usually of eastern and southern exposures. These reptiles live in river valleys, woody canyons (including dense Colchic forest with evergreen understorey) and in treeless riversides, sea and lake shores (Sevan).

In the Tabasaran district of Dagestan, snakes were recorded at 100–250 m asl in a rough terrain along the northern foothills of the Greater Caucasus Ridge, in the Rubas riverside covered by poplar forests with *Phragmites communis*, *Typha angustifolia* and *Bolboschoenus maritimus*. The sympatric species are *Natrix natrix*, *Emys orbicularis*, *Mauremys caspica* and *Pelophylax ridibun-*



Fig. 54. A drawing of the dice snake, *Tropidonotus hydrus* (= *Natrix tessellata*) from the book “Fauna Caspio-Caucasia nonnullis observationibus novis” by E.I. Eichwald (1841).



Fig. 55. Dice snake, *Natrix tessellata* – Khosrov Reserve, Armenia

dus. In the Itum-Kalinskaya Depression, this species is common in the riparian *Hippophae rhamnoides* forest with the undergrowth of *Berberis vulgaris* and *Rosa canina* growing along the Chanty-Argun floodplain. Dice snakes share this habitat with *Hyla orientalis*, *Bufo viridis* and *Pelophylax ridibundus*. In the surroundings of the Mt. Chayniza (Gobustan Reserve, Azerbaijan), snakes are found in *Salsola gemmascens* – *S. nodulosa* desert on a vast maritime terrace among the scattered steep hills intersected by ravines and gullies. The other reptiles living here are *Eremias velox*, *Ophisops elegans*, *Testudo graeca*, *Telescopus fallax*, *Xerotyphlops vermicularis*, *Eirenis collaris*, *Platyceps najadum*, *Dolichophis schmidtii*, *Hemorrhois ravergieri* and *Macrovipera lebetina*. Snakes also occur here in a narrow strip of tamarisk-scrub sand desert along the ephemeral creek where the patches of scrubs are scattered among the tamarisk trees. The shrubs are represented by *Caragana* sp. and

Salsola ericoides. The sympatric reptiles are *Ophisops elegans*, *Hemorrhois ravergieri* and *Macrovipera lebetina*. In the Lachin district, dice snakes occur on interchanging rocky and gentle (<30°) hills at 600–800 m asl in the Aker riverside. The species *Lacerta media*, *Darevskia raddei*, *Paralaudakia caucasia*, *Xerotyphlops vermicularis*, *Eirenis modestus*, *E. collaris*, *Platyceps najadum*, *Macrovipera lebetina* and *Bufo viridis* live here as well.

In Armenia's Arpa River basin, between Eghegnadzor and Areni, dice snakes occur at 800–1000 m asl in the rocky canyon covered with riparian forests dominated by *Salix australior* and *Ulmus carpinifolia* with the accompanying species *Morus alba*, *Elaeagnus caspica* and *Tamarix meyeri*. The sympatric species are *Bufo viridis*, *Hyla savignyi*, *Pelophylax ridibundus*, *Pseudopus apodus*, *Ophisops elegans*, *Lacerta media*, *Hemorrhois ravergieri*, *Dolichophis schmidtii* and *Macrovipera lebetina*.



Map 8. Distribution map of *Natrix tessellata*.

Dice snakes can also be found in phryganoid vegetation on the right steep (up to 40°) bank of the Arpa River which is exposed to the southeast and covered by *Rhamnus pallasii* and *Ephedra procera*. Snakes share this habitat with *Xerotyphlops vermicularis*, *Dolichophis schmidtii*, *Hemorrhhois ravergieri*, *Eirenis punctatolineatus*, *E. collaris*, *Heremmites septemtaeniatus transcausicus* and *Bufo viridis*. In the Meghri district (southern Armenia), *N. tessellata* is recorded in the Meghri riverhead and on the southern macroslope of the Meghri Ridge, in phryganoid oakeries of *Quercus macranthera* with stand density 0.1–0.3. The other reptiles are *Darevskia raddei*, *Lacerta media*, *L. strigata*, *Ablepharus bivittatus*, *Montivipera raddei*, *Paralaudakia caucasia*, *Platyceps najadum* and *Dolichophis schmidtii* (Tuniyev et al., 2011).

Dice snake is able to imitate defensive behavior of Lebetine viper (Tuniyev et al., 2011).

On the Black Sea coast of the Caucasus and in the Ciscaucasus, dice snakes are not recorded at more than 600 m asl, but in the southern Transcaucasus they move up to 2000 m. These reptiles can swim off the seacoast and hunt on sea fishes.

Conservation status. Abundance is rather stable, in some places big congregations are formed. Before the 1940s, ca. 30,000 skins of dice snakes were purveyed per annum on the Caspian Sea (Markov, 1934). Protected in reserves and national parks of the Caucasus (Kavkazsky, Pitsunda-Mussera, Colchic, Kyzyl-Agach, Sevan, Khosrov Forest and others) (Tuniyev et al., 2011).

Subfamily Colubrinae Opperl, 1811

Genus *Dolichophis* Gistel, 1868

Dolichophis Gistel 1868, Die Lurche Europas. Ein Beitrag zur Lehre von der geographischen Verbreitung derselben. In: Gistel, J. (Ed.), Blicke in das Leben der Natur und des Menschen. Verlag von Ed. Wartig, Leipzig: 274 p. (144–167).

Type species. *Coluber caspius* 1789 (in Van Wallach et al., 2014). The valid name is *Dolichophis caspius* (Gmelin, 1789).

Large snakes of body length occasionally exceeding 2500 mm. The head is large and its cervical interception is clear-cut. The body is cylindrical, almost round in section. The scales are smooth aligned in 19 rows around the middle of the body. Each scale has two apical fossae. The ventral scales form a longitudinally extended lateral ridge. The ventral scales are 189–211, subcaudal 80–113 pairs, supralabial 8, sometimes 7–9. The anal scute is divided.

The genus includes 4 species: *Dolichophis caspius* (Gmelin, 1789), *Dolichophis cypriensis* (Schätti, 1985), *Dolichophis jugularis* (Linnaeus, 1758) and *Dolichophis schmidtii* (Nikolsky, 1909) Their distribution is spread over the East Mediterranean (including big islands), steppes of South-east Europe (Moldova, Russia, Ukraine), Caucasus, Turkey, Iraq, Syria, Lebanon, Israel, Jordan, western and northern Iran and south-western Turkmenistan. There are two species living in the Caucasus.

Caspian whip snake – *Dolichophis caspius* (Gmelin, 1789) (Fig. 56–57)

Coluber caspius Gmelin, 1789, Caroli a Linne Systema Nature. Tom.I. Pars III. G.E. Beer, Lipsiae, (1), 112: (1033–1516) pp.

Terra typica. In the original description – “Ad litora maris caspi” (coast of the Caspian Sea); “Jaikische Steppen, Unterlauf des Ural-Flussen” – Yaik Steppe, lower Ural River (in Mertens, Müller, 1928; Schätti, 1988d; Ščerbak, Böhme, 1993); lower Volga River (in Ananjeva et al., 2006).

Type specimens. Holotype, not designated, location unknown (Van Wallach et al., 2014).

Distribution. Europe from Hungary along the Danube River to southern Romania, Moldova, southern Ukraine and Crimea and then to the Rostov Province,

North Caucasus and western Transcaucasus (an isolated population in north-eastern Anatolia), Povolzhie or Volga Region (Volgograd and Astrakhan provinces) and northwards to 50° N. In the east, the Caspian whip snake permeates into Asia, the Volga-Ural interfluvium in western Kazakhstan.

Until recent times, this species was considered as subspecies *Coluber* (= *Dolichophis*) *jugularis caspius* (Gmelin, 1779), *Coluber* (= *Dolichophis*) *jugularis jugularis* (Linnaeus, 1758) (Europe), *Coluber* (= *Dolichophis*) *jugularis schmidtii* (Nikolsky, 1909) and *Coluber* (= *Dolichophis*) *jugularis asianus* (Boettger, 1879) (northwestern Iraq and northeastern Syria) (Terentiev, Chernov, 1949; Bannikov et al., 1977).

Distribution in the Caucasus. A foothill strip along the Black Sea coast from Sukhumi to the Taman Peninsula inclusive, steppe and forest-steppe zones in the Krasnodar Territory and the Republic of Adygheya, Stavropol Territory, northern foothills of the Karachaevo-Cherkessk Republic, Kabardino-Balkaria, North Ossetia-Alania, Chechen Republik and Dagestan (Map 9). On the western coast of the Caspian Sea including Chechen Island (Mazanaeva, Sultanova, 2001), it reaches the boundary of Dagestan and Azerbaijan (Khachmas) where it is sympatric with the closely related *Dolichophis schmidtii*, proving the species-level identity of these taxa. Isolated populations are recorded in Georgia in the east suburb of Rustavi, Kvemo Kartli Region in the valley of the Kura River (Bekoshvili, Doronin, 2015) and in the Artvin Depression, Çoruh riverside in the Turkish part of the Caucasus Ecoregion. This snake was recorded in chestnuts in the lower part of the gorge of Murgul River and on the right bank of Chorokh River opposite the city of Artvin. Apparently, there is a small isolated population of this species in the Artvin Basin and in the vicinity of town of Borchkha. During five seasons we only saw it there twice (B. Tuniyev et al., 2014).

Habitats. In the Black Sea region of the Caucasus, this species occurs in a variety of habitats: broadleaf (mainly oak) forests, juniper and pistachio sparse forests, sometimes also polydominant broadleaf-mixed Colchic-type forests with evergreen understorey. In the Ciscaucasus, it is confined to forest-steppes, steppes and semi-deserts). The preference is given to hard clayey slopes and ravine brinks covered by trees and shrubs. In the North Caucasus, snakes permeate into sand hills (Nogayskaya Steppe) and floodplains (Priazovskie Plavni) where they actively swim and hunt in reeds.



Fig. 56. Caspian whip snake, *Dolichophis caspius*, adult individual – vicinity of Sochi, Krasnodar Territory, Russian Federation.



Fig. 57. Caspian whip snake, *Dolichophis caspius*, juvenile individual – vicinity of Novorossiysk, Krasnodar Territory, Russian Federation.



Map 9. Distribution map of *Dolichophis caspius*.

In the Dagestan part of the Nogayskaya Steppe, near the Chervlenye Buruny village snakes live in fescue-wormwood steppe dominated by *Artemisia lercheana*, *A. taurica*, *A. arenaria*, *Festuca sulcata* and patchily scattered *Juno caucasica* and *Tulipa biebersteiniana*, as well as in forbs-cereal-moss meadow-steppe and *Cotinus-Rhamnus* forest-steppe. In meadows, the dominant species are *Euphorbia* sp., *Orchis* sp., *Phleum pratense*, *Poa bulbosa*, *Cardamine* sp. and others. The moss *Forstula* sp. *synusia* is common.

In forest-steppe, the trees *Cotinus coggygria* and *Rhamnus pallasii* prevail. Singular individuals of *Populus hybrida* grow near the artesian springs. Herbal composition is identical to what is described above. In the Shelkovsky district of Chechen Republik, near the

Lake Budary and in adjoining Tersko-Kumsky sands of the Nogayskaya Steppe, whip snakes are common in scrublands dominated by *Rhamnus pallasii* on sand slopes. The lizard *Lacerta strigata* is common here, but *Eremias arguta* and *Pseudopus apodus* are rare. These species can be frequently found in *Cotinus-Rhamnus* communities growing on northern slopes with dominant *Cotinus coggygria*, sub-dominant *Rhamnus pallasii* and singular *Rosa* sp., *Crataegus pallasii*, *Lonicera* sp. and *Prunus stepposa*. The dominant herbs are *Asparagus* spp.

In Shelkovsky district, Chechen Republik, Caspian whip snakes are also found in forest glades, *Elaeagnus angustifolius* plantations and other places with near-surface groundwater and dense grass cover be-

neath the trees of *Elaeagnus angustifolia*. A wide assortment of suitable habitats can be added by wetlands, reedbeds on the Lake Budary and its derivative lakelets. The sympatric reptiles in these habitats are two species of *Natrix*, *Lacerta strigata* and quite rare *Pseudopus apodus*. Since recent times, in the Nogayskaya Steppe the species also spreads over the high sand hills with scattered vegetation. In the Artvin Depression of Turkey, it occurs among cliffs with sparse Mediterranean vegetation composed of *Pinus pinea*, *Arbutus andrachne*, *Cistus tauricus* and *C. salviifolius*.

Conservation status. At the workshop on IUCN assessment of Palearctic reptiles and amphibians in Antalya, Turkey in September 2008, its status was designated as LC. As a species of decreasing population and shrinking habitats, the Caspian whip snake is included in the Red Data Books (Vulnerable) of the Krasnodar Territory (2017), Adygheya (2012), Kabardino-Balkaria (2000), North Ossetia-Alania (1999), and Ingushetia (2007) republics, Stavropol Territory (2013), Kalmykia (2013) and Astrakhan Province (2014). Caspian whip snakes live well in human-transformed landscapes like settlements, vineyards, garbage dumps, tea plantations and others.

Population decline is linked with direct killing by humans and road kills on highways of the Taman Peninsula and near Gelenjik. Whip snakes verge on the brink of extinction on the Black Sea coast; to the south of Tuapse they survive only in isolated populations. Population density is low everywhere, except for some sites in the north-western Transcaucasus and plains of Dagestan. This species is protected in Sochi National Park, Dagestansky and Rostovsky Reserves. Parts of populations are safeguarded in the Khosta district of Kavkazsky Biosphere Reserve (yew-boxwood grove) and in a number of sanctuaries (Priazovsky, Bolshoi Utrish, Abrausky, Psebaisky, Samursky and others). It is essential to establish Novorossiyskiy Reserve (Tuniyev, Nilson, 1995) and several zoological micro-sanctuaries or natural monuments in sites with viable populations. Species conservation on the federal level is recommended.

Red-bellied racer – *Dolichophis schmidtii* (Nikolsky, 1909) (Figs. 58–59)

Coluber schmidtii Nikolsky, 1909, New for the Caucasus species of reptiles. *Izvestiya Kavkazskogo muzeya*. Tiflis, vol. IV: 303.

Terra typica. 1) “Deirušty ad fl. Bolgar-čai, Mugan merid. 27.III.1907 (leg. Schmidt et Schelkovnikov); in salsis Adži, Mugan centr. 29.III.1907 (leg. Schmidt et Schelkovnikov); pag. Ešakči, regio septentr. distr. Lenkoran. 29.IV.1907 (leg. Kaznakov and Schelkovnikov); Tiflis, hortus botanicus. (leg. W.Klippert)” – from A.M. Nikolsky’s (1909a) description. Then he wrote (p. 305): “*This snake was found in 1907 by A.N. Kaznakov, R.G. Schmidt and A.B. Shelkovnikov during their trips to the Mugan Steppe, in the number of 6 individuals in different parts of the Mugan Steppe, namely near the Anji alkaline lands, in the vicinity of the Deirushty village in the southern Mugan and not far from the Eshakchi village in the north of the Lenkoran district. Moreover, 2 individuals were recorded by V. Klipper in the botanic garden of Tiflis*” (Nikolsky, 1909a).

2) “Deirushty am Fluß Bolgar-Tschai, Salzsteppe Adshi (mittlere Mugan-Steppe), Eschaktschi (Lenkoran-Gebiet) und Tiflis” – in Mertens, Wermuth, 1960; Ščerbak, Böhme, 1993.

3) Transkaukasus [“Mugan-Wüste, Lenkoran District und Tiflis”] – in Schätti, 1988d.

4) “Lenkoran i Saliy, Talyshskie gory (Azerbaijan)” (Lenkoran and Saliy, Talysh Mts. (Azerbaijan) – in Ananjeva et al., 2006.

5) Terra typica restricta: “in salsis Adži, Mugan centr.” [= Adzhi village, Azerbaijan] – in Vedmederya et al., 2009 (the *terra typica* is restricted because of lectotype designations).

Type specimens. The type series consisted of 8 juvenile individuals – syntypes [maximum size: SVL 390 mm, Lcd 87 mm (c.304–305)]. Two syntypes were found in collections of the Natural History Museum of Kharkov University which allowed to designate the lectotype as MNKNU 14935 (“in salsis Adži, Mugan centr” [= Adzhi village, Azerbaijan]. Leg.: R. G. Schmidt and A. B. Schelkovnikov, 29.III.1907] and paralectotype MNKNU 14934 (“pag. Ešakči, regio septentr. Distr. Lenkoran” (= Eshakchi village, Lenkoransky District, Azerbaijan). Leg.: A. N. Kaznakov and A. B. Schelkovnikov, 29.III.1907 – in Vedmederya et al., 2009).

Taxonomic notes. In the original description of *Coluber schmidtii*, Nikolsky (1909a) wrote: “On plastic characters, the described species is very similar with the species *C. quadrivirgatus* Boie [= *Elaphe quadrivirgata* (Boie, 1826) – islands of Kunashir and Hokkaido, Japanese islands], and in Boulenger’s *Catalogue of the Snakes in the British Museum I did not find any differences of this species from C. schmidtii*”.



Fig. 58. Red-bellied racer, *Dolichophis schmidtii*, adult individual – Meghri, Armenia.



Fig. 59. Red-bellied racer, *Dolichophis schmidtii*, juvenile individual – Meghri, Armenia.



Map 10. Distribution map of *Dolichophis schmidtii*.

A comparison of geographically so distant species from different genera looks unjustified. The description of snake colouration by Nikolsky (1909a) is incomplete: “The top of the body is gray with 6 longitudinal rows of small black speckles; the top of the head is gray with elongated and vague black blotches; ... the belly is white, without blotches; the lower side of the tail is yellowish”. It does not correspond the colouration of adult *Coluber schmidtii* (*Dolichophis schmidtii*), nor it agrees with amended descriptions of colour patterns in adult snakes provided by Nikolsky in his subsequent publications.

In the most valuable works by Nikolsky “Reptiles and amphibians of the Caucasus” (1913) [*Zamenis gemonensis* (Laurenti, 1768) (in part of the East

Transcaucasus = *Dolichophis schmidtii*)] and “Fauna of Russia and adjacent countries. Reptiles” (1916) a [*Zamenis gemonensis schmidtii* (Nikolsky, 1909) (= *Coluber schmidtii* Nikolsky, 1909)], colouration is described as follows: “Cherry or red-brown on the top, bright coral with nacre-pink tints on the bottom; juveniles are gray with six rows of longitudinal rows of small black speckles on the top”. This description fully coincides with diagnostic colour pattern of *Dolichophis schmidtii* (Nikolsky, 1909a). The body size of *Coluber* (= *Dolichophis*) *schmidtii* indicated by Nikolsky (total length up to 390 mm, tail length up to 87 mm) clearly confirm his subsequent conclusion that in the species description he dealt only with juveniles, so the description was incomplete and colour patterns could

be attributed only to immature individuals. Adults occasionally reach over 2500 mm in length, including a tail, but are usually 1600–1700 mm. Over age, they change body colour from gray to red-brown and even to crimson.

Distribution. The area from central Anatolia to Syria, Lebanon and the eastern Transcaucasus and then through northern Iran to southwestern Turkmenistan.

Until recently, the red-bellied racer (*Dolichophis schmidti*) was considered as a subspecies *Coluber jugularis schmidti* (Nikolsky, 1909) (= *C. jugularis erythrogaster* Fischer, 1832). In the northwestern limit of its distribution range, it inhabits southwest regions of South Ossetia in semiarid landscapes on the low altitudes where it is quite rare (Tuniyev et al., 2017).

Distribution in the Caucasus. Northern Turkey, Iran, Armenia, eastern Georgia, South Ossetia, Azerbaijan and southern Dagestan (Map 10). In Dagestan, this racer co-exists with the closely related *Dolichophis caspius*, what confirms species distinctiveness of both these taxa.

Habitats. In the northern part of their range, red-bellied racers occur in foothill and maritime zones up to 200 m asl. In the eastern and southern Transcaucasus, they move up to 1600 m and in the Meghri Ridge of southern Armenia they cross the 2000 m line. Racers also live in riverine areas, on arid and waterless shrubby slopes, in mountain steppes, juniper sparse forests, orchards and coastal sands, sometimes in sub-alpine meadows. They prefer the habitats with dense vegetation, near the water. In Gobustan Reserve of Azerbaijan, racers inhabit a large maritime terrace with scattered steep hills interspersed by ravines and gullies at 400–600 m asl. Habitats represent the *Salsola nodulosa* desert in which racers are sympatric with *Eremias velox*, *Ophisops elegans*, *Telescopus fallax*, *Xerotyphlops vermicularis*, *Eirenis collaris*, *Platyceps najadum*, *Hemorrhais ravergieri*, *Natrix tessellata* and *Macrovipera lebetina*.

In the Lachin district, near the Mishny village, racers live in precipitous and rocky terrain in the middle elevations of the Lesser Caucasus. On cliffs and screes, vegetation comprises the primary areas and the secondary after-forest communities. The north-western slopes hanging over the right bank of the Aker River are widely covered by sibiljak comprising *Quercus macranthera*, *Spiraea crenata*, *Cotinus coggygria*, *Lonicera iberica*, *Cerasus mahaleb*, *Rosa* sp., *Berberis orientalis*

and *Viburnum lantana*. The singular individuals of *Palurus spina-christi*, *Amygdalus fenzliana*, *Pyrus zangezura*, *Crataegus orientalis*, *Juniperus oblonga*, *Ephedra procera*, *Cotoneaster* sp. and *Jasminum fruticans* also grow here. In these communities, the red-bellied racer co-exists with *Darevskia raddei*, *D. portschinskii* and *Paralaudakia caucasia*.

In Armenia, between Eghegnadzor and Areni along the Arpa River, racers occur in riparian forests growing in the rocky V-shaped meridian canyon at 800–1000 m asl. The sympatric reptiles are *Pseudopus apodus*, *Opisops elegans*, *Lacerta media*, *Natrix tessellata*, *Hemorrhais ravergieri* and *Macrovipera lebetina* and the dominant trees are *Salix australior*, *Ulmus carinifolia*, *Morus alba*, *Elaeagnus caspius* and *Tamarix meyeri*. This species can also be found in phryganoid habitats on the right steep (up to 40°) bank of the Arpa covered mostly by *Rhamnus pallasii* and *Ephedra major procera*. The other reptiles living here are *Xerotyphlops vermicularis*, *Natrix tessellata*, *Hemorrhais ravergieri*, *Eirenis punctatolineatus*, *E. collaris*, *Heremites septemtaeniatus*, and *Bufo viridis*. In the Meghri district of southern Armenia, racers are recorded in the Meghri riverhead, on the southern macroslope of the Meghri Ridge, in the phryganoid oakeries of *Quercus macranthera* with crown density 0.1–0.3. The sympatric reptiles are *Darevskia raddei*, *Lacerta media*, *Lacerta strigata*, *Ablepharus bivittatus*, *Natrix tessellata*, *Montivipera raddei*, *Paralaudakia caucasia* and *Platyceps najadum*. In the surroundings of Yerevan city, the red-bellied racer co-exists with *Macrovipera lebetina* in ravines with smooth slopes, tuff outcrops on ravine brinks and tuff breakstones among the ruderal vegetation composed of *Avena* sp., *Pyrethrum tamrutense*, *Pyrethrum* sp., *Artemisia* sp., *Salsola gemmascens*, with singular *Euphorbia* sp. and *Allium* sp.

Conservation status. At the workshop on IUCN assessment of Palearctic reptiles and amphibians in Antalya, Turkey in September 2008, its status was designated as LC. This species is quite sparse in the Caucasus and never forming high-density populations. It is preserved in some protected areas of the Transcaucasus (Khosrov Forest, Shikahogh, Turianchay, Vashlovani). It is listed in the Red Data Books of Republic of Dagestan (2009) and South Ossetia (2017). It is essential to establish a protected area in the foothills of Dagestan in order to protect the red-bellied racer and other Mediterranean and Asia Minor species.

Genus *Hemorrhois* Boie, 1826

Hemorrhois Boie, 1826, Generaltübersicht der Familien und Gattungen der Ophidier. Isis von Oken, Jena, 19 (10): 982 (981–982).

Type species. *Coluber hippocrepis* Linnaeus, 1758 (in Van Wallach et al., 2014). The valid name is *Hemorrhois hippocrepis* (Linnaeus, 1758).

Large snakes reaching a length 2000 mm. Usually, body length including a tail does not exceed 1500 mm. Tail length is about one-third of body length. The head is large and has clear cervical interception. There are 21–25 scales around the middle of the body. The maxillary teeth posteriorly enlarge and 2–3 rear teeth are separated from the anterior teeth by a small diatema.

This genus comprises 4 species: *Hemorrhois ravergieri* (Menetries, 1832), *H. nummifer* (Reus, 1834), *H. hippocrepis* (Linnaeus, 1758) and *H. algirus* (Jan, 1863). They live in North Africa, South Europe, Turkey, Transcaucasus, Central Asia, Iraq, Iran, Afghanistan and northern Pakistan, also permeating into north-western China (Xinjiang), western Kyrgyzstan, southern and eastern Kazakhstan. The Caucasus gives home to two cryptic species: *Hemorrhois ravergieri* and

H. nummifer. Interestingly, these snakes can mimic large venomous snakes (viperids) with whom they often co-exist. The most remarkable examples are imitations of *Macrovipera lebetina* and *Montivipera xanthina* by *Hemorrhois ravergieri* and *H. nummifer*

Leaden-coloured racer – *Hemorrhois nummifer* (Reuss, 1834) (Fig. 60)

Coluber nummifer, Reuss, 1834, Zoologische Miscell., Reptilien. Ophidier. Abh. Mus. Senckenberg, 1: 135(127–162).

Terra typica. In the original description – “Ägypten” (Egypt).

Type specimens. SMF 7407 (in Boettger, 1898).

Distribution. Mediterranean (Cyprus) and Aegean (Rhodes, Xanthos) islands, Anatolia, Middle East including the Sinai Peninsula, north-western Egypt, northern Iraq, north-eastern Iran, southern Transcaucasus, Central Asia and Kazakhstan. The sympatry zone with the similar-looking spotted whip snake (*Hemorrhois ravergieri*) extends from Anatolia in the west to Central Asia in the east (Schätti, Agasian, 1985; Tuniyev, 1997a; Ananjeva et al., 1998,



Fig. 60. Leaden-colored racer, *Hemorrhois nummifer* – Ekhegnadzor, Armenia.



Map 11. Distribution map of *Hemorrhois nummifer*.

2006). Possibly, this phenomenon can be considered as a good example of sympatric cryptic species (Tuniyev, 1997a). In Turkey flattened individual was found above Ardanuch settlement and was recorded on the large scree of the upper part of the watershed range of Tortum River and its left tributary near Nikah settlement (Tuniyev et al., 2014). Probably it is the westernmost record of semidesert Iranian inhabiting the same biotopes with *Hemorrhois ravergeri*.

Distribution in the Caucasus. Ararat Valley and surrounding mountains (Armenia), Nakhichevan Republic, northern Turkey and northern Iran (Map 11).

Habitats. Racers usually occur on open scrubby stony slopes and cliffs, in riparian woodlands and arid canyons. They can also be encountered in ruins and or-

chards near villages and sometimes permeate into human settlements. In the vicinity of the Nrnadzor village (Meghri district, southern Armenia), racers were recorded in a meridian canyon with numerous branches and outcrops, in juniper sparse forest on ridgetops and on westerly and northerly exposed slopes. In habitats where the leaden-coloured racer co-exists with *Ophisops elegans*, *Eremias strauchi* and *Testudo graeca*, the dominant plants are *Juniperus foetidissima* and *J. polycarpus* mixed with *Quercus infectoria* and *Celtis glabrata*. The second storey is represented by *Berberis orientalis*, *Rhamnus pallasii*, *Lonicera iberica* and *Juniperus oblonga*.

This racer is distributed at lower elevations than *Hemorrhois ravergeri*; in the Ararat Valley, its records do not exceed 1300 m asl. The aposematic behaviour

(head flattening like in viperids) is recorded. Such imitations can be particularly efficient in combination with the mimicry of sympatric vipers (*Montivipera xanthina*, *M. palaestinae*, *Macrovipera lebetina obtusa*, *M. lebetina chernovi*, *M. lebetina turanica*) coloured alike *Hemorrhoids nummifer*

Conservation status. At the workshop on IUCN assessment of Palearctic reptiles and amphibians in Antalya, Turkey in September 2008, its status was designated as LC. This species is quite rare in the Caucasus, which represents the northern margin of its global range. It is protected in Khosrov Forest and Erebuni Reserves of Armenia.

Spotted whip snake – *Hemorrhoids ravergieri* (Ménétriés, 1832) (Fig. 61)

Coluber ravergieri Ménétriés, 1832, Catalogue raisonné des objets de zoologie recueillis dans un voyage Caucase et jusqu'aux frontières actuelles de la Perse enterpris par ordre de S.M. l'Empereur. Acad. Imper. Sciences, St. Petersburg, 4, 271: 69(59–74) (No 235).

Terra typica. “Bakou, Georgia” (Baku, Azerbaijan and Georgia; from the original description in Ménétriés, 1832: 69).

Type specimens. ZISP 1750 (Zoological Museum of the Imperial Academy of Sciences, No. 1750, in Nikolsky, 1916: 103).

Distribution. From eastern Turkey and the East Caucasus through Iran, Central Asia (Turkmenistan, Uzbekistan, Tajikistan) and Afghanistan to southern Kazakhstan and north-western China (Xinjiang) (Böhme, 1993a). In Anatolia, Transcaucasus and Central Asia the spotted whip snake is sympatric with the leaden-coloured racer (Schätti, Agasian, 1985). Correct determination of distribution areas of these two species in the eastern Transcaucasus and Central Asia is complicated due to troubles with identification of *Coluber ravergieri* and *C. nummifer* from published descriptions which often lack essential details. Like *C. nummifer*, *C. ravergieri* demonstrates the aposematic behaviour and mimicry of sympatric viperids (*Macrovipera lebetina* group, *Montivipera xanthina* group). *C. r. glazunovi* (Nikolsky, 1896) described from Tajikistan has been currently considered as a junior synonym of *C. ravergieri ravergieri*, which is quite an arguable approach. Possibly, the population from Chinese Turkestan which deviated too far from the Caucasian and Central Asian populations of *C. ravergieri* should also



Fig. 61. Spotted whip snake, *Hemorrhoids ravergieri* – Kasakh Gorge, Armenia.



Map 12. Distribution map of *Hemorrhhois ravergieri*.

be considered as a distinct subspecies. Notably, the Central Asian whip snake populations often contain black-headed individuals which are never recorded so far in the Caucasus.

Distribution in the Caucasus. From the foothills of Dagestan through the Kura-Arax Lowland to eastern Georgia, Armenia, Zuvand (Azerbaijan), northeast Turkey (B. Tuniyev et al., 2014) and Iran. Possibly, this species also occurs in semi-arid depressions of Dagestan; more research is required to confirm this (Map 12).

Habitats. Like leaden-coloured racers, spotted whip snakes live in arid habitats on shrubby and stony slopes and cliffs, in riparian thickets and canyons. In the meantime, whip snakes live at higher el-

evations and move up to 2400 m asl in Turkey and the Transcaucasus, occurring in juniper sparse forests, subalpine oakeries of *Quercus macranthera*, screes, phrygana and siblijak. In Chayniza (Gobustan Reserve, Azerbaijan), snakes live on a maritime terrace with scattered steep slopes interspersed by ravines and gullies and covered by *Salsola gemmascens* – *S. nodulosa* desert. The sympatric reptiles are *Eremias velox*, *Ophisops elegans*, *Testudo graeca*, *Telescopus fallax*, *Xerotyphlops vermicularis*, *Eirenis collaris*, *Platyceps najadum*, *Dolichophis schmidtii*, *Natrix tessellata* and *Macrovipera lebetina*. In this reserve, snakes occur also in a narrow sand desert strip along the ephemeral creek with tamarisks and semishrubs. The subshrubs are represented by *Caragana* sp. and *Salsola ericoides*.

The species *Ophisops elegans*, *Natrix tessellata* and *Macrovipera lebetina* co-exist with whip snakes in this habitat. In the Lachin district, near the Mishny village, snakes are recorded in typical East Mediterranean secondary forests (*Paliurus spina-christi*, *Amygdalus fenzliana*, *Rosa canina*) replacing the cut primeval woodlands on the southeastern slopes. The herbs *Stachys* sp. and *Thymus* sp. dominate in the herb-shrub layer, giving home to *Darevskia raddei*, *Lacerta media* и *Platyceps najadum*.

In the Arpa River basin, between Eghegnadzor and Areni (Armenia), snakes are recorded in a narrow 20–60 m wide strip of riparian forests dominated by *Salix australior* and *Ulmus carpinifolia* and supplemented by *Morus alba*, *Elaeagnus caspica* and *Tamarix meyeri*. The sympatric reptiles are *Pseudopus apodus*, *Ophisops elegans*, *Lacerta media*, *Dolichophis schmidti*, *Natrix tessellata* and *Macrovipera lebetina*. Whip snakes were also found on the right slopes of the Arpa River, on steep slopes covered by *Rhamnus pallasii* and *Ephedra procera* where the reptile fauna also included *Heremites septemtaeniatus*, *Natrix tessellata*, *Dolichophis schmidti*, *Xerotyphlops vermicularis*, *Eirenis punctatolineatus*, *E. collaris* and *Macrovipera lebetina*. In the Meghri Ridge, near the Nrnadzor village, whip snakes inhabit a meridian rocky canyon with numerous branches covered by *Paliurus*, *Punica* and *Punica-Paliurus* types of sibiljak on semi-desert and mountain steppe soils. The sympatric reptiles are *Xerotyphlops vermicularis*, *Eirenis collaris*, *Macrovipera lebetina*, *Telescopus fallax* and *Malpolon insignitus*. Here snakes also live at more than 1500 m asl in grass oakeries, on northern and north-western exposures. These oakeries represent a high and well-developed forest of crown density up to 1.0 and two-storey stand. The first storey consists of *Quercus macranthera*, *Fraxinus oxycarpa* and *Celtis glabrata*. The second storey includes *Berberis orientalis*, *Lonicera iberica* and *Padellus mahaleb*. Extra-storey vegetation is represented by large *Vitis silevstris*. The herbal storey is composed of *Melandrium boissieri*, *Dictamnus caucasicus*, *Vinca herbacea* and *Plantago lanceolata*. It was recorded on the large scree of the upper part of the watershed range of Tortum River and its left tributary near Nikah settlement, in vicinity of Delal village on the tributary of Arax River in 17 km eastwards Khorosan town, in Giseldere gorge below Sarijan village (Murat River basin). Widely presented in semidesert belt of southeast Anatolia (B.Tuniyev et al., 2014).

Conservation status. Ecology, population status and abundance are poorly studied. At the workshop on IUCN assessment of Palearctic reptiles and amphibians in Antalya, Turkey in September 2008, its status was designated as LC. This species is more widespread in the Caucasus than *H. nummifer*. Included in the Red Data Book of Dagestan (2009). In the Transcaucasus, it is protected in Khosrov Forest, Shikahogh, Vashlovani and Tuianchay Reserves and Vashlovani National Park. It is essential to establish a protected area in the foothills of Dagestan to preserve this species and other Mediterranean and Asia Minor species.

Genus *Platyceps* Blyth, 1860

Platyceps Blyth, 1860, Report of Curator. Zoological Department. Journ. and Proc. Asiat. Soc. Bengal, Calcutta, 29 (1): 114 (87–115).

Type species. *Coluber ventromaculatus* Gray, 1834 in Gray & Hardwicke, 1830–1835 (Van Wallach et al., 2014). The valid name is *Platyceps ventromaculatus* (Gray, 1834).

Middle-sized (total length including a tail is up to 1300 mm, usually smaller), slender snakes with a long tail (half the body length) and a clear cervical interception. The nostril is split between the two nasal scutes. The lateral lines of the frontal scute are usually concave. The scales have poorly developed longitudinal costae. The pupil is round. The subcaudal scutes are arranged in two rows. The maxillary teeth posteriorly increase in size. The rear maxillary teeth are separated from the anterior teeth by a small diastema. The ventral scutes are 200–240, subcaudal – 94–140 pairs, supralabial – 7–9, the anal scute is divided.

This genus comprises 27 species distributed from North and North-East Africa to western India and Pakistan through the Mediterranean, Arabian Peninsula, Iran, Iraq, Afghanistan and the Caucasus. These are *Platyceps afarensis* Schätti et Ineich, 2004, *P. bholanathi* (Sharma, 1976), *P. brevis* (Boulenger, 1895), *P. collaris* (Müller, 1878), *P. elegantissimus* (Günther, 1878), *P. florulentus* (Geoffroy-St-Hilare, 1827), *P. gracilis* (Günther, 1862), *P. insulanus* (Mertens, 1965), *P. karelini* (Brandt, 1838), *P. ladacensis* (Anderson, 1871), *P. largeni* (Schätti, 2001), *P. messanai* (Schätti et Lanza, 1989), *P. najadum* (Eichwald, 1831), *P. noeli* Schätti, Tillack et Kucharzewski, 2014, *P. rhodorachis* (Jan, 1865), *P. roger-*

si (Anderson, 1893), *P. saharicus* (Schätti et McCarthy, 2004), *P. scortecchi* (Lanza, 1963), *P. sinai* (Schmidt et Marx, 1956), *P. sindhensis* Schätti, Tillack et Kucharzewski, 2014, *P. somalicus* (Boulenger, 1896), *P. taylori* (Parker, 1949), *P. tessellata* (Werner, 1910), *P. thomasi* (Parker, 1931), *P. variabilis* (Boulenger, 1905), *P. ventromaculatus* (Gray, 1834) (Schätti et al., 2014).

The fauna of the former USSR included 3–4 species depending on views on the taxonomic status of *Coluber* (= *Platyceps*) *atayevi* Tuniyev et Shammakov, 1993. Following its description, it was named differently as the species *Coluber* (= *Platyceps*) *atayevi* (Ananjeva et al., 1998) or the subspecies *Coluber* (= *Platyceps*) *najadum atayevi* (Ananjeva et al., 2006; Schätti, 2004a). As new information on *Platyceps najadum* continues to come, taxonomic distinctiveness of subspecies becomes a topical issue, which may upgrade some taxa to a species level. In this monograph, we adhere to a viewpoint that the Caucasus is inhabited by one species (Darevskij, Ščerbak, 1993), but preliminary data show great variations in the various parts of the species distribution range in the Caucasus where animals differ in size and color patterns.

Dahl's whip snake – *Platyceps najadum* (Eichwald, 1831) (Figs. 62–64)

Tyria najadum Eichwald, 1831, *Zoologia specialis quam expositis animalibus tum vivis, tum fossilibus potissimum Rossiae in universum, et Poloniae in specie, in usum lectionum publicarum in Universitate Caesarea Vilnensi habendarum. Pars posterior* (=pt. 3). Josephi Zawadzki, Vilnae: 395 pp., 1 pl.

Tyria ocellata Eichwald, 1831 – “Quellen bei Pjatigorsk und Kislovodsk, Kaukasus” – Pyatigorsk and Kislovodsk (Mt. Beshtau), Caucasus (in Darevskij, Ščerbak, 1993).

Coluber olivaceus Dwigubskij, 1832 – Südöstliches Transkaukasien (South-East Caucasus) – in Darevskij, Ščerbak, 1993.

Terra typica. In the original description – “Baku, Transkaukasien”, Baku, Azerbaijan (Ananjeva et al., 2006); Transcaucasus (Darevskij, Ščerbak, 1993).

Type specimens. Holotype, not designated, a 760 mm specimen (K.E.I. Eichwald, 1825–1826), location unknown. (Van Wallach et al., 2014).

Distribution. Western and south-western parts of former Yugoslavia, western Albania, Greece, southern



Fig. 62. A drawing of the Dahl's whip snake, *Tyria najadum* (= *Platyceps najadum*) from the book “Fauna Caspio-Caucasia nonnullis observationibus novis” by E.I. Eichwald (1841).

Bulgaria, Asia Minor, Syria, Israel, northern Jordan, Iraq, northern Iran, south-western Turkmenistan and the Caucasus. Intraspecific systematics and distribution of taxa are in a focus of many scientists. At present, 5–6 subspecies are usually considered on the base of differences in their size, pholidosis, and colour patterns. The subspecies *Platyceps najadum dahlii* (Schinz, 1833) lives in the Balkans, Cyprus, western Turkey, Syria and Iraq. *P. n. kalymnensis* (Schneider, 1979) is found only on the Kalymnos Island in the Aegian Sea. The nominate subspecies *P. n. najadum* occurs in most of the Caucasus and in Asia Minor. Southeastern Azerbaijan is inhabited by *P. n. albitemporalis* (Darevsky et Orlov, 1994). *P. n. atayevi* (Tuniev et Shammakov, 1993) is confined to southern Turkmenistan (western and central Kopetdag Mts. from Karakaly in the west to the Sulukly Spring in the east) and northern Iran. The taxonomic status of this subspecies is arguable, possibly



Fig. 63. Dahl's whip snake, *Platyceps n. najadum* – North Ossetia-Alania, Russian Federation.



Fig. 64. Dahl's whip snake, *Platyceps n. najadum*, melanist – Pitsunda, Abkhazia.



Map 13. Distribution map of *Platyceps najadum*.

it should be assigned a species status as suggested by the authors of its description. The species *Platyceps rubriceps* (Wenzmer, 1919) living in the European and southwestern parts of Turkey, southern Bulgaria, Syria and Israel was until recently designated as a subspecies of *Platyceps najadum*. Some populations containing completely black melanistic individuals are known from the Black Sea coast of the Caucasus (Kudepsta, Akhshtyr, Adler, Pitsunda, Gudauta, Novyi Afon). The issue of taxonomic status of snakes from the Black Sea coast of the Caucasus differing by their large size, morphology and melanists remains unresolved.

Distribution in the Caucasus. In the Russian part of the Caucasus, Dahl's whip snakes live in the foothills and mountains of Dagestan, Chechen Republik,

Ingushetia, North Ossetia-Alania and the adjacent areas of the Stavropol Territory. An isolated western enclave is known from the Black Sea coast of the Krasnodar Territory and in Abkhazia. Another isolated population lives on the Black Sea coast of Adjara and Lazistan. The main range is spread over the eastern Transcaucasus: Azerbaijan (including Talysh Mts. and Zuvand), most of Armenia and eastern Georgia (Map 13).

The subspecies *Platyceps najadum albitemporalis* occurs near Lenkoran in southeastern Azerbaijan.

Platyceps najadum albitemporalis (Darevsky et Orlov, 1994)

Coluber najadum albitemporalis Darevsky and Orlov, 1994, The systematic position of the slender racer *Coluber najadum* (Eichwald) from south-east Az-

erbaijan, and some remarks on the herpetological fauna of this region. *Rus. J. Herpetol.*, 1(2): 93(93–97).

Terra typica. In the original description – “6 km west of Lenkoran, south-eastern Azerbaijan”.

Type specimens. Holotype: ZIL (=ZISP) 20305 (adult male), paratypes: ZIL (=ZISP) 20302, 20303, 20304, 20306, 20307, 20308, 20309.

Habitats. *Platycephalus najadum najadum* is a eurytopic snake living in xerophytic landscapes. It occurs in open stony semi-deserts and wormwood steppes, among rocky outcrops and screes, on shrubby and woody slopes of foothills and mountains, in xeromorphic scrubs, juniper sparse forests, oakeries, glades, orchards, vineyards and among ruins of old constructions. In Armenia it is distributed up to 2200 m asl, in the North Caucasus up to 1600 m and on the Black Sea coast no higher than 300 m. On the Mt. Aragats it is recorded in stony mountain steppe at more than 2000 m asl along with *Pelias eriwanensis*. On the Black Sea coast, it lives in semi-arid pistachio and juniper sparse forests and humid polydominant mixed subtropical forests with evergreen understorey. In the North Caucasus, Dahl’s whip snakes occur in semi-arid depressions of Jurassic shales, inhabiting the eastern slopes covered by sibiljak and oreoxerophytic vegetation and the slopes with forest derivatives in the Mineralnye Vody group of laccolites. In Dagestan’s branches of the Atlybuyunsky Ridge, on the northeastern slopes at 400–600 m asl Dahl’s whip snakes occur in intrazonal vegetation among the rocks and screes covered by *Juniperus oblonga*, *Jasminum fruticans*, *Juno caucasica* and *Thymus* sp. In the Itum-Kalinsky Depression of Chechen Republic, snakes live in oreoxerophytic East Mediterranean secondary and, occasionally, primary sibiljak with *Paliurus spina-christi* and *Rhamnus pallasii*.

This species is also recorded in mixed sibiljak covering most of the left bank of the Chanty-Argun River and both slopes of the depression. *Paliurus spina-christi* is a dominant species. The other important plants growing along the streams are *Celtis glabrata*, *Rhamnus pallasii*, *Rosa* sp., *Spiraea hypericifolia*, *Crataegus* sp., *Malus orientalis*, *Prunus cerasifera* and *Berberis vulgaris*. The herbal storey is represented by *Asparagus* sp., *Salvia daghestanica* and *Stipa capillata*. The other reptiles living here are *Lacerta strigata*, *Anguis fragilis*, *Coronella austriaca*, *Zamenis hohenackeri*, *Pelias lotievi* and *P. dinniki*. Whip snakes also live in ash-hornbeam oakeries with two-storey stand. The first storey of crown density 0.6–0.8 comprises the

dominant *Quercus petraea* and sub-dominant *Carpinus caucasia* and *Fraxinus excelsior*, with scattered *Alnus incana*, *Populus tremula* and *Pyrus caucasica*. The second storey (crown density 0.3–0.8) is represented by *Corylus* sp. and *Swida australis*, adding *Berberis* sp. and *Spiraea hypericifolia* on glades and forest margins. The herbal storey is motley, comprising mesophilic forest and meadow species. Dahl’s whip snakes are rare in petrophilic vegetation of the Itum-Kalinskaya Depression composed of *Saxifraga* sp., *Valeriana alliarifolia*, *Campanula tridentata*, *Asplenium trichomanes*, *A. ruta-muraria* and many others.

In Gobustan Reserve of Azerbaijan, whip snakes are recorded at 400–600 m asl on a large maritime terrace with scattered steep hills interspersed by ravines and gullies. The dominant habitat is *Salsola gemmascens* – *S. nodulosa* desert. The sympatric reptiles are *Eremias velox*, *Ophisops elegans*, *Telescopus fallax*, *Xerotyphlops vermicularis*, *Eirenis collaris*, *Dolichophis schmidtii*, *Hemorrhois ravergieri*, *Natrix tessellata* and *Macrovipera lebetina*.

In the Lachin district, near the Mishny village, this species co-exists with *Darevskia raddei*, *D. portschinskii*, *Lacerta media*, *Pseudopus apodus*, *Anguis fragilis* and *Eirenis modestus* in secondary post-forest sibiljak that replaced the cut primary oakeries on the left bank of the Aker River, cliffs and screes of the Aker canyon. This snake is also recorded in typical East Mediterranean secondary forests growing on the south-eastern slopes and dominated by *Paliurus spina-christi*, *Amygdalus fenzliana* and *Rosa* sp. The species *Stachys* sp. and *Thymus* sp. dominate in the herbal storey, providing habitats for whip snakes co-existing with *Darevskia raddei*, *Lacerta media* and *Hemorrhois ravergieri*.

Some records of this species are known from thorny tragacanth and sainfoin cushion plant communities on the southern slopes in subalpine meadows and also in the Aker River canyon on interchanging rocky and gentle (up to 30°) slopes at 600–800 m asl with dominant *Juniperus foetidissima* and *J. polycarpos*. *Lacerta media* inhabit these places as well as *Darevskia raddei*, *Paralaudakia caucasia*, *Xerotyphlops vermicularis*, *Eirenis modestus*, *E. collaris*, *Natrix tessellata*, *Macrovipera lebetina* and *Bufo viridis*.

In the Meghri district of southern Armenia, Dahl’s whip snakes occur in the Meghri riverhead and in branches of the southern macroslope of the Meghri Ridge, in phryganoid oakeries of crown density 0.1–0.3 comprising mainly *Quercus macranthera*. The sympatric reptiles are

Darevskia raddei, *Lacerta media*, *L. strigata*, *Ablepharus bivittatus*, *Natrix tessellata*, *Montivipera raddei*, *Paralaudakia caucasia* and *Dolichophis schmidti*.

The subspecies *Platyiceps najadum albitemporalis* is a typical representative of the relict Talysh-Hyrcanian fauna of the western sub-region of the Mediterranean zoogeographical region. Apart from *Platyiceps najadum albitemporalis*, local relict herpetofauna consists of *Bufo eichwaldi*, *Rana macrocnemis pseudodalmatina*, *Darevskia chlorogaster*, *Zamenis persicus* and *Gloydius caucasicus*. Moreover, some forest-dwelling species from the North and West Caucasus survive here in distantly isolated relict populations. These are *Lisotriton vulgaris lantzi*, *Triturus karelinii*, *Darevskia praticola* ssp. and *Anguis fragilis*. The most remarkable plant relicts are stands of *Taxus baccata* (Darevsky, Orlov, 1994), *Parrotia persica*, *Zelkova carpinifolia*, *Quercus castaneifolia* and others.

Conservation status. At the workshop on IUCN assessment of Palearctic reptiles and amphibians in Antalya, Turkey in September 2008, its status was designated as LC. As a species of limited distribution and decreasing numbers, the Dahl's whip snake is included in the Red Data Books of the Krasnodar Territory (2017), North Ossetia-Alania (1999), Republic of Ingushetia (2007) and Stavropol Territory (2013). The species is preserved in Sochi, Vashlovani and Hyrcanian National Parks, Pitsunda-Mussera, Khosrov Forest, Vashlovani and Lenkoran Reserves. A part of its range falls within the Khosta district of Kavkazsky Biosphere Reserve (yew-boxwood grove).

Genus Smooth snakes – *Coronella* Laurenti, 1768

Coronella Laurenti, 1768, Specimen Medicum, Exhiben Synopsis Reptilium Emendatam cun Experimentis circa Venena et Antidota Reptilium Austriacorum, quod Autoritate et Consensu. Wien, J. Thomae Trattnem: 84(1–214), tab. V, fig. 1.

Type species. *Coluber laevis* Lacépède (= *Coronella austriaca* Laurenti, 1768) designated by Boie (1826) – in Williams, Wallach, 1989. The valid name is *Coronella austriaca* Laurenti, 1768.

Middle-sized snakes having a more or less flattened head with a less distinct cervical interception. Body length with a tail is seldom over 800 mm, usually 600–700 mm. The pupil is round. The scales are

smooth, with two apical pores on each. The subcaudal scutes are arranged in two rows, the anal scute is divided. 150–200 ventral scutes; subcaudal 40–72 pairs, maxillary 7, seldom 8. There are 19 rows around the midbody. The maxillary teeth increase posteriorly, but the last two teeth are not increased and not separated from other teeth by a diastema. The supratemporal is at least twice as shorter than the skull length and its posterior end does not protrude over the posterior edge of the braincase.

The genus comprises 3 species: *Coronella austriaca* Laurenti, 1768, *C. brachyura* (Günther, 1866) and *C. girondica* (Daudin, 1803). *C. austriaca* is widespread in Europe (except for the southern Iberian Peninsula, northern Scandinavia and large Mediterranean islands), West Asia (Caucasus, northern Iran and Asia Minor) and Central Asia (Mugojary, western Kazakhstan). Phylogeography and study of genetic structure revealed (Jablonski et al., 2018) that the Iranian clade is both phylogenetically and geographically closely related to the Transcaucasian clade. Since they form a common higher-order clade sister to the Eastern clade, the authors hypothesize that the common ancestor of these clades originated from the region of Caucasus or Transcaucasia and subsequently dispersed both northward (Eastern clade) and southward (Iranian clade 1). There is one species occurring in the Caucasus.

Smooth snake – *Coronella austriaca* Laurenti, 1768 (Fig. 65–66)

Coronella austriaca Laurenti, 1768, Specimen Medicum, Exhiben Synopsis Reptilium Emendatam cun Experimentis circa Venena et Antidota Reptilium Austriacorum, quod Autoritate et Consensu. Wien, J. Thom. Trattnem: 84(1–214), tab. V, fig. 1.

Terra typica. “circa Viennam” and “America” [= vicinity of Vienna, Austria and America]. Restricted to Austria *fide* Mertens & Müller (1928: 48) (Van Wallach et al., 2014).

Type specimens. Not designated (Van Wallach et al., 2014).

Distribution. Almost all Europe, except for Ireland, part of England, northern Scandinavia, central and southern Iberian Peninsula and the Mediterranean islands. One of the most northward-distributed boreal species reaching the latitude 62°N in Scandinavia. Its range is spread to western Kazakhstan (southern Mugojary) in the east, northern parts of Asia Minor, Iran and



Fig. 65. Smooth snake, *Coronella austriaca* – Dagestan, Russian Federation.

the Caucasus in the southeast. North Eurasia is inhabited by the nominate subspecies *C. a. austriaca* Laurenti, 1768 that is continuously distributed over all European part of Russia to the Tula and Ryazan provinces in the north, and further to southern parts of western Siberia, Kazakhstan, Caucasus and northern Asia Minor. Some northern records are known from the Ivanovo and Vologda provinces and the south of the Republic of Komi. The second subspecies *C. a. fitzingeri* (Bonaparte, 1840), which is distinguished by its monochromatic colouration, lives in the southern Iberian Peninsula and Sicily. Some publications (Bannikov et al., 1977; Ananjeva et al., 2006) provide erroneous information about occurrence in the southern Iberian Peninsula.

Distribution in the Caucasus. Almost all parts of the isthmus to the south of the Kuma-Manych Depression, reaching the northern parts of Turkey and Iran (including the Talysh Mts. and Alborz Mts.) (Map 14). It is absent in semi-deserts of the western Caspian Sea, Ap-

sheron Peninsula, Kura-Arax Lowland and proper Ararat Valley, and does not move over the elevation 3100 m asl. In the Caucasus, smooth snakes are polymorphic in various physico-geographical regions, so the description of some intraspecific taxa, which originated under long-term isolation and different ages of populations, is potentially possible.

Habitats. Smooth snakes live in steppes, meadow-steppes, forest-steppes, broadleaf, conifer and mixed forests, preferring the sun-heated glades. In the Caucasus, this species is also known to inhabit stony and arid mountain grasslands and scrubby slopes. In the eastern and southern Transcaucasus, these snakes usually occur at elevations no less than 1100–1200 m asl. In the West Caucasus, they live from the sea level up to alpine meadows, reaching 3000 m and more. In the East Caucasus, altitudinal distribution is limited by 600–3000 m, seldom up to 3100 m asl, including the foothill steppes and arid sparse forests, montane forests, oreoxero-



Map 14. Distribution map of *Coronella austriaca*.

phytic mountain steppes, subalpine and alpine meadows up to the boundary with the subnival zone. In the Itum-Kalinsky Depression, Chechen Republik smooth snakes can be found in oreoxerophylic East Mediterranean secondary, sometimes primary, thorny vegetation (sibljak) dominated by *Paliurus spina-christi*, as well as in petrophilic communities (see the Dahl's whip snake above) and subalpine meadows. The other reptiles living here are *Lacerta strigata*, *Anguis fragilis*, *Platycephalus najadum*, *Zamenis hohenackeri*, *Pelias lotievi* and *P. dinniki*. Contrary to *P. najadum* and *Z. hohenackeri* which are rare on the left side of the Itum-Kalinskaya Depression, smooth snakes are common among the cliffs and screes covered by petrophilic vegetation comprising *Saxifraga* sp., *Valeriana* sp., *Campanula*

tridentata, *Asplenium trichomanes*, *A. ruta-muraria* and other plants.

Conservation status. At the workshop on IUCN assessment of Palearctic reptiles and amphibians in Antalya, Turkey in September 2008, its status was designated as LC. In most of the West Caucasus and the Armenian Highland, the smooth snake is a common, but sparsely distributed species. It is rare in other parts of the Caucasus and included in the Red Data Book of the Stavropol Territory (2013) and Kalmukia Republic (2013). This species is preserved in a number of protected areas: Kavkazsky, Teberdinsky, Kabardino-Balkarsky, North-Ossetian, Zakataly, Geygöl, Hyrcanian, Shikahogh, Khosrov Forest, Dilijan, Lagodekhi, Batsara-Babaneuri, Kintrishi, Gumista,

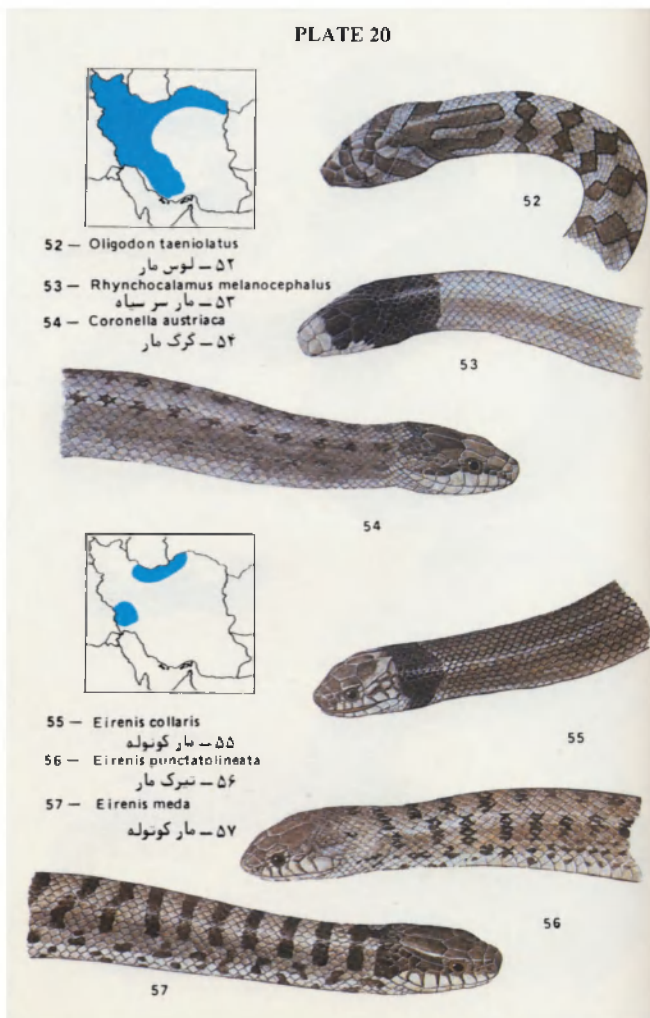


Fig. 66. A drawing of the smooth snake, *Coronella austriaca* in the same figure plate with *Eirenis collaris*, *Eirenis punctatolineatus* and *Rhynchocalamus melanocephalus* from the book “The snakes of Iran” by M. Latifi (1991).

Pitsunda-Mussera, Sochi, Prielbrusie, Alania, Ritsa and Sevan.

Genus Dwarf snakes – *Eirenis* Jan, 1863

Eirenis Jan, 1863, Enumerazione sistematica degli ofidi appartenenti al gruppo Coronellidae. Arch. Zool. Anat. Phis., 2(2): 256(213–330).

Type species. *Coronella modesta* Martin, 1838 (Van Wallach et al., 2014).

Quite small cryptic fossorial snakes with body length up to 750 mm, usually 400–500 mm, including a tail. The cervical interception is weak and the head is covered on top by large and symmetrical scutes. The lateral lines of the frontal scute are straight. The nostril is in one whole scute. The pupil is round. The scales

are smooth, with one apical pore and arranged in 15 or 17 longitudinal rows around the midbody. 7 supralabial scaled, 8–9 sublabials. The subcaudal scales form two longitudinal rows. The maxilla is not bent upwards and has 14–22 teeth without a diastema. The palatal bones have up to 12–14 teeth and the pterygoid has up to 22 teeth, which decrease in size posteriorly. Dwarf racers feed on invertebrates, predominantly orthopterous insects. The notable results of study of the Palearctic species of the genus *Contia* Girard, 1853 (= *Eirenis*), particularly in the Caucasus, were published in the late 1800s and early 1900s (Elpatievsky, 1902; Nikolsky, 1913, 1916; Terentiev, Chernov, 1940; 1949; Chernov, 1948). Stickel (1951) considered the characters that differed between the Nearctic genus *Contia* and the Palearctic genus *Eirenis*. In the past decades, serious changes were made in taxonomy of *Eirenis*: new species and subspecies were discovered, distribution ranges were clarified and a number of phylogenetic reconstruction scenarios were suggested (Eiselt, 1971; Bannikov et al., 1977; Başoğlu, Baran, 1980; Darevsky, Bakradze, 1982; Dotsenko, 1985a,b, 1987, 1989; Demirsoy, 1996; Baran, 1976, 2005; Baran, Atatür, 1998; Ananjeva et al., 1998, 2006; Schmidtler, 1988, 1993, 1997; Marx, 1968; Schmidtler, Baran, 1993a,b; Schmidtler, Eiselt, 1991; Schmidtler, Lanza, 1990; Schmidtler, Schmidtler, 1978; Nagy et al., 2003; Rajabizadeh et al., 2012a, 2015; Mahlow et al., 2013; Van Wallach et al., 2014).

The genus comprises 16 species distributed in North-East Africa, South-West Asia from the Arabian Peninsula to Pakistan and north-western India, some Mediterranean and Aegean islands, the Caucasus and southern Turkmenistan: *E. aurolineatus* (Venzmer, 1918); *E. bakkariensis* Schmidtler et Eiselt, 1991; *E. barani* Schmidtler, 1988; *E. collaris* Ménériés, 1832; *E. coronella* (Schlegel, 1837); *E. coronelloides* (Jan, 1862); *E. decemlineatus* (Dumeri et Bibron, 1854); *E. eiselti* Schmidtler et Schmidtler, 1978; *E. levantinus* Schmidtler, 1993; *E. lineomaculatus* Schmidt, 1939; *E. medus* (Chernov, 1940); *E. modestus* (Martin, 1838); *E. punctatolineatus* (Boettger, 1892); *E. rechingeri* Eiselt, 1971; *E. rothii* Jan, 1863; *E. thospitis* Schmidtler et Lanza, 1990.

There are four species in the fauna of the Caucasus. Dotsenko (1989) suggested to split the genus *Eirenis* into 2 subgenera: *Eirenis* Jan, 1863 (type species *Coronella modesta* Martin, 17 scales around the middle of the body; species from the south-eastern and southern parts of the range: *E. modestus*, *E. punctatolineatus*,

E. decemlineatus, *E. lineomaculatus*) and *Collaria* Dot-senko, 1989 (type species *Contia collaris* Ménétriés, 15 scales around the middle of the body; species from the north-west of the range: *E. collaris*, *E. eiselti*, *E. rothi*, *E. coronella*, *E. medus*, *E. rechingeri*). Nagy et al. (2003) published results of their molecular study revealing a sistergroup relationship between *Eirenis* and the genus *Hierophis*, and including the formerly separate *Pseudocyclophis persicus* in *Eirenis*.

Collared dwarf snake – *Eirenis collaris* (Ménétriés, 1832) (Figs. 67–68)

Coluber collaris Ménétriés, 1832, Catalogue raisonné des objets de zoologie recueillis dans un voyage Caucase et jusqu'aux frontières actuelles de la Perse

enterpris par ordre de S.M. l'Empereur, Acad. Imper. Sciences, St.Petersburg, 4, 271: 67(59–74).

Terra typica. In the original description – “pres du Bechbarmak, non loin de la mer Caspienne”, Mt. Beshbarmak, Divichin district, Azerbaijan (in Ananjeva et al., 2006).

Type specimens. Lectotype ZISP 1546.

Distribution. Two subspecies [*Eirenis c. collaris* and *E. c. macropilatus* (Werner, 1903)] occur in eastern Turkey, neighbouring parts of Iran, Iraq, Syria, Lebanon, Israel and the East Caucasus. The following taxa were described from eastern Turkey: *E. aurolineatus* (Venzmer, 1918); *E. barani barani* Schmidtler, 1988; *E. barani bishofforum* Schmidtler, 1997; and *E. eiselti* Schmidtler et Schmidtler, 1978.

Distribution in the Caucasus. The nominate subspecies is known from the northern parts of Turkey and



Map 15. Distribution map of *Eirenis collaris*.



Fig. 67. Collared dwarf snake, *Eirenis collaris* – Shikahogh Reserve, Armenia.

Iran, south-eastern Georgia, southern Armenia, Azerbaijan and the foothills of Dagestan (Map 15). The subspecies *E. c. macrospilotus* was described from 2 specimens collected in the vicinity of the Mt. Ararat. There is a record of one individual of *E. c. macrospilotus* (Werner, 1903) in the Agri Province of Turkey (Darevsky, Bakradze, 1982).

***Eirenis collaris macrospilotus* (Werner, 1903)**

Contia collaris var *macrospilota* Werner, 1903, Über Reptilien und Batrachier aus Westasien (Anatolien und Persien). Abhand. Akad. München, Klasse II, XXII, Abt. II, 381. The valid name is *Eirenis collaris macrospilotus* (Werner, 1903).

Terra typica. “Hochgebirgslagen westlich des Ararat-Gebiets”, mountains to the west of Ararat, delineated by Eiselt (1982).

Type specimens. Type specimens must be regarded as lost (Eiselt, 1982).

Habitats. Individuals live in open stony areas of clay and wormwood semi-deserts and also on gentle and moderately steep slopes covered by sparse xerophilic vegetation, particularly on soft, weakly stony and semi-

sandy soils. In mountains, it is known from elevations up to 1700 m asl. In wormwood semi-deserts of the Tabasaransky district in Dagestan, these snakes occur in habitats dominated by *Artemisia fragrans* with singular individuals of *Iris furcata* and *Geranium* sp. The snakes *Xerotyphlops vermicularis* and *Telescopus fallax* are sympatric. In Azerbaijan, collared dwarf snakes are recorded in *Salsola gemmascens* – *S. nodulosa* desert in Gobustan Reserve and on interchanging rocky and gentle (up to 30°) slopes of the Aker riverside at 600–800 m asl covered by the juniper *Juniperus foetidissima* and *J. polycarpos* sparse forests.

In Armenia's Arpa River basin, between Eghegnadzor and Areni, dwarf snakes occur in the V-shaped rocky meridian canyon at 800–1000 m asl in riparian pistachio *Pistacea mutica* forests stretched as a narrow strip along the left bank. The forest stand is very sparse (over 5 m between the trees) and sub-dominated equally by *Acer ibericum*, *Crataegus orientalis*, *Celtis caucasica*, *Amygdalus fenzliana* and *Rhamnus pallasii*. The dominant herbs are *Artemisia fragrans*, *Stachys inflata* and *S. stschegleewii*. Snakes can also be recorded in

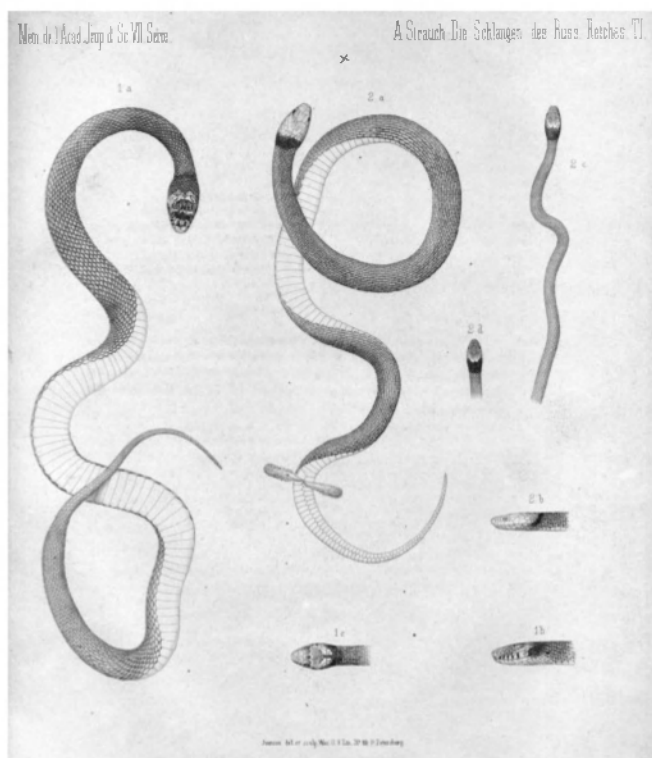


Fig. 68. A drawing of the collared dwarf snake *Ablabes collaris* (= *Eirenis collaris*) in the same figure plate with *Ablabes modestus* (= *Eirenis modestus*) from the book “Die Schlangen des Russischen Reiches” by A.A. Strauch (1873).

phryganoid communities on the southeastern and steep (up to 40°) right bank of the Arpa covered by *Rhamnus pallasii* and sub-dominant *Ephedra major procera*, as well as sibiljak on terraces (see habitats of the sympatric *Xerotyphlops vermicularis*).

In the Meghri district of Armenia, dwarf snakes were recorded in the vicinity of the Nmadzor village, in the meridian canyon with numerous branch gorges covered by *Paliurus*, *Punica* and *Paliurus-Punica* types of sibiljak growing on semi-desert and mountain steppe soils with numerous rocky outcrops. The dominant plants are *Paliurus spina-christi* and *Punica granatum* and the sympatric reptiles are *Xerotyphlops vermicularis*, *Macrovipera lebetina*, *Telescopus fallax* and *Malpolon insignitus*. In Shikahogh Reserve, they live in the natural grove of *Platanus orientalis* along the Tsav River.

Conservation status. This species is quite rare on the northern periphery of its range, but already in southern Dagestan it becomes common (up to 3 individuals/ha). At the workshop on IUCN assessment of Palearctic reptiles and amphibians in Antalya, Turkey in September 2008, its status was designated as LC. Its status is designated in the Georgian Red List as

VU B2a. In most of its range it is a common species and during some seasons it becomes numerous. In the southern Transcaucasus, it is preserved in Khosrov Forest, Shikahogh, Eldar, Vashlovani and Turianchay Reserves and in Vashlovani National Park. It is essential to establish a protected area in the Russian Federation to safeguard the existence of this species and other Mediterranean and Asia Minor species.

Ring-headed dwarf snake – *Eirenis modestus* (Martin, 1838) (Figs. 69–70)

Coronella modesta Martin, 1838, On some snakes collected during the Euphrates expedition (*Coluber chesneii*, *Coronella multicincta*, *Coronella modesta*, *Coronella pulchra*, *Vipera euphratica*). Proc. Zool. Soc. London, 6: 82(81–83).

Terra typica. “Trabzon (=Trebizonde =Trapezund)” – Schmidtler, Baran, 1993b; Trabzon (Turkey). Mahlow et al. (2013) wrote that whether Trabzon is the actual collecting site, can not yet be clarified with certainty.

Type specimens. Syntypes (4), 4BMNH 1850.10.21.21–22, longest syntype 292 mm (Van Wallach et al., 2014).

Distribution. Mediterranean and Aegian islands to eastern Turkey, Syria, Iraq, East Transcaucasus and western Iran. Several subspecies were described so far: *E. m. semimaculatus* (Böttger, 1876) from the Lesbos Island (Greece), *E. m. cilicius* Schmidtler, 1993 from southern Anatolia, *E. m. werneri* (Wettstein, 1937) from the Alazonisi Island near the Furni Island in the Aegian Sea and nominate *E. m. modestus* (Martin, 1838) from the Caucasus.

Distribution in the Caucasus. Sporadically distributed in the Transcaucasus within eastern Georgia, Armenia and Azerbaijan and in mountainous Dagestan, North Caucasus (Map 16).

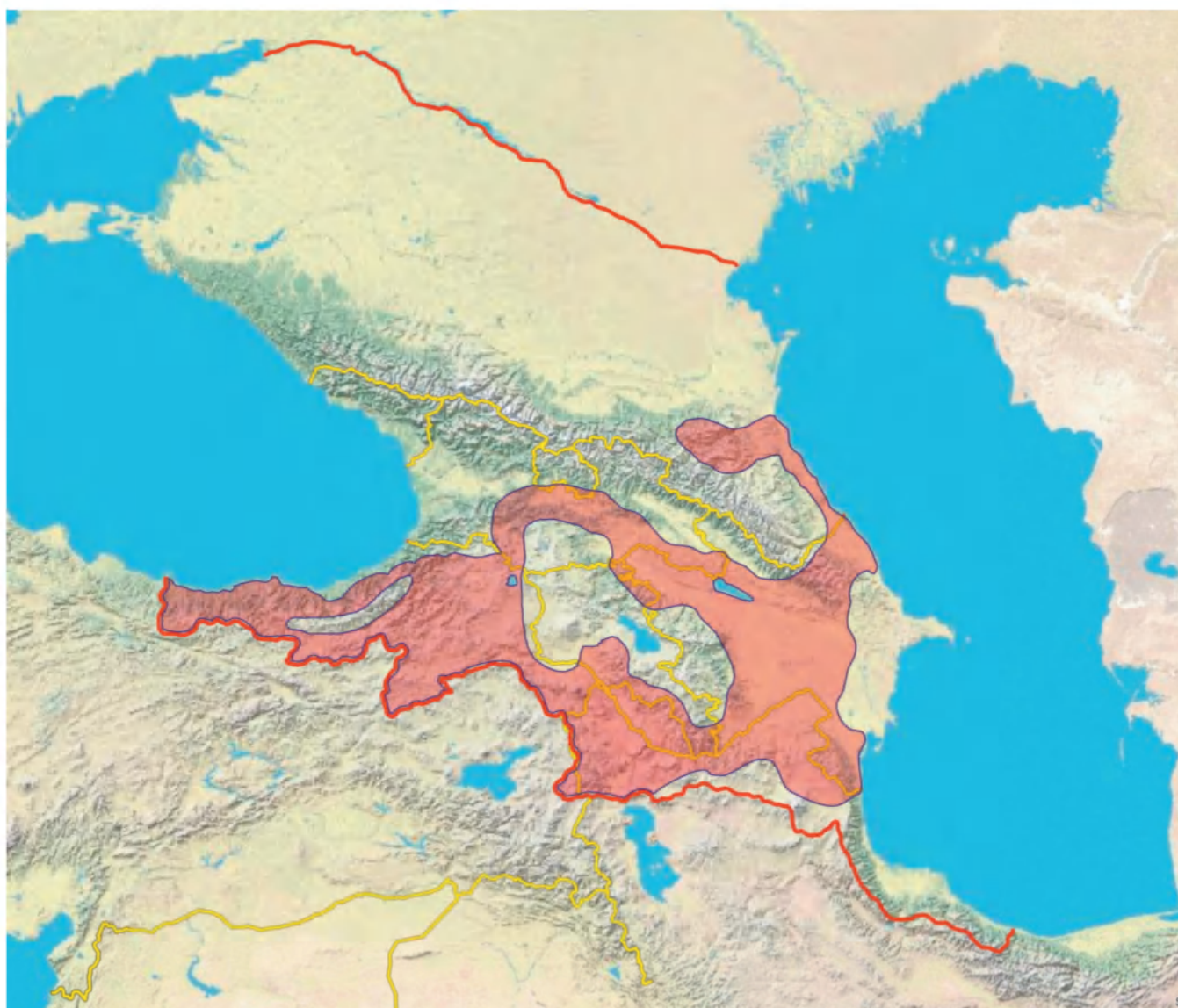
Habitats. Ring-headed dwarf snakes occur on gentle and moderately steep slopes, usually stony ones covered by sparse arid vegetation. Sometimes they can also be found in open areas of wormwood-broomsedge steppes or in sparse broadleaf forests. Like all species of this genus, these snakes are often recorded from April to early June, usually under the stones, but with the onset of summer heat and vegetation dryout they move deep into the soil and seeing them in this period is almost unlikely. Only strong downpours with thunderstorms in July-August can drive them out to the surface for a short emergence and even basking. In the surroundings of Lachin, ring-headed dwarf snakes are



Fig. 69. Ring-headed dwarf snake, *Eirenis modestus*, adult individual – Gekhard, Kotai district, Armenia.



Fig. 70. Ring-headed dwarf snake, *Eirenis modestus*, juvenile individual – Gekhard, Kotai district, Armenia.



Map 16. Distribution map of *Eirenis modestus*.

recorded on interchanging rocky and gentle (up to 30°) slopes of the Akera River at 600–800 m asl in juniper *Juniperus foetidissima* and *J. polycarpus* sparse forests where they co-exist with *Xerotyphlops vermicularis*, *Eirenis collaris*, *Platyceps najadum* and *Macrovipera lebetina*.

Conservation status. Ecology, population status and abundance are poorly studied. Big congregations of dwarf snakes, numbering over 20 individuals over 2 hours of surveys, were recorded in eastern Georgia near Tbilisi, in Lachin district of Azerbaijan and Khosrov Forest Reserve of Armenia. This species is quite common and widespread in the foothills and mountains of Dagestan in the basins of Kara-Koisu, Avarskoe Koisu and Andiyskoe Koisu up to 1500 m asl. At the

workshop on IUCN assessment of Palearctic reptiles and amphibians in Antalya, Turkey in September 2008, its status was designated as LC. Its protection has been ensured in Khosrov Forest and Shikahogh Reserves. It is also recorded near the boundary of Dagestansky Reserve.

Dark-headed dwarf racer – *Eirenis persicus* (Anderson, 1872) (Fig. 71)

Cyclophiops persicus Anderson, 1872, On some Persien, Himalayan and others reptilies. Proceedings of the Zoological Society of London, 392: 371–404.

Terra typica. In the original description – “Busshire, Persia”; Bushehr, Iran (Bannikov et al., 1977;



Map 17. Distribution map of *Eirenis persicus*.

Ananjeva et al., 2006), "Bushehr, South Iran, ca. 28° 55' N, 50° 50' E, approx. 20 m a.s.l. (Mahlow et al., 2013).

Type specimens. ZSI, Calcutta Holotype ZSI 4828 fide Sclater (1891), Das et al. (1998), Mahlow et al., 2013 and Van Wallach et al., 2014.

Distribution. Widespread from southeastern Turkey and Iraq in the west to Pakistan and north-western India in the east. This species also occurs in southern Turkmenistan (Kopetdag, Badkhyz, Karabil) and the extreme south of Armenia where it is represented by the subspecies *Eirenis p. persicus*. In the Kopetdag Mts. it is known from elevations up to 1000 m asl. In Armenia, the only record came from a steep stony slope of the Tsiranidzor Canyon, in semi-desert (Aghasyan, 1987b).

Distribution in the Caucasus. The only record (Aghasyan, 1987b) was made in the Tsiranidzor Canyon, southern foothills of the Meghri Ridge in front of the Arax River, Armenia (Map 17). Most likely, this is an extreme northwestern limit of species distribution. Further south, the range is spread southeastwards to Iran and, passing by the Lake Van from the south, it extends to Cilicia in southeastern Turkey.

Habitats. In Armenia, a dwarf racer was found under the stone on a steep slope in the ecotone of wormwood semi-desert and *Paliurus-Punica sibiljak* about, 700 m asl. Vegetation of local screes is represented by *Arum elongatum*, *Vinca herbacea*, *Asparagus verticillatus*, *Ceterach officinarum* and *Cheilanthes persica*. The species *Salix australior*, *Rubus* sp. and *Ficus carica*



Fig. 71. Dark-headed dwarf snake, *Eirenis persicus* – Kopetdag, Turkmenistan.

grow near springs. An individual of *Eirenis collaris* was found 5 m away from the dwarf racer record.

Conservation status. In Turkmenistan, this species is common in the Kopetdag Ridge and rare in Badkhyz and Karabil. At the workshop on IUCN assessment of Palearctic reptiles and amphibians in Antalya, Turkey in September 2008, its status was designated as LC. In the Caucasus, the dark-headed dwarf racer is one of the rarest reptiles distributed in the north-western margin of its global range. It is listed in the Red Book of animals of the Republic of Armenia (2010: CR B2ab(i,ii,iii). Here, it is protected in Arevik National Park.

Dotted dwarf snake – *Eirenis punctatolineatus* (Boettger, 1892) (Figs. 72–73)

Cyclophis modestus var. *punctatolineata* Boettger, 1892, Drei neue colubriforme Schlangen. Zool. Anz., 15: 417–420.

Terra typica. Armenia.

Type specimens. Not designated.

Distribution. Arax River basin in the Transcaucasus, eastern Turkey, western Iran and eastern Iraq. A closely related species *E. thospitis* Schmidtler et Lanza, 1990 was described from the area in 2–3 km N NE of Van, about 2000 m elevation (E Turkey) The Caucasus is inhabited by the subspecies *E. p. punctatolineatus* (Boettger, 1892).

Distribution in the Caucasus. Southern Armenia, southwestern and southeastern Azerbaijan, Turkish and Iranian parts of the Caucasus (Map 18).

Habitats. Dotted dwarf snakes live on gentle, very stony hills and in semi-deserts with sparse herbal cover and xerophilic scrubs. In the Arax River basin in Armenia, snakes reach the elevations up to 2000 m asl. In Armenia, between Eghegnadzor and Areni in the Arpa riverside, snakes occur in the V-shaped rocky canyon at 800–1000 m asl in riparian pistachio forests stretched as a narrow (20–60 m) strip along the left bank, on the western slopes.

In this landscape, forest stand is sparse (more than 5 m between the trees) and the dominant species is *Pistacia mutica*. The supplementary tree species are equally



Map 18. Distribution map of *Eirenis punctatolineatus*.

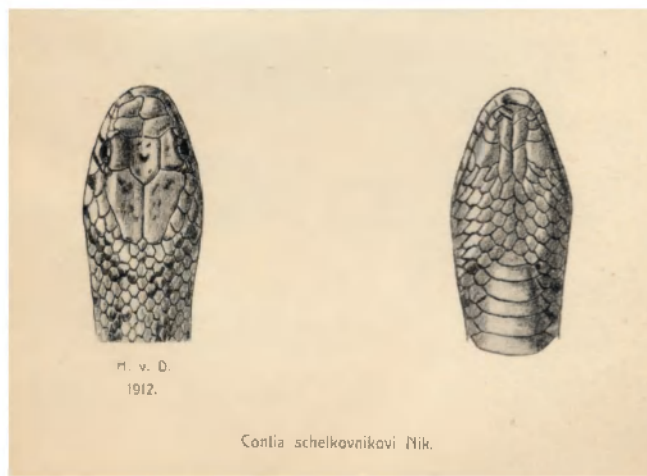


Fig. 72. Images of the dotted dwarf snake *Contia schelkovnikovi* (= *Eirenis punctatolineatus*) from the book “The reptiles and amphibians of the Caucasus” by A.M. Nikolsky (1913).



Fig. 73. Dotted dwarf snake, *Eirenis punctatolineatus* – Khosrov Reserve, Armenia.

represented *Acer ibericum*, *Crataegus orientalis*, *Celtis caucasica*, *Amygdalus fenzliana* and *Rhamnus pallasii*. The main herbs are *Artemisia fragrans*, *Stachys inflata* and *S. stschegleewii*. The sympatric reptiles are *Xerotyphlops vermicularis*, *Eirenis collaris*, *Eryx jaculus* and *Macrovipera lebetina*. In the Meghri district of southern Armenia, near the Nrnadzor village, snakes live in the meridian canyon with numerous branch gorges, in Paliurus, Punica and Paliurus-Punica siblijak growing on semi-desert and mountain steppe soils with rocky outcrops. The dominant trees are *Paliurus spina-christi* and *Punica granatum*.

Along the altitudinal gradients, the dotted dwarf snake takes an intermediate position between the colored dwarf snake and the ring-headed dwarf snake.

Conservation status. Ecology, population status and abundance are poorly studied. In some sites (Hrazdan Gorge in Armenia) density can be as high as 10 individuals/km walked. This species is quite abundant on the Akhtamar Island on the Lake Van. At the workshop on IUCN assessment of Palearctic reptiles and amphibians in Antalya, Turkey in September 2008,

its status was designated as LC. The species is protected in Khosrov Forest Reserve in Armenia. Possibly, it occurs also in other protected areas of the Caucasus.

Genus *Elaphe* Fitzinger, 1833

Elaphe Fitzinger, 1833, Ueber die Ausarbeitung einer Fauna des Erzherzogtumes Oesterreich ... in Beiträge zur Landeskunde Oesterreich's unter der Enns. Erster Band. F. Becker'schen Universitäts Buchhandlung, Wien, 1: 280–430.

Type species. *Elaphe parreyssii* Wagler, 1833 (= *Coluber* Wagler (= *Coluber quatuorlineatus* Lacépède, 1789) – designated by Van Wallach et al., 2014. The valid name is *Elaphe quatuorlineata*.

Large and medium snakes of body length 800 mm to over 1600 mm. Including a tail, body length can reach over 2000 mm. The maxillary teeth are same-size, 12–22 and arranged in a continuous row. The anterior mandibular teeth are longer than the posterior ones. The cervical interception is clear-cut. The pupil is round. The subcaudal scutes are arranged in two rows.

The scales are smooth or having uncertain ridge. The lateral edges of the frontal scales are straight. These snakes kill their prey by constricting. They live in a variety of habitats from semi-arid and arid landscapes to montane forests, seashores and volcano slopes with geothermal springs. All *Elaphe* spp. are well-skilled in climbing and can manifest themselves as both terrestrial and semi-arboreal species.

Until recently, the genus *Elaphe* sensu lato comprised more than 50 species widespread in North and Central Americas, Asia including the Greater Sunda Islands and the Philippines, South and Central Europe. It was proved that *Elaphe* sensu lato is not a monophyletic species, but a complex of 12–14 genera depending on views on systematics of this group. According to morphological, biochemical and molecular studies (Lenk et al., 2001a; Lenk, Wüster, 1999; Helfenberger, 2001; Schulz, 1996; Utiger et al., 2002, 2005), *Elaphe* s.l. includes the following genera: *Bogertophis* Dowing et Price, 1988 (type species: *Coluber subocularis* Brown, 1901); *Coelognatus* Fitzinger, 1843 (type species: *Coluber radiatus* Boie, 1827); *Elaphe* Fitzinger, 1828 (type species: *Coluber quatuorlineatus* Lacépède, 1789); *Euprepiophis* Fitzinger, 1843 (type species: *Coluber conspicillatus* Boie, 1826); *Gonyosoma* Wagler, 1828 (type species: *Gonyosoma oxycephalum* Wagler, 1828); *Oocatochus* Helfenberger, 2001 (type species: *Tropidonotus rufodorsatus*, Cantor, 1842); *Oreophis* Utiger, Helfenberger et Schätti, 2002 (type species: *Coluber porphyraceus* Cantor, 1839); *Orthriophis* Utiger, Helfenberger et Schätti, 2002 (type species: *Cynophis moellendorffii*, Boettger, 1886); *Pantherophis* Fitzinger, 1843 (type species: *Coluber guttatus*, Linnaeus, 1758); *Pseudelaphe* Mertens et Rosenberg, 1943 (type species: *Coluber flavirufus* Cope, 1867); *Rhinechis* Wagler, 1833 (type species: *Coluber scalaris* Schinz, 1822); *Zamenis* Wagler, 1830 (type species: *Coluber Aescilapi* Lacépède, 1789 = *Natrix longissima* Laurenti, 1768 – indicated later, Fitzinger, 1843).

There are 3 genera designated in the fauna of the northern Eurasia: *Elaphe*, *Rhinechis* and *Zamenis*. The monotypical genus *Rhinechis* [*R. scalaris* (Schinz, 1822)] lives in Spain and southern France. For the Caucasus, we consider *Elaphe* sensu stricto and *Zamenis*. Here, the genus *Elaphe* sensu stricto consists of 2 species (*E. dione* and *E. sauromates*) and the genus *Zamenis* numbers 4 species (*Z. hohenackeri*, *Z. longissimus*, *Z. persicus*, *Z. situla*).

Steppes ratsnake – *Elaphe dione* (Pallas, 1773) (Figs. 74–75)

Coluber dione Pallas, 1773, Reise durch verschiedene Provinzen des Russischen Reichs. St.Petersburg, Kayserlichen Academie der Wissenschaften, vol. 2: 717(1–744).

Terra typica. Mertens and Mülller (1928) designated the *terra typica restricta* as “Vorposten Gratscheffskoi, bei Semijarsk, oberstes Irtysh-Gebiet, Bezirk Semipalatinsk. Heute Kazachstan”; “near Semiyarsk, upper Irtysh riverside, Semipalatinsk Province” (Kazakhstan) – in Schulz (1996), Ananjeva et al. (1997, 1998, 2006), Van Wallach et al. (2014).



Fig. 74. A drawing of the steppes ratsnake, *Elaphe dione* in the same figure plate with *Elaphe sauromates*, *Elaphe longissima*, *Elaphe hohenackeri* (= *Elaphe sauromates*, *Zamenis persicus*, *Zamenis hohenackeri*) from the book “The snakes of Iran” by M. Latifi (1991).

Type specimens. Not designated (Obst, Ščerbak, 1993; Ananjeva et al., 1997; Schulz, 1996; Van Wallach et al., 2014).

Distribution. Western Ukraine, Rostov, Volgograd and Astrakhan provinces in Russia through the Volga-Ural interfluvium, Central Asia (except for sand deserts) and Kazakhstan to southern Siberia and Far East (Amur Province, Khabarovsk and Primorsky Territories). Steppes ratsnakes also occur in Mongolia, northern China and Korea. Some records are known from the Caucasus and islands in the Caspian and Aral Seas. The species *Elaphe czerskii* described by A.M. Nikolsky from the Primorsky Territory can possibly be considered as the subspecies *Elaphe dione czerskii* (Nikolsky, 1914). The subspecies *Elaphe dione*

niger Golubeva, 1923 and *Elaphe dione tenebrosa* Sobolevsky, 1929 described from western Siberia and the Altai Mts. have been perceived as invalid. The final verdict on the taxonomic status of the steppes ratsnake will be made after the revision of huge amounts of materials collected across the vast range of this trans-Palaearctic species. This species is known to have numerous colour and morphological variations in the eastern part of its distribution area, particularly in southern Siberia, Altai Mts., Mongolia, Chinese Central Asia and central China.

Distribution in the Caucasus. There is some information about the occurrence of the steppes ratsnake in the eastern Transcaucasus, mainly in Azerbaijan, eastern Georgia (southern slopes of the Greater Cau-



Map 19. Distribution map of *Elaphe dione*.



Fig. 75. Steppes ratsnake, *Elaphe dione* – Nogai steppe, northern Dagestan, Russian Federation.

casus Ridge – Lagodekhi Reserve) and northern Iran (Map 19). Some findings from Georgia and Armenia are caused by misidentification of *E. hohenackeri*. This species is also known from some sites in the Stavropol Territory and Dagestan, whereas the records from the Krasnodar Territory need confirmation.

Habitats. The steppes ratsnake is one of the most widely distributed Palearctic species and its habitats are very diverse. This snake occurs in steppes, riparian forests, floodplains, riversides, sparse broadleaf and conifer forests, scrublands, reedbeds, alpine and subalpine meadows, and in margins of wetlands. It also lives in arid landscapes), alkaline lands, stony and clay semi-deserts and rocky seashores. Habitats in the Caucasus are poorly studied and most of records are confined to the areas near water bodies in steppes. Near Budenovsk, on the Kuma River this snake inhabits the beds of *Phragmites australis* along the river course and irrigation canals.

Conservation status. Not threatened in most of its range. At the workshop on IUCN assessment of Palearctic reptiles and amphibians in Antalya, Turkey in September 2008, its status was designated as LC. In the Caucasus, it is rare and occurring in a limited number of sites. It is included in the Red Data Books of the Stavropol Territory (2002). Possibly, it also lives in Rostov Reserve.

Eastern four-lined ratsnake – *Elaphe sauromates* (Pallas, 1811) (Figs. 76–77)

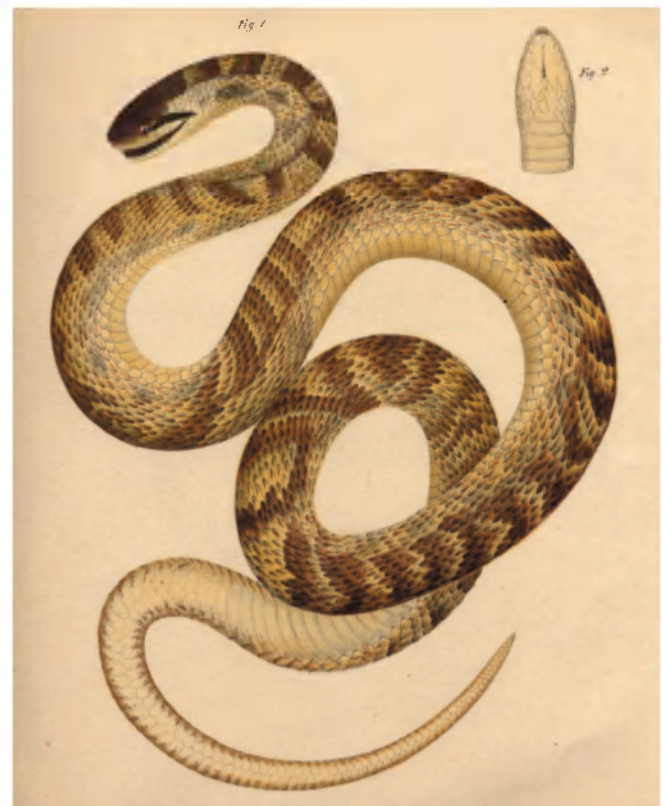


Fig. 76. A drawing of the Eastern four-lined ratsnake, *Tropidonotus sauromates* (= *Elaphe sauromates*) from the book “Fauna Caspio-Caucasia nonnullis observationibus novis” by E.I. Eichwald (1841).



Map 20. Distribution map of *Elaphe sauromates*.

Coluber sauromates Pallas, 1811(1814), Zoographia Rosso-Asiatica, sistens Omnium Animalium in Extenso Imperio Rossico. Volumen Tertium (=3). Caes. Acad. Sci., Petropoli (=St.Petersburg), vii, 42(428), cxxv pages.

Terra typica. Mertens and Müller (1928) designated the *terra typica restricta* as “Landenge bei Perekop, Taurien, Süd-Russland”; “An isthmus near the town of Perekop, Tauria” (Kherson Province, Crimea, Ukraine) (Schulz, 1996; Ananjeva et al., 2006).

Type specimens. Not designated.

Distribution. Bulgaria and Romania to the east of the Danube and Prut Rivers, Moldova, southern Ukraine, steppes of southern Russia (Rostov and Astrakhan, vicinity of Novorossiysk), Caucasus, eastern

Turkey, north-western Iran, extreme north-west of Turkmenistan and western Kazakhstan eastwards to the Aral Sea. Earlier was considered as a subspecies of the four-lined ratsnake *E. quatuorlineata sauromates* (Lacépède, 1789).

Distribution in the Caucasus. North-western Ciscaucasus (Novorossiysk to Kabardinka), Kalmykia, Chechen Republik, Stavropol Territory, Ingushetia, Dagestan, Transcaucasus (eastern Georgia, Armenia, Azerbaijan), eastern Turkey and north-western Iran (Map 20).

Habitats. *E. sauromates* usually occurs in arid landscapes, steppes, semi-deserts and forest-steppes (in both foothills and plains), stony and sandy deserts, scrubby slopes with rocky outcrops, forest glades and sparse forests. In the northern part of the Kara-Bogaz-Gol Lagoon,



Fig. 77. Eastern four-lined ratsnake, *Elaphe sauromates* – Meghri, Armenia.

this snake lives on hard loamy soils covered by saxaul, saltwort and other xerophytic plants. In the central part of the Ustyurt Plateau, it inhabits firmly fixed saxaul-covered sands, clay deserts and saline lands. In the Transcaucasus, four-lined ratsnakes move up to 2500 m asl and often occur in oakery glades and juniper sparse forests. In the Meghri district of southern Armenia, near the Lichk village, ratsnakes were recorded in subalpine grass oakery with one-storey forest stand dominated by *Quercus macranthera* and scattered trees of *Acer hyrcanum*, *Pyrus zangezura* and *Betula litwinowii*. The dominant grasses are *Poa pratensis*, *P. alpina*, *Anthoxanthum odoratum* and *Koeleria caucasica*.

Conservation status. Population has been declining because of large-scale transformations of virgin lands in steppes and other plains. As a species of declining population, *E. quatuorlineata sauromates* was listed in the Red Data Books of Azerbaijan (2013, VU), Ukraine (2009), Kazakhstan (2010, category 3, poorly studied species) and Turkmenistan (2011, category 3, marginal and rare species). It was also included in the Red Data Books of the Krasnodar Territory (2017, Near

Threatened, category 3), Kabardino-Balkaria (2000), North Ossetia-Alania (1999), Kalmykia (2013) republics and Stavropol Territory (2013). According to the workshop on IUCN assessment of Palearctic reptiles and amphibians in Antalya, Turkey in September 2008, its status was designated as LC. *E. sauromates* is protected in Dagestansky, Khosrov Forest, Vashlovani and Eldar Reserves and in Vashlovani National Park. It is essential to establish Novorossiysk Reserve, which would incorporate the species habitats in the Krasnodar Territory (Tuniyev, Nilson, 1995).

Genus *Zamenis* Wagler, 1830

Zamenis Wagler, 1830, Natürliches System der Amphibien, mit vorangehender Classification der Säugthiere und Vogel. Ein Beitrag zur vergleichenden Zoologie. J. G. Gotta'schen Buchhandlung, München: vi, (188): 354.

Type species. *Zamenis aesculapii* (= *Coluber aesculapii* Lacépède, 1789; = *Natrix longissimus* Laurenti,

1768). The valid name is *Zamenis longissimus* (Laurenti, 1768).

Large and middle-sized snakes. Most of them have body length 850–1000 mm and, with a tail, 1000–1300 mm. Only *Elaphe longissima* from South Europe can reach over 2000 mm, including a tail. The maxillary teeth are nearly same-size, 15–24 and arranged in a continuous row. The anterior teeth are slightly bigger than the posterior ones. The cervical interception is clear-cut. The pupil is round. The pterygoid bones do not have crests on the dorsal side. There are 21–27 scales (usually 23–25) around the middle of the body. The ventral scales are 195–260; the subcaudal scales are arranged in two rows, each of 61–93 scales. The anal shield is divided. The scales are smooth. The lateral edges of the frontal scale are straight. These snakes kill their prey by constricting. They live in a variety of habitats from semi-arid and arid landscapes to montane forests, seashores and volcano slopes with geothermal springs. All *Zamenis* spp. are well-skilled in climbing and can manifest themselves as both terrestrial and semi-arboreal species.

There are five species of this genus living in Asia Minor, Europe (Spain through South Europe including Sicily and some Aegean islands to the Carpathians, southern Moldova and lower Yuzhnyi Bug River) and the Caucasus. These are *Zamenis hohenackeri* (Strauch, 1873); *Z. lineatus* (Camerano, 1891); *Z. longissimus* (Laurenti, 1768); *Z. persicus* (Werner, 1913) and *Zamenis situla* (Linnaeus, 1758). There are no contemporary records confirming the presence of *Zamenis situla* in the Transcaucasus, so the earlier statements of species presence should be refuted (Szczerbak, 2003). Biogeographical and molecular dating analyses (Salve et al., 2018) suggest an origin of the ancestor of *Rhinechis* and *Zamenis* in the Aegean region with early cladogenesis during the Late Miocene associated with the Aegean arch formation and support a scenario of east to west diversification.

There are three species occurring in the Caucasus Ecoregion.

Transcaucasian ratsnake – *Zamenis hohenackeri* (Strauch, 1873) (Figs. 78, 79)

Coluber hohenackeri Strauch, 1873, Die Schlangen des Russischen Reichs, Systematischer und Zoogeographischer Beziehung, Mémoires de L'Académie

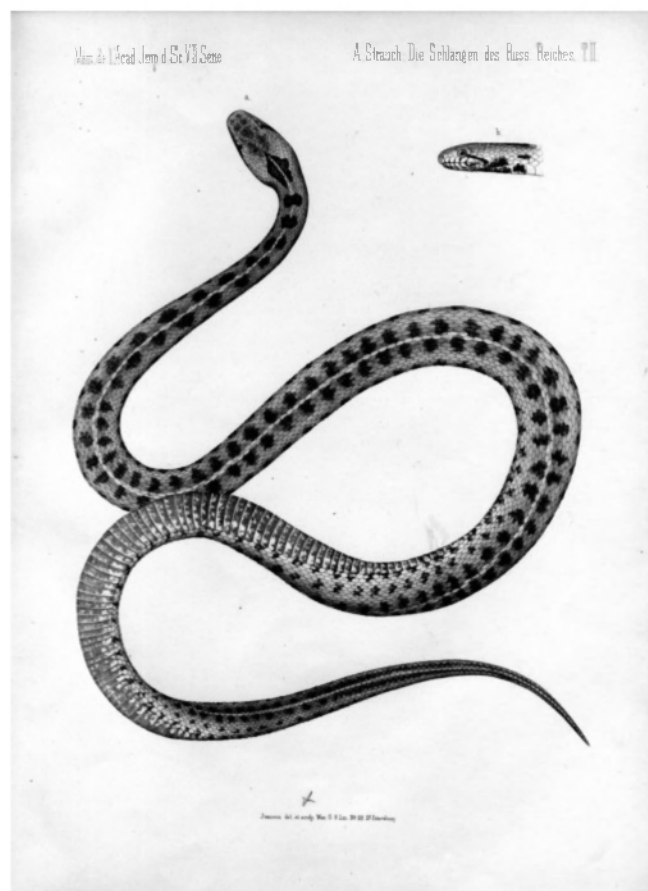


Fig. 78. A drawing of the Transcaucasian ratsnake, *Coluber hohenackeri* (= *Zamenis hohenackeri*) from the book “Die Schlangen des Russischen Reiches” by A.A. Strauch (1873).

des Impériale des Sciences de St.-Petersburg, VII Série, Tom XXI (4): 69 – tab. II (1–287 + VI tab.).

Terra typica. In the original description – “Kolonie Helenendorf (=Chanlar), Elisabethpol (=Gänçä, =Kirowabad), Tiflis (=Tbilisi)], Kaukasus”. Bishoff (1993) designated the *terra typica restricta* as “Chanlar, Aserbaidžan”; “The German colony Elenendorf (=Khanlar) and Elizavetpol (=Gyanja) [Azerbaijan]; Tiflis (=Tbilisi, Georgia)” – Schulz, 1996, Ananjeva et al., 2006. Because the lectotype was selected, we describe the *terra typica* as “Tbilisi, Georgia, Transcaucasus”.

Type specimens. In the original description (p. 73) – 5 syntypes in collections of Zoological Museum of the Imperial Academy of Sciences: No. 1642 (Kolonie Helenendorf), 1625 (Elisabethpol), 1636 (Tiflis), 1629–1630 (Kaukasus). Three syntypes are found and the lectotype ZISP 1636 and paralectotypes ZISP 1629 и ZISP 1642 are identified.

Distribution. Israel, Lebanon, Asia Minor, East Caucasus and northwestern Iran. The nominate subspe-



Fig. 79. Transcaucasian ratsnake, *Zamenis hohenackeri* — Khosrov Reserve, Armenia.

cies *Z. h. hohenackeri* (Strauch, 1873) lives in most of its range. The other subspecies *Z. h. taurica* Werner, 1898 inhabits the Cilician Taurus in southeastern Turkey and, as an isolated population, the Mt. Hermon in southern Lebanon and northern Israel (Bischoff, 1993). Recent molecular and morphological data (Hermann et al., 2018) provide sufficient evidence to support three distinct lineages within the *Z. hohenackeri* complex. These represent the subspecies *Z. h. hohenackeri*, *Z. h. tauricus*, and a lineage from southwestern Turkey described as a distinct subspecies *Z. h. lyciensis* Hoffmann, Mebert, Schulz, Göçmen, Helfenberger et Böhme, 2018. The pattern of divergence and distribution of the lineages demonstrate the association with geo-climatic events (Jandzik et al., 2013).

Zamenis hohenackeri lyciensis Hoffmann, Mebert, Schulz, Göçmen, Helfenberger et Böhme.

Distribution in the Caucasus. Eastern Georgia, Armenia, Azerbaijan and neighbouring areas of Turkey and Iran (Map 21). In the Russian part of the Caucasus, the Transcaucasian ratsnake occurs sporadically in North Ossetia-Alania, Dagestan, Chechen Republik and Ingushetia.

Habitats. This snake species lives in mountainous habitats among the rocky outcrops with woodlands and scrubs, riparian thickets and forest margins and stony mountain xerophytic steppes. In the North Caucasus, it inhabits semi-arid montane depressions with oreoxerophilic vegetation (sibljak, phrygana) and mountain steppes. In the Itum-Kalinskaya Depression in Chechen Republik, ratsnakes are recorded in mixed sibljak covering most of the left bank of the Chanty-Argun River. The dominant trees are *Paliurus spina-christi* and (along the streams) *Celtis glabrata*. The sub-dominants are *Rhamnus pallasii*, *Rosa* sp., *Spiraea hypericifolia*, *Crataegus* sp., *Malus orientalis*, *Prunus cerasifera* and *Berberis vulgaris*. The storey of herbs and shrubs comprises the *Asparagus* sp., *Salvia daghestanica* and *Stipa capillata*. The sympatric reptiles are *Lacerta strigata*, *Anguis fragilis*, *Coronella austriaca*, *Platyceps najadum*, *Pelias lotievi* and *P. dinniki*.

This species also lives in two-storey ash-hornbeam oakeries in Chechen Republik. The first storey of crown density 0.6–0.8 is composed of *Quercus petraea*, sub-dominant *Carpinus caucasia* and *Fraxinus excelsior* and scattered *Alnus incana*, Popu-



Map 21. Distribution map of *Zamenis hohenackeri*.

Ilex tremula and *Pyrus caucasica*. The second storey (density 0.3–0.8) comprises the *Corylus* sp., *Swida australis*, *Berberis* sp. and *Spiraea hypericifolia*. The herbal cover is motley, comprising mesophilic forest and meadow species.

Like *Platyceps najadum*, the Transcaucasian ratsnake seldom occurs on the left bank of the Itum-Kalinskaya Depression among the petrophilic vegetation composed of *Saxifraga* sp., *Valeriana alliariifolia*, *Campanula tridentata*, *Asplenium trichomanes*, *A. rutanuraria* and others. In the Çoruh River basin in Turkey, it lives on volcanic slopes with abundant breakstones and scrublands. In the Kazbekovsky district of Dagestan, it is recorded in broadleaf forests and semi-arid depressions in the lower Sulak River.

Conservation status. At the workshop on IUCN assessment of Palearctic reptiles and amphibians in Antalya, Turkey in September 2008, its status was designated as LC. Population of this species is under severe human pressures of habitat transformation and loss. It is included in the Red Book of animals of the Republic of Armenia (2010: VU B1ab(iii)) and Georgia (1982, category 2). Now, it is listed in the Red Data Book of the Russian Federation (2001) as a marginal and sporadically distributed species and in the Red Data Books of North-Ossetia-Alania (1999), Ingushetia (2007) and Dagestan (2009). *Z. hohenackeri* is protected in Borjomi-Kharagauli National Park, Liakhvi and Saguramo Reserves in Georgia, Zakataly, Pirkulin and Turianchay Reserves in Azerbaijan and Khosrov Forest Reserve in Armenia.

**Aesculapian snake – *Zamenis longissimus*
(Laurenti, 1768)** (Fig. 80–81)

Natrix longissima Laurenti, 1768, Specimen Medicum, Exhibens Synopsis Reptilium Emendatam cum Experimentis circa Venena et Antidota Reptilium Austriacorum, quod Autoritate et Consensu. Viennae, Joan. Thom. Trattner: 74(1–214).

Terra typica. Mertens and Müller (1928) designated the *terra typica restricta* as “Wien”; Vienna, Austria (Böhme, 1993b; Schulz, 1996; Ananjeva et al., 2006).

Type specimens. Not designated (Schulz, 1996).

Distribution. It spans from northeastern and eastern Spain through Central and South Europe (including Sicily and some Aegian islands) to East Europe

(Carpathians, southern Moldova, lower Yuzhnyi Bug River), northern Asia Minor and the Caucasus. The patterns of intraspecific taxonomy remain unclear. The nominate subspecies *Z. l. longissimus* (Laurenti, 1768) lives in most of its range. The other two subspecies are *Z. l. romanus* (Suckow, 1798) from the southern Apennines and Sicily and *Z. l. rechinyeri* Werner, 1932 from the Amorgos Island in Greece. Snakes from the isolated populations in Adygheya, Black Sea coast of the Krasnodar Territory, Abkhazia and Adjara-Lazistan are morphologically different. Information about the Aesculapian snake in eastern Georgia’s foothills of the Greater Caucasus (Lagodekhi Reserve) is very limited.

Distribution. The range is split into at least four patches: (1) foothills of the Krasnodar Territory from the



Map 22. Distribution map of *Zamenis longissimus*.



Fig. 80. Aesculapian snake, *Zamenis longissimus*, adult individual – vicinity of Dagomys, Krasnodar Territory, Russian Federation.



Fig. 81. Juvenile Aesculapian snake, *Zamenis longissimus*, Krasnodar Territory, Russian Federation.

Markotkh Ridge to the Psou River and then through Abkhazia to Sukhumi in the east; (2) Azishtau Ridge in the Republic of's northern macroslope of the Greater Caucasus Ridge; (3) Lagodekhi in eastern Georgia; (4) eastern foothills of the Colchic Lowland – Adjaria and Lazistan in Turkey (Map 22). The record on the Mt. Ararat, 50 km to the east of Aralyk in the ecotone of irrigated lands and stony steppe (Schweger, 1994) remains an emigma which puts serious corrections into the distribution of *Zamenis longissimus* in the Transcaucasus. To reliably delineate the range of this snake in the Caucasus Ecoregion, it is essential to clarify its distribution in Lagodekhi on the southern macroslope in the Greater Caucasus and, possibly, in western Azerbaijan's Zakataly and also to confirm the presence on the Mt. Ararat.

Habitats. This species lives in foothills in beech forests, mixed broadleaf forests with evergreen understorey, riparian polydominant forests, hornbeam forests, ecotones of beech and oak forests, tea plantations, hazel orchards, glades, wet meadows, sparse shrublands, slopes of woody canyons and overgrown outcrops, pistachio and juniper sparse forests, sibljak and steep maritime cliffs.

Conservation status. The Aesculapian snake was listed in the Red Data Books of the USSR (1984) and Georgian SSR (1982, category 2). Later, as a species of decreasing population and relict distribution it was included in the Red Data Books of the Russian Federation (2001, category 2), the Krasnodar Territory (2017, Vulnerable VU B2b, category 2) and Ukraine (2009). At the workshop on IUCN assessment of Palearctic reptiles and amphibians in Antalya, Turkey in September 2008, its status was designated as LC.. It is protected in Caucasian, Utrish, Pitsunda-Mussera, Sataplia, Kintrishi, Lagodekhi and Pskhu-Gumista Reserves, Sochi and Ritsa national parks, Abrau and Tuapse sanctuaries. It is essential to establish Novorossiysk Reserve in the area from the Cape Bolshoi Utrish to the Mt. Papay inclusive (Tuniyev, Nilson, 1995).

Persian ratsnake – *Zamenis persicus* (Werner, 1913) (Figs. 82,83)

Coluber persicus Werner, 1913, Neue oder seltene Reptilien und Frösche des Naturhistorischen



Fig. 82. Persian ratsnake, *Zamenis persicus*, black moph – Talysh mountains, Azerbaijan.



Map 21. Distribution map of *Zamenis persicus*.

Museum in Hamburg. Mitt naturhist. Mus. Hamburg, 30: 1–51.

Terra typica. Barferush, Mazandaran, northern Iran.

Type specimens. The description was made from a collection specimen (juvenile male) collected by F. Bruns in a period of 20–26 July 1909 and stored at Museum of Natural History of Hamburg (Germany) until it was lost during the World War II (Schulz, 1996; Van Wallach et al., 2014).

Distribution. Forests of southeastern Azerbaijan (Lenkoran, villages Shaghagach and Gugavar, foothills of the Talysh Mts.) and the lower belt of the Alborz Ridge along the Caspian Sea coast in Iran (Gilan and Mazandaran provinces). For a long time, this species

was considered as *Elaphe longissima persica* (= *Zamenis longissimus*).

Distribution in the Caucasus. Distribution of the Persian ratsnake in the region fully coincides with the total range of this narrowly endemic species (Map 23).

Habitats. Hyrcanian forests.

Conservation status. Ecology and population status are poorly studied. At the workshop on IUCN assessment of Palearctic reptiles and amphibians in Antalya, Turkey in September 2008, its status was designated as DD. Protected in Hyrcanian National Park. The Persian ratsnake snake is listed in the Red Book of the Republic of Azerbaijan (2013).



Fig. 83. Persian ratsnake, *Zamenis persicus*, brown morph – Talysh mountains, Azerbaijan.

Genus Ground snakes – *Rhynchocalamus* Günther, 1864

Rhynchocalamus Günther, 1864, Report on a collection of reptiles and fishes from Palestine. Proc. Zool. Soc. London: 491(488–493).

Type species. *Rhynchocalamus melanocephalus* (Jan, 1862) (= *Homalosoma melanocephala* Jan, 1862) (Van Wallach et al., 2014). The valid name is *Rhynchocalamus melanocephalus* (Jan, 1862).

Small snakes visually resembling some species of the genus *Oligodon* Boie, 1827 which were lumped together for a long time (Darevsky, 1970). The intermaxillary scute is large and strongly bent upwards to the upper surface of the snout, wedging deeply into the internasals. The width of the frontal scute is equal or a bit longer than its length. The nostril is in one whole scute. The body scales are smooth. The ventral scutes are 181–229, subcaudal – 53–68 pairs, the anal scute is divided, supralabial scutes 6–7. There are 15 rows of scales around the middle of the body. The small zygomatic scute is absent, one preorbital scute; one or two postorbital scutes; the lower mandibular scutes are indistinct.

The maxillary teeth are 5–6, of which the last two are much bigger than the anterior ones. There is no diastema. The palatal and pterygoid bones are toothless. Reduction of dentition is associated with specialized feeding on soft-bodied insects (termites, ants, centipedes) and their eggs.

The genus comprises 5 species distributed in the Middle East from south-eastern Turkey and the eastern Transcaucasus in the north to the south-western Arabian Peninsula in the south: *Rhynchocalamus arabicus* Schmidt, 1933, *R. dayanae* Tamar, Šmid, Göğmen, Meiri et Carranza, 2016, *R. ilamensis* Fathinia, E. Rastegar-Pouyani, N. Rastegar-Pouyani et Darvishnia, 2017, *R. melanocephalus* (Jan, 1862) and *R. satunini* (Nikolsky, 1899) (Tamar et al., 2016; Fathinia et al., 2017). Study of molecular phylogeny and micro CT-scanning revealed extreme cryptic biodiversity in Kukri snakes. These results led to description of new genus *Muhtarophis barani* (Olgun, Avci, Ilgaz, Üzum et Yilmaz, 2007) for *Rhynchocalamus barani* (Serpentes: Colubridae) (Olgun et al., 2007; Avci et al., 2015). The species *R. arabicus* Schmidt, 1933 occurs on the Arabian Peninsula. The distribution of *Rhyn-*

chocalamus species is patchy and limited. The range of *R. melanocephalus* is restricted to the Levant and Sinai while *R. satunini* is confined to the Irano-Anatolian region and in particular the Caucasian ecoregion) (Šmid et al. 2015). One species, *R. satunini* occurs in Armenia and Nakhichevan (Azerbaijan)

Satunin’s Kukri Snake – *Rhynchocalamus satunini* Nikolsky, 1899 (Fig. 84)

Contia satunini Nikolsky, 1899, Ann. Mus. Zool. Akad. Imp. Sci. St.-Petersburg, 4: 449 (449–451). *Rhynchocalamus melanocephalus satunini* (Nikolsky, 1899) – in I.S. Darevsky, 1970, Zool. Zhurn., vol. XLIX, No. 11: 1685–1690.

Terra typica. In the original description – “near the Migry village of the Elizavetpol Province, on the Arax River (collector K. Satunin)”, vicinity of Meghri, Armenia.

Type specimens. ZISP 9343.

Distribution in the Caucasus. A limited number of records are known from the left bank of the Arax River in southern Armenia and Nakhichevan (Azerbaijan), from Yerevan suburbs in the west to the Shvanidzor village in the east (southern foothills of the Meghri Ridge) (Map 24).

Habitats. These snakes live on arid, stony slopes with sparse herbal and scrubby vegetation, in wormwood semi-deserts, *Zygophyllum* communities and *Paliurus sibiljak*. In mountains, they reach 1000 m asl.



Map 24. Distribution map of *Rhynchocalamus satunini*.



Fig. 84. Satunin's kurki snake, *Rhynchocalamus satunini* – vicinity of Erevan, Armenia.

Conservation status. At the workshop on IUCN assessment of Palearctic reptiles and amphibians in Antalya, Turkey in September 2008, its status was designated as LC. As a rare species prone to imminent extinction for adverse habitat changes (category 3), the black-headed ground snake is included (as *Rhynchocalamus melanocephalus*) in the Red Books of animals of the Republic of Armenia (2010: VU B2ab(I,iii) and Red Book of the Republic of Azerbaijan (2013). Possibly, it also lives on the Urts Ridge to the south-west of Khosrov Forest Reserve. Protected in Arevik National Park.

Genus Cat snakes – *Telescopus* Wagler, 1830

Telescopus Wagler, 1830, *Natürliches System der Amphibien, mit vorangehender Classification der Säugthiere und Vogel. Ein Beitrag zur vergleichenden Zoologie*. J. G. Gotta'schen Buchhandlung, München:182(1–354).

Type species. «*Coluber* sp. plate v» – Savigny in Geoffroy, 1829 (= *Telescopus obtusus* Reuss,

1834, = *Coluber dhara* Forsskål, 1775) (Welch, 1883; Leviton et al., 1992; Van Wallach et al., 2014). The valid species name is *Telescopus dhara obtusus* (Reuss, 1834).

Middle-sized slender snakes of body length 800–1800 mm. The body is cylindrical, slightly flattened. The head is covered by large regular-shaped scutes and separated from the neck by a clear-cut cervical interception. The eyes are medium-sized, with a vertical pupil. The scales are smooth and arranged in 19–23 rows. The ventral scutes are 170–275, subcaudal – 33–86 pairs, supralabial scutes 7–9. The anal scute is divided or whole. The maxillary bone has 10–12 teeth which posteriorly decrease in size and a pair of large, grooved teeth separated by a diastema. In the mandible, the anterior teeth are larger than the posteriors. Grooved teeth are common in many colubrids of Asia and Africa from the subfamily Colubrinae, but it is not a taxonomic character of phylogenetic value. Colubrinae have all types of dentition, from small and same-size teeth on the maxillae, dentals, pterygoids and palatines to different levels of heterodontism, presence of diastema and full or partial loss of dental and pterygoid teeth.

Cat snakes are nocturnal, terrestrial and living predominantly in foothills and plain deserts and semi-deserts, moving up to 2000 m asl. They feed mainly on lizards, sometimes also on small birds and mammals, and kill their prey by venom. These snakes are oviparous, laying 5–15 eggs in a clutch.

Cat snakes are distributed in South Europe, South-West Asia and Africa. The genus includes 11–12 species, including one in Turkmenistan and Iran [*Telescopus rhynopoma* (Blanford, 1874)] and one in the Caucasus (*Telescopus fallax*).

Mediterranean Catsnake – *Telescopus fallax* (Fleischmann, 1831) (Figs. 85–86)

Tarbophis fallax Fleischmann, 1831, Dissertatio inauguralis sistens Dalmatiae Nova Serpentum Genera quam gratiosi medicorum ordinis auctoritate in Regia

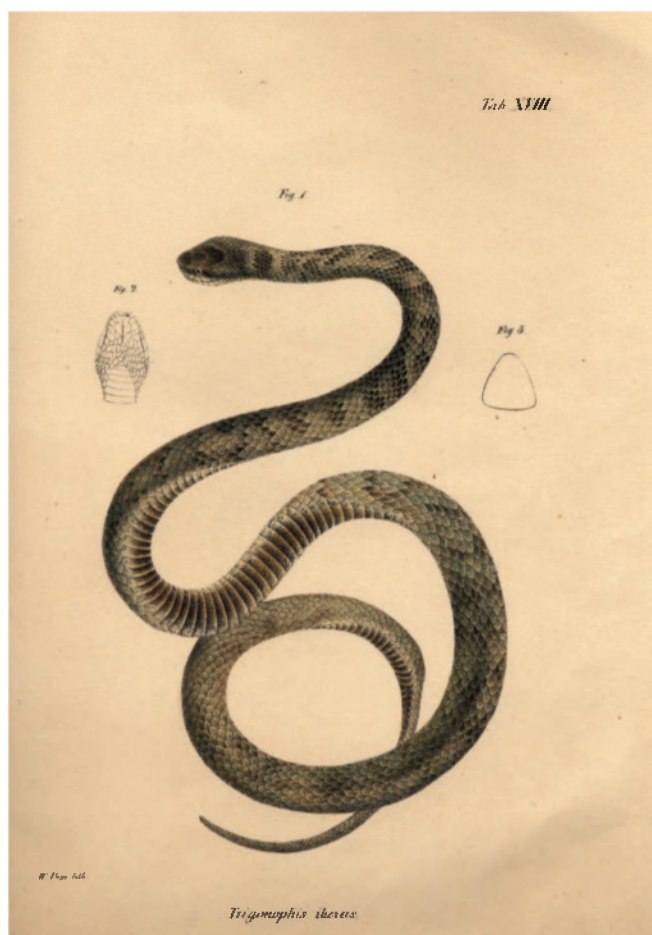


Fig. 85. A drawing of the Mediterranean catsnake, *Trigonophis iberus* (= *Telescopus fallax iberus*) from the book “Fauna Caspio-Caucasia nonnullis observationibus novis” by E.I. Eichwald (1841).

Literarum Universitate Friderico – Alexandrina pro impetrandis Doctoris Medicinae, Chirurgiae atque Artis obstetricae Summis honoribus et privilegiis eruditorum examini submitit. Comissis C. Heyderi, Erlangae: 18 (35).

Terra typica. “Triest” [delineated by Mertens and Müller (1928)]; Triest (Adriatic Sea coast, Italy) (Grillitsch, Gllillitsch, 1999; Ananjeva et al., 2006).

Type specimens. Holotype, none designated, location unknown (Van Wallach et al., 2014).

Distribution. Balkan Peninsula, Aegian and Mediterranean islands, Iran, Iraq, Syria, Lebanon, Turkey and Israel. In Russia, it is known from records in Dagestan.

There are 7 subspecies: *T. f. fallax*, *T. f. cyprianus* Barbour et Amaral 1927, *T. f. iberus* (Eichwald, 1831); *T. f. intermedius* Gruber, 1974, *T. f. multisquamatus* Wettstein, 1952; *T. f. pallidus* Stepanek, 1944 and *T. f. syriacus* (Boettger, 1896). Dagestan and the Transcaucasus (Armenia, Azerbaijan and eastern Georgia) are inhabited by *T. fallax iberus* (Eichwald, 1831).

Telescopus fallax iberus (Eichwald, 1831)

Trigonophis iberus Eichwald, 1831, Zoologia specialis quam expositis animalibus tum vivis, tum fossilibus potissimum Rossiae in universon, et Poloniae in Specie in usum lectionum publicarum in Universitate Caesarea Vilnensi habendarum, Pars posterior, Vilnae, III: 175 (404), 2 pl.

Terra typica. In the original description – “Tiflis” (=Tbilisi), Georgia.

Type specimens. Not designated.

Distribution in the Caucasus. It is distributed from the foothills of Dagestan in the north along the Caspian Sea coast to Azerbaijan, eastern Georgia, Armenia and adjacent areas of Turkey and Iran in the south (Map 25). Nordmann (1840: p. 343, pl. 4, fig. 2) mentioned *Dipsas fallax* (= *T. fallax iberus*) from collections made by Demidov in the lower Kuban River. Nikolsky (1913) wrote that this record “is hardly possible, ... and its locality can be mistaken”. There is no any other specimen recorded or collected beyond the East Caucasus, except this one which is stored at Zoological Institute RAS.

Habitats. Mediterranean cat snakes occur on stony slopes covered by sparse herbal vegetation and scrubs. This species lives in mountain xerophytic steppes, semi-deserts and, very seldom, in margins of montane forests. In the north of the range, in Dagestan, it is common in



Map 25. Distribution map of *Telescopus fallax iberus*.

dry foothills dominated by wormwood *Artemisia fragrans* semi-deserts. In wormwood semi-deserts of Dagestan's Tabasaransky district, in the Rubas riverside soosan snakes inhabit areas with *Artemisia fragrans* and singular *Iris furcata* and *Geranium* sp. The sympatric reptiles are *Xerotyphlops vermicularis* and *Eirenis collaris*. In Gobustan Reserve of Azerbaijan, these snakes live in *Salsola gemmascens* – *S. nodulosa* desert along with *Xerotyphlops vermicularis*, *Eirenis collaris*, *Platyceps najadum*, *Dolichophis schmidtii*, *Hemorrhhois ravergieri*, *Natrix tessellata* and *Macrovipera lebetina*.

In the Meghri district of Armenia, snakes are recorded near the Nrnadzor village in the meridian canyon with branches covered by *Paliurus*, *Punica* and *Paliurus-Punica sibiljak* growing on semi-desert and moun-

tain steppe soils with numerous rocky outcrops. The dominant plants are *Paliurus spina-christi* and *Punica granatum* and the sympatric reptiles are *Xerotyphlops vermicularis*, *Macrovipera lebetina*, *Telescopus fallax* and *Eirenis collaris*. In the Abovian suburbs (Armenia), this species was found in stony mountain steppe at the upper limit of altitudinal distribution.

Conservation status. At the workshop on IUCN assessment of Palearctic reptiles and amphibians in Antalya, Turkey in September 2008, its status was designated as LC. As a threatened and rare species occurring in the marginal areas of its global range, the Mediterranean cat snake is listed in the Red Data Books of the Russian Federation (2001), Red Book of the Republic of Armenia (2010: VU B2ab(I,ii) and Dagestan (2009).



Fig. 86. Mediterranean catsnake, *Telescopus fallax iberus* – Khosrov Reserve, Armenia.

It is protected in Vashlovani Reserve and National Park, Georgia, Arevik National Park, Armenia and possibly occurs also in other protected areas of the Caucasus.

FAMILY LAMPROPHIIDAE Fitzinger, 1843

Lamprophiids are a very diverse (~320 species) group of snakes. Many of them are terrestrial but some are fossorial (e.g. *Amblyodipsas*), arboreal (e.g. *Langaha*), or semi-aquatic (e.g. *Lycodonomorphus*). They inhabit deserts, grasslands, temperate and tropical forests, steppes and mountains. These snakes feed on mammals, birds, reptiles, amphibians, fish, and invertebrates, some of them use constriction to kill their prey (e.g. *Boaedon*), whereas others are highly venomous and dangerous to humans (e.g. *Atractaspis*). The modern classification was offered by Pyron et al. (2011, 2013). According to their results lamprophiids are more closely related to elapids. Most species are oviparous (Kelly et al., 2011).

Subfamily Psammophiinae Boie in Fitzinger, 1826

Subfamily Psammophiinae containing more than 50 species belonging to following genera *Dipsina* Jan, 1862, *Hemirhagerhis* Boettger, 1893, *Malpolon* Fitzinger, 1826, *Mimophis* Günther, 1868, *Psammophis* Fitzinger, 1826, *Psammophylax* Fitzinger, 1843, *Rhagerhis* Peters, 1862 and *Rhamphiophis* Peters, 1854. Two genera, *Malpolon* and *Psammophis* are presented in the Caucasian Ecoregion.

Genus *Malpolon* Fitzinger, 1826

Malpolon Fitzinger, 1826, Neue Classification der Reptilien nach ihren Natürlichen Verwandtschaften. Nebst einer Verwandtschafts-Tafel und einem Verzeichnisse der Reptilien-Sammlung des k. K. Zoologischen Museums zu Wien. J.G. Huebner, Wien: viii, 66 pp.

Type species. *Natrix lacertina* (= *Coluber monspessulanus* Hermann, 1804) (Van Wallach et al., 2014).

Large snakes of body length up to 1800 mm. The head is elongated and tapered, well separated from the neck by the cervical interception. The top of the head is clearly concave. The tail is long. There are 17–19 rows of scales around the middle of the body. The scales are smooth; in adults they have quite clear longitudinal median grooves. The ventral scales are 155–190 and the subcaudal scales are 48–110 pairs. The anal shield is divided. The maxilla has 10–17 small teeth of same size and 1–2 large teeth with an external groove that are located in the posterior region and separated from the anterior teeth by a diastema. By this character, *Malpolon* snakes belong to opisthoglyphous snakes (not a taxonomic category). The pupil is round.

There are three species in this genus distributed in the Mediterranean, South Europe, North Africa, Arabian Peninsula, Asia Minor, Central Asia and the Caucasus: *Malpolon insignitus* (Geoffroy De St-Hilaire, 1827), *Malpolon moilensis* (Reuss, 1834) and *Malpolon monspessulanus* (Hermann, 1804). These snakes live in dry steppes and foothill areas. Their activity is crepuscular. Recent molecular genetic research (Carranza et al., 2006) has demonstrated that a high level of

genetic divergence in the eastern clade of *M. monspessulanus* indicates an early dispersion and distribution of taxa through northern Lybia and Egypt to Syria, Iraq and Iran and across the Mediterranean Turkey to the Aegean Archipelago and the Balkans.

There is one species living in the Caucasus.

Eastern Montpellier Snake – *Malpolon insignitus* (Geoffroy, 1827) (Fig. 87)

Coluber insignitus Geoffroy in Savigny, Description des reptiles qui se trouvent en Egypte. In Savigny M.J.C.I. de (ed.), Description de l' Egypte pendant l'expédition de l'armée française (1798–1801). Histoire naturelle, Paris: Imprimerie Impériale: 121–160.

Type locality: “Egypte” [= Egypt]. Restricted to lower Egypt *fide* Mertens et Müller (1928) (Van Wallach et al., 2014)).

A valid species *fide* Carranza et al. (2006: 538)

Distribution in the Caucasus. It is known that the range in the Caucasus Ecoregion is split into two areas. The northern area is located in the East Ciscaucasus, forming a geographical isolate spread in Russia



Fig. 87. Eastern Montpellier snake, *Malpolon insignitus* – Nyuvadi, Armenia.



Map 26. Distribution map of *Malpolon insignitus*.

(eastern Kalmykia, Stavropol Territory, Rostov Province, and some sites on the left bank of the Volga River in the Astrakhan Province). The southern area covers almost all Azerbaijan, southern Armenia, southeastern Georgia, north-western Turkey and north-western Iran (Map 26). As this snake is recorded in northeastern Azerbaijan close to Dagestan, possibly it also occurs in maritime areas of Dagestan. No similar disjunctions in distribution of other Mediterranean species are known in the Caucasus.

Habitats. In the Transcaucasus, Eastern Montpellier snakes occur in dry stony semi-deserts with rough terrain and rocky outcrops and also in arid steppes, fixed sands and arid sparse forests. In the Meghri district of southern Armenia, these snakes are recorded near the

Nrnadzor village in the meridian canyon with branches covered by Paliurus, Punica and Paliurus-Punica types of sibiljak growing on semi-desert and mountain steppe soils with numerous outcrops. The dominant plants are Paliurus spina-christi and Punica granatum. The sympatric reptiles are *Xerotyphlops vermicularis*, *Eirenis collaris*, *Macrovipera lebetina* and *Telescopus fallax*. In this district, snakes also inhabit *Salsola* sp. semi-deserts with *Stachys inflata*, *Allium* sp. and *Thymus kotschianus* on breakstones. In the Ciscaucasus, snakes live in clayey-sandy wormwood-grass steppes, sands and sometimes in floodplain meadows

Conservation status. Population size is not high, but stable. The main threat is habitat loss to human activities. At the workshop on IUCN assessment of Pal-

earctic reptiles and amphibians in Antalya, Turkey in September 2008, its status was designated as LC (<https://www.iucnredlist.org/species/157253/5061050>). Its status is designated in the Georgian Red List as VU B2a. As a species of decreasing population, it is included in the Red Data books of Astrakhan Province (2014), Stavropol Territory (2013) and Republic of Kalmykia (2013). Protected in Eldar, Vashlovani and Turianchay Reserves and in Vashlovani National Park.

Genus *Psammophis* Boie in Fitzinger, 1826

Psammophis Boie, 1826, Generalübersicht der Familien und Gattungen der Ophidien. Isis von Oken, Jena, 19(10): 981–982.

Type species. *Psammophis sibilans* (Linnaeus, 1758) [= *Coluber sibilans* Linnaeus] – in Van Wallach et al. (2014). The valid name is *Psammophis sibilans*.

Slender, long and very mobile snakes. Body length can reach 2200 mm, but is usually 1000–1300 mm. The narrow head is tapered and poorly separated by the cervical inter-

ception. The eyes are large and the pupil is round. The frontal scale is long and narrow. The top of the head is covered by large symmetrical scutes. The scales are smooth with an apical pore on each scale. The subcaudal scales are arranged in two rows. The maxillary teeth differ in size: the median of 10–13 is the largest and the posterior 1–2 teeth are grooved and separated from a row of small teeth by a diastema. By this trait, *Psammophis* snakes belong to opisthoglyphous snakes. These snakes live predominantly in open arid areas with sparse scrubs, including deserts. They are active hunters; some of them prey exclusively on lizards. Activity is diurnal. Oviparous, laying 3–20 elongated eggs in a clutch.

There are more than 30 species in this genus widely spread in Africa, South and West Asia. One species, *P. condanarus* (Merrem, 1820), permeates eastwards to Thailand and central Vietnam. There is one species in the Caucasus.

Steppe ribbon racer – *Psammophis lineolatus* (Brandt, 1838) (Fig. 88)

Coluber (Taphrometopon) lineolatus Brandt, 1838, Note sur quatre nouvelles espèces de serpents de la côte



Fig. 88. Steppe ribbon racer, *Psammophis lineolatus* – western Karakum desert, Turkmenistan.



Map 27. Distribution map of *Psammophis lineolatus*.

occidentale de la mer Caspienne et de la Perse septentrionale par M. Kareline. Bull. Ac. St.-Petersburg, III (16) : 243(241–244).

Terra typica. In the original description – “desert ad. m. Casp.”; eastern coast of the Caspian Sea – Ananjeva et al. (2006).

Type specimens. Holotype ZISP 2042 (Coll. Karelin, 1837: Lit. orient. m. Caspii).

Distribution. Southern Kazakhstan and Central Asia to southern Mongolia, northwestern China, Pakistan, Afghanistan, Iran and the extreme south of the Transcaucasus.

Distribution in the Caucasus. The steppe ribbon racer is known only from the Nakhichevan Depression in the middle part of the Arax River basin (Az-

erbaijan) separated from Armenia’s Ararat Valley by the anticlinorium of the Volchie Vorota (Wolf Gates) (Darevsky, 1959; Bannikov et al., 1977) (Map 27). Until now, only two specimens are collected. The first was collected by I.S. Darevsky in May 1957 10 km to the north of the state border with Iran, near the village of Kyarim-Kuli-Diza. The second specimen was collected by N.N. Scherbak in 1974 4 km to the north of the Diza village. Now it has been stored at the National Museum of Natural History of the National Academy of Sciences of Ukraine (Dotsenko, 2003). Given that most of the Nakhichevan Depression is located in Iran, new records of this snake can be expected there. Recently (Doronin, 2016) a third known specimen of *Psammophis lineolatus* (Brandt, 1836) from the Caucasus (near the Anabad

village, Ordubad district, Nakhchivan Autonomous Republic of Azerbaijan) was recorded.

Habitats. Steppe ribbon racers inhabit open arid areas, most frequently deserts, where they live in fixed and half-fixed sands, rarely in clayey wormwood and wormwood-saltwort semi-deserts and takyr. They often reach the heights over 2600 m asl in Afghanistan, 1700 m in Kyrgyzstan, 1500 m in Tajikistan and up to 1000 m in Turkmenistan' Kopetdag Mts. In the Caucasus, this species lives only in the hottest depression of the entire Caucasian isthmus whose climate differs even from the adjacent Ararat Valley.

Conservation status. At the workshop on IUCN assessment of Palearctic reptiles and amphibians in Antalya, Turkey in September 2008, its status was designated as LC. Beyond the Caucasus, the steppe ribbon racer is a common species of stable population size, but in the Caucasus it is a rare reptile distributed in the extreme north-western periphery of its global range. It is listed in the Red book of the Republic Azerbaijan (2013).

FAMILY VIPERS – VIPERIDAE Laurenti, 1768

The head of viperids is usually wide, with a clear-cut cervical interception, covered on top by small scales or large scutes. The body is thick, with a short tail. The pupil is vertical. The mobile maxilla is significantly shortened. There is a deep notch on the anterosuperior edge of the maxilla in snakes of the subfamily Crotalinae, but it is absent in Viperinae Laurenti, 1768. The maxilla is attached to the prefrontal by its anterior side, allowing it to take a vertical position to the cranial axis with mouth opening. The large tubular fangs are connected with venom glands and located in the posterior part of the maxilla. The palatal, pterygoid and dental bones have teeth. The rudimentary pelvis and hind limbs are absent. The Crotalinae species have well-developed heat-sensing pits between a nostril and an eye, so are called the pit vipers.

Viperids comprise the terrestrial, fossorial and arboreal forms. Species inhabiting high latitudes and elevations are usually diurnal, but a majority of tropical vipers is nocturnal. The family includes both ovoviviparous and oviparous species. All vipers are venomous. Their venom is predominantly hemotoxic, i.e. affecting the blood and blood-forming organs. Snake-bitten animals

die from blood incoagulation and many internal hemorrhages. Vipers are very dangerous to humans. Deaths from inenommation are numerous and even when recovering victims suffer from strong necrotic processes in muscles and bones and from diseases resulting from lesions of kidneys and the liver. Viper venoms have been widely used in pharmacology and medicine, particularly for diagnostic tests, making these reptiles commercial venom producers (Ananjeva, Orlov, 2005).

The family Viperidae comprises about 270 species belonging to 35–40 genera from 4 subfamilies – Azemiopinae Liem, Marx et Rabb, 1971 (southern China and northern Vietnam), Crotalinae Oppel, 1811 (Asia, North, Central and South Americas), Causinae Cope, 1860 (sub-Saharan Africa) and Viperinae Laurenti, 1768 (Europe, Africa, continental Asia, Taiwan, eastern Java, Lesser Sunda Islands and Ceylon). The Viperidae are absent in Australia, Oceania, Papua New

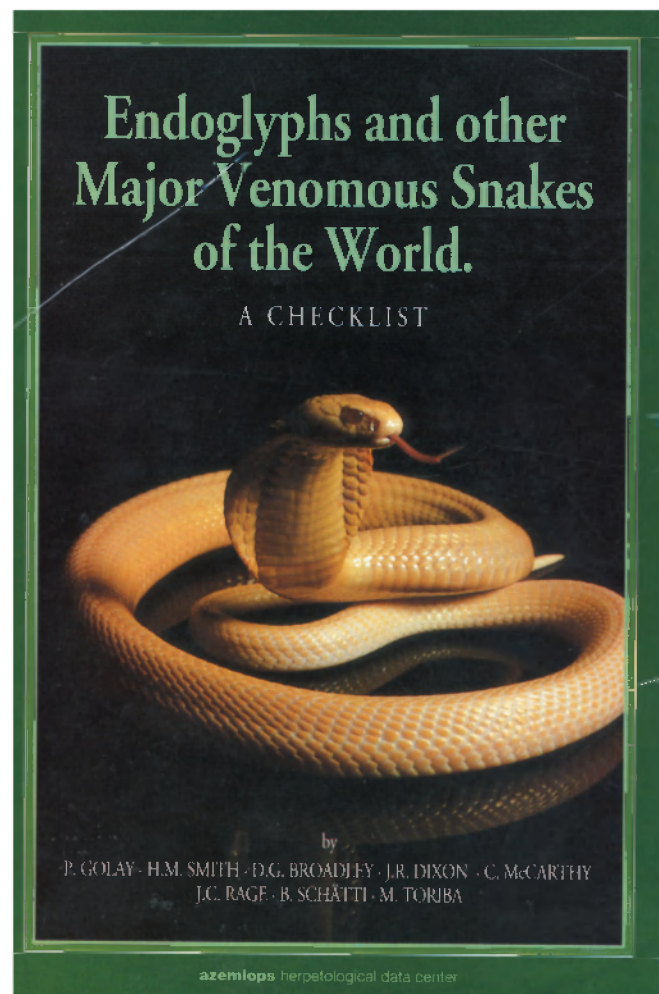


Fig. 89. Cover page of the book “Endoglyphs and other major venomous snakes of the world” by F. Golay et al. (1993).

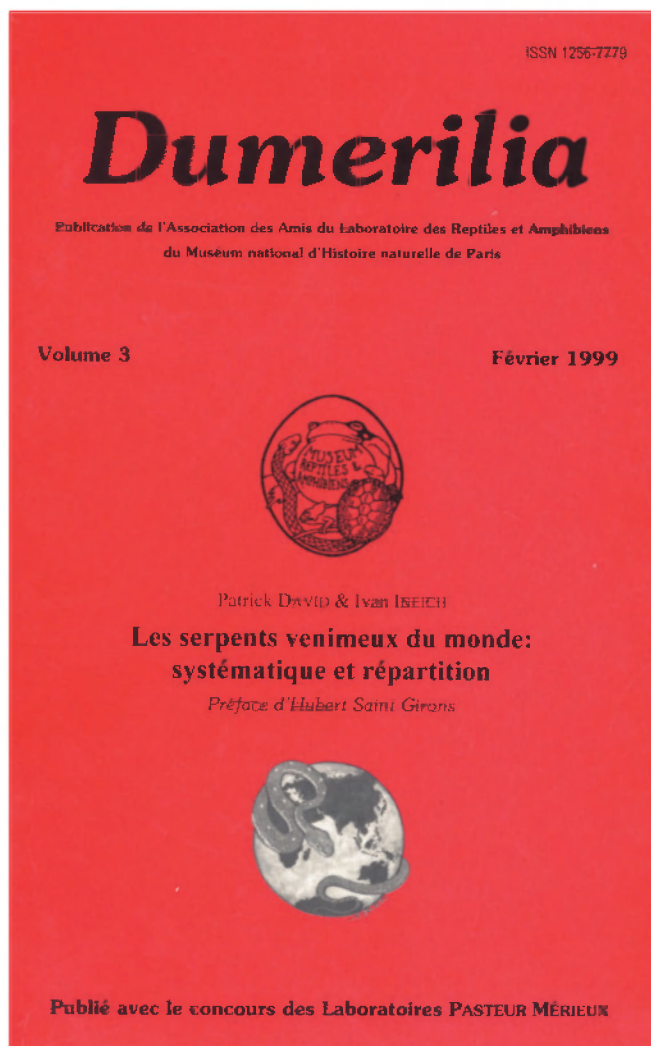


Fig. 90. Cover page of the book “Les serpents venimeux du monde: systématique et répartition” by P. David and I. Ineich (1999).

Guinea and Madagascar (Marx, Rabb, 1965; Gloyd, Conant, 1990; David, Ineich, 1999; McDiarmid et al., 1999; Gumprecht et al., 2004; Wüster et al., 2008).

In spite of their relatively low diversity (ca. 9% of all colubroid snakes), vipers demonstrate high variation in morphology and ecological niches, occupying dominant positions in many ecosystems (Greene, 1994, 1997). They act as model organisms in today’s evolutionary, phylogenetic, morphological and ecological studies (Groombridge, 1986; Herrmann et al., 1987, 1992; Madsen, Shine, 1994; Madsen et al., 1999; Lenk et al., 2001b; Martins et al., 2001; Wüster et al., 2004; Araújo, Martins, 2006; Ineich et al., 2006). Special chapters in modern revisions (Figs. 89–90) of the world’s venomous snakes and a volume of *Handbuch der Reptilien und Amphibien Europas* (3/IIB, 1999) (Fig. 91) are devoted to the Viperidae. There is a monograph on venomous snakes of Europe and the *Vipera* snakes of

Asia and Africa (Fig. 92). International conferences have been regularly held to address this group of snakes, e.g. a symposium within the World Congress of Herpetology (Prague, 1997), Symposium on Biology of Pit Vipers (Arlington TX, 1989), 1st International Conference on Biology of the Vipers (Uppsala, Sweden, 2000), 2nd International Conference on Biology of the Vipers (Porto, Portugal, 2007) (Fig. 93), the 2th Biology of the Vipers Conference (Calci, Pisa, Italy, 2010), the 4th Biology of the Vipers Conference (Athens, Greece, 2014) and the 5th Biology of the Vipers Conference (Chefchaouen, Morocco, 2017). The proceedings of these conferences are published in “Phylogeny and Systematics of the Viperidae” (1999) (Fig. 94), “Biology of the Pitvipers” (1992) and “Biology of the Vipers” (2002).

Special attention should be paid to research of viperid venoms, their evolution and role in trophic adaptations (Daltry et al., 1996; Chijiwa et al., 2003; Creer et al., 2003; Sanz et al., 2006). The results of morpho-

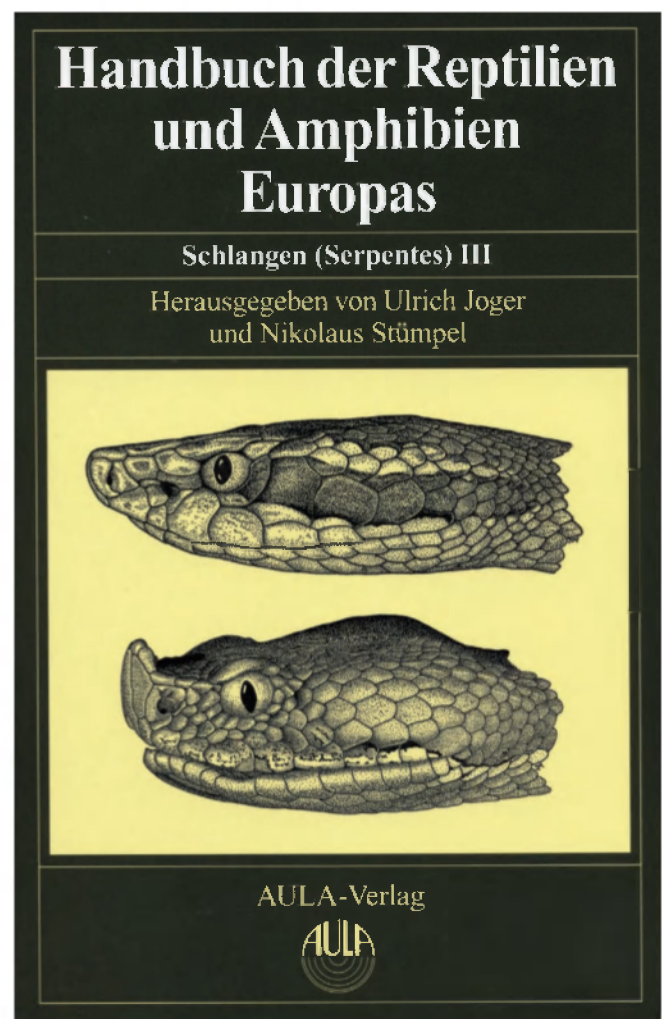


Fig. 91. Cover page of the book “Handbuch der Reptilien und Amphibien Europas”. Vol. 3/IIB (1999).

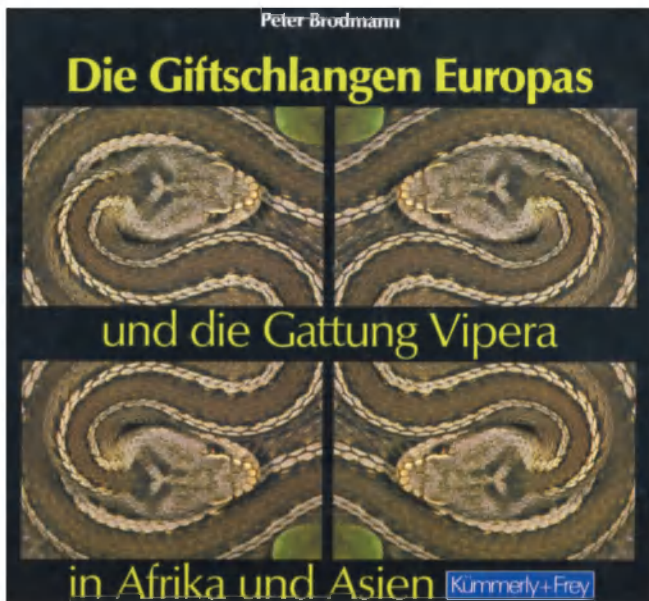


Fig. 92. Cover page of the book “Die Giftschlangen Europas und die Gattung *Vipera* in Afrika und Asien” by P. Brodmann (1987).

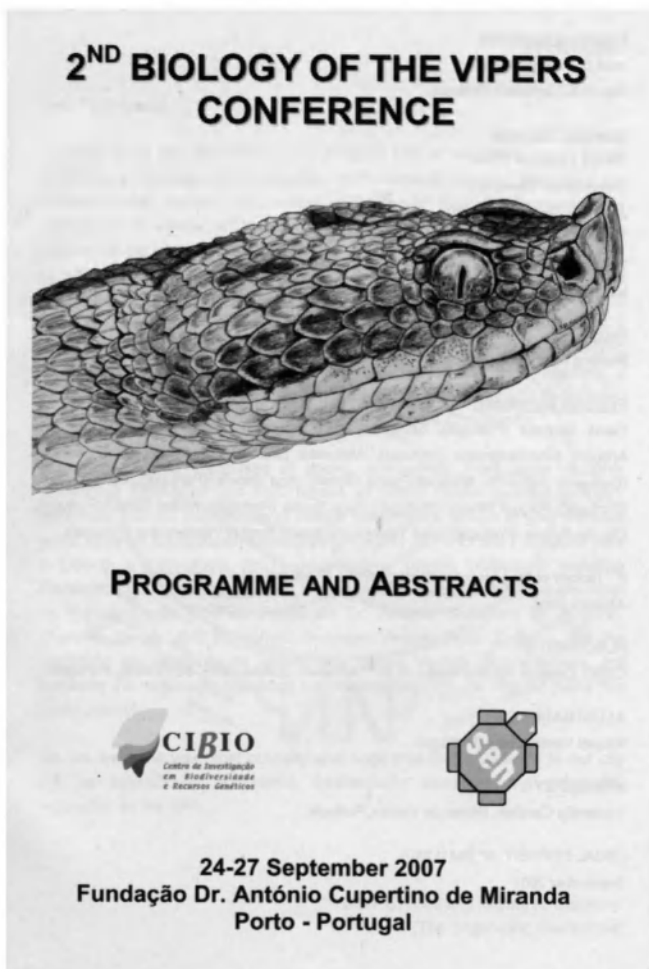


Fig. 93. Cover page of the proceedings of the 2nd Biology of the Vipers Conference in Portugal (2007).

logical (Jackson, 2003, 2007) and toxicological (Fry et al., 2003; Fry, Wüster, 2004) studies show that the venom apparatus appeared in the early stages of the radiation of the colubroid snakes (Fry et al., 2006), then it disappeared in some lineages or reached high levels of advancement, like in vipers (Vidal, 2002).

This family includes a number of rare and poorly studied species. Nineteen species are listed on the IUCN Red List of Threatened Species and 3 species from the North Palearctic were included in the Red Data Book of the USSR (1984). A number of taxa are protected by the Bern Convention, listed in regional Red books or protected at local

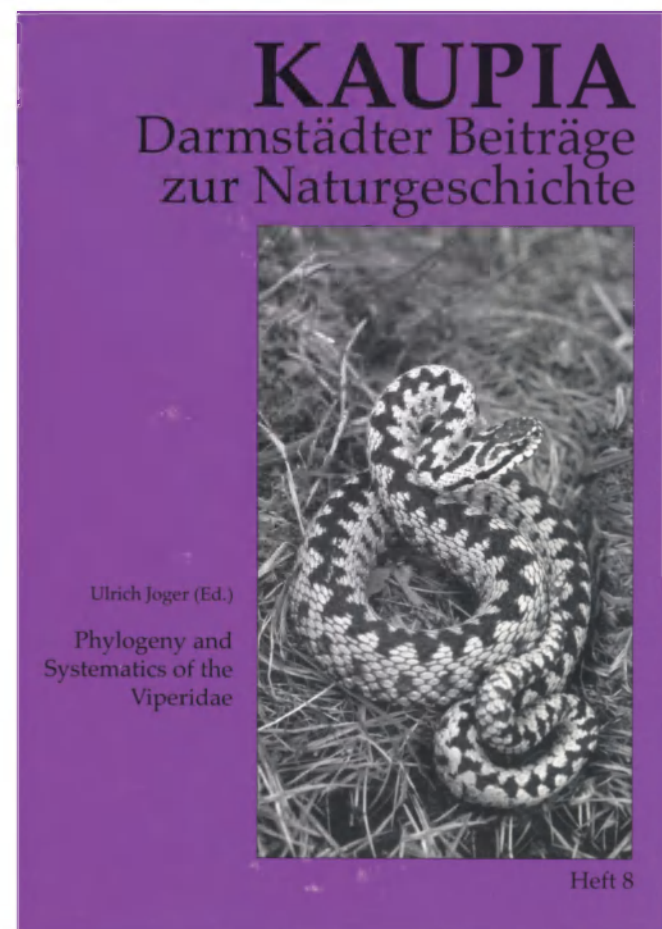


Fig. 94. Cover page of the proceedings “Phylogeny and Systematics of the Viperidae” U. Joger (ed.) (1999).

scales. Like most of other snakes, vipers are mainly threatened by human-induced habitat loss and transformations and their conservation is often formal or insufficient.

An ever-growing interest to conservation of Caucasian vipers as an indispensable part of the region’s biodiversity has been realized in joint and multilateral international projects (Figs. 95–101).



Fig. 95. Participants of the Caucasian herpetological expedition. Grozny. 1990. From left to right: A.A. Iogansen, N.L. Orlov, N.B. Ananjeva, R. Macey, A.V. Lotieva, Yu.I. Kaverkin (top row); T. Papenfuss (bottom row).



Fig. 96. Caucasian Reserve, Russian Federation. 1990. From left to right: Claus Andrén, Boris Tuniyev, Göran Nilson and Nikolai Orlov.

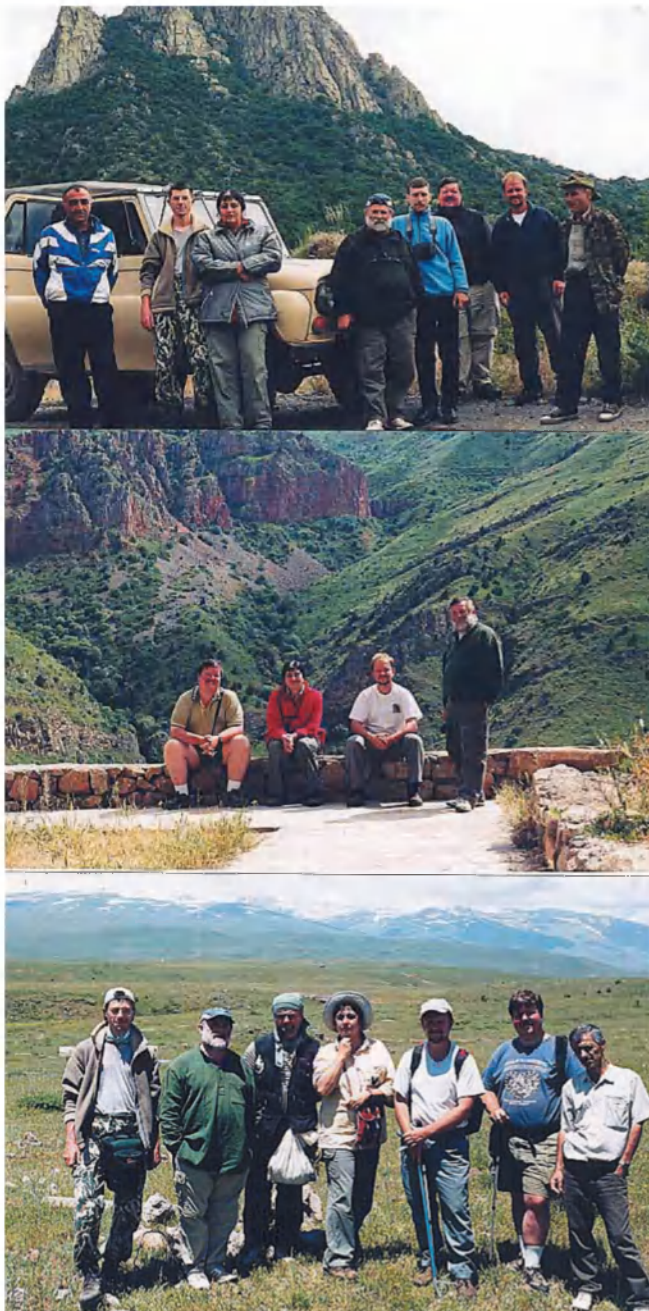


Fig. 97. Armenia. 2004. Roman Khalikov, Nikolai Orlov, Akexander Malkhasyan, Natalia Ananjeva, Jeff Etling, Andy Snyder and Aram Agasyan (photo at the bottom of the picture).

There are 5 genera of this family in the fauna of the Caucasus belonging to two subfamilies (Crotalinae: *Gloydius* and Viperinae: *Macrovipera*, *Pelias*, *Montivipera* and *Vipera* sensu stricto). Indications of the genus *Pseudocerastes* Boulenger, 1896 [*P. persicus* (Dumeril, Bibron et Dumeril, 1854)] in the eastern Transcaucasus [Soganlug near Tiflis (Tbilisi, Georgia) and Ashtarak village of the Erivan Province (=Armenia)] (Nikolsky, 1913, 1916) are erroneous. Most likely, these records

should be attributed to *Pseudocerastes persicus* brought from Persia (Iran) or southeastern Turkey.

Subfamily Pit vipers – Crotalinae Oppel, 1811

Genus Pit vipers – *Gloydius* Hoge et Romano-Hoge, 1981

Gloydius Hoge et Romano-Hoge, 1981, Poisonous snakes of the world. Part I. Check list of the pit vipers. Viperoidae, Viperidae, Crotalinae. Mem. Inst. Butantan, São Paulo (1979) 42/43: 194(179–310).

Type species. “*Trionocephalus halys*; Boie, 1827 [= *Halys halys*; Gray, 1849; = *Gloydius halys* (Pallas, 1776)]” – designated by Hoge and Romano-Hoge (1981).

Medium-sized snakes, up to 800 mm in length. The large, wide head is covered on top by nine large scales, which form a flat shield. The cervical interception is clear-cut. The snout tip is slightly turned up, but without additional cutaneous protuberances. The pupil is vertical. The body scales have a costa and two apical pores each. The subcaudal scutes are arranged in two rows. The ultimate-row scales near the tail tip have longer length than width. All species are venomous, having paired tubular fangs on a very mobile maxilla. The supratemporal bones are very short and not extending over the posterior of the braincase. Generally, cranial bones are thin, lightweight and ensuring high kinesis of the skull. The ectopterygoid is rather straight. As in most viperids, the venom of the *Gloydius* species is hemotoxic, leading to hemorrhages, thromboses and intense necroses. However, these pit vipers and their close relatives (rattlesnakes) also produce neurotoxins which affect the nervous system and kill an organism by causing the paralysis of the respiratory centre and other ganglia. So, the venom of these snakes makes a dual effect on their victims: the first stage is neurotoxic and the second is hemotoxic (common for proper viperids).

For a long time the *Gloydius* species were referred to the genus *Agkistrodon* s.l. which is now split into 5 genera:

- 1) *Calloselasma* Cope, 1860 – Indochina and Indonesia (Java and Sumatra). 1 species
- 2) *Deinagkistrodon* Gloyd, 1979 – southern China, including Taiwan, and northern Indochina. 1 species



Fig. 98 Caucasian Reserve, Russian Federation. 2005. Nikolai Orlov and Boris Tuniyev.



Fig. 99. Berd, Armenia. 2006. From left to right: Bob Murphy, Lesley Lewcock, Nikolai Orlov, Aram Aghasyan and Alexander Malkhasyan. 2006.



Fig. 100. Leningrad (St.Petersburg). 1988. From left to right: Nikolai Orlov, Wolfgang Böhme, Ilya Darevsky, Leo Borkin, Natalia Ananjeva.



Fig. 101. Ulrich Joger. 2006.

3) *Hypnale* Fitzinger, 1843 – Ceylon and southern India. 3 species

4) *Agkistrodon* Beauvois, 1799 (s.s.) – North and Central Americas, southwards to northwestern Costa Rica inclusive. 3 species

5) *Gloydius* comprising 17 species: *Gloydius angusticeps* Shi, Yang, Huang, Orlov et Li, 2018; *G. blomhoffii* (Boie, 1826), *G. brevicaudus* (Stejneger, 1907), *G. caucasicus* (Nikolsky, 1916), *G. halys* (Pallas, 1776), *G. himalayanus* (Gunther, 1864), *G. intermedius* (Strauch, 1868), *G. lijianlii* Jiang et Zhao, 2009, *G. liupanensis* Liu, Song et Luo, 1989, *G. monticola* (Werner, 1922), *G. qinlingensis* (Song et Chen, 1985), *G. rickmersi* Wagner, Tiutenko, Borkin et Simonov, 2015, *G. rubromaculatus* Shi, Li et Liu, 2017, *G. shedaoensis* (Zhao, 1979), *G. strauchi* (Bedriaga, 1912), *G. tsushimaensis* (Isogawa, Moriya et Mitsui, 1994) and *G. ussuriensis* (Emelianov, 1929).

They live in a vast area from Asia Minor to East Asia including Mongolia, China, Korea, Japan (except for the Ryukyu Archipelago), Pakistan, northern India, Nepal, Iran, Afghanistan, Central Asia, Kazakhstan and southern Azerbaijan. In general, this genus is distrib-

uted in the Palearctic zoogeographical region. There is one species (*G. caucasicus*) occurring in the Caucasian Ecoregion (Asadi et al., 2018).

Caucasian pitviper – *Gloydus caucasicus* (Nikolsky, 1916) (Figs. 102–103)

Ancistrodon halys caucasicus Nikolsky, 1916, Presmykayuschiesia (Reptilia). Vol II. Ophidia. Fauna Rossii i sopredelnykh stran. Petrograd, Imperatorskaya akademiya nauk: 274–276 (1–349), 8 Plates.

Terra typica. Erroneously defined as “vicinity of Kirovsk town, Lenkoran district, Azerbaijan, approximate 38°29′N, 48°43′E” because of erroneous designation of the neotype ZISP 2200 (Orlov, Barabanov,

1999, 2000; Orlov et al., 2002). As the syntypes were found in MNKNU and the lectotype MNKNU 14942 was identified (Vedmederya et al., 2009), the *terra typica* should be re-defined as “Dzhi village, Arusskaja obschina, Lenkoran uezd” (= Dzhi village, Lenkoran district, Azerbaijan).

Type specimens. Lectotype MNKNU 14942 (collectors A.N. Kaznakov and A.B. Shaposhnikov, 18 July 1906).

A.M. Nikolsky (1916, p. 276) wrote: “*The Caucasian Museum sent me several individuals collected by A.N. Kaznakov and A.B. Shaposhnikov in the following localities of the Lenkoran district: Mashkhan, Gyugavar, Khanbulag and the Dzhi village of the Arusskoe community. A.B. Shelkovnikov and A.N. Kaznakov*



Map 28. Distribution map of *Gloydus caucasicus*.



Fig. 102. Caucasian pitviper, *Gloydius caucasicus* – Astara region, Azerbaijan.



Fig. 103. Caucasian pitviper, *Gloydius caucasicus* – Elburs, Iran.

found this snake in Mashkhan to the south of Lenkoran in forest, almost at sea level, and near the Dzhi village in a totally treeless landscape at 700 m and in cliffs at 2200 m above sea level”.

Distribution. *G. caucasicus* (Nikolsky, 1916) inhabits southeastern Azerbaijan, southern Turkmenistan (Kopetdag), northern Iran (Alborz and Kopetdag Mts.) and northwestern Afghanistan to the north of Gerat. In the Caucasus Ecoregion, it occurs in southeastern Azerbaijan (Lenkoran Lowland, Talysh Mts. and Zuvand) and the adjacent areas of the Alborz Ridge in Iran (Map 28).

Habitats. In the Caucasus, these snakes inhabit lowland subtropical Hyrcanian forests, montane broad-leaf forests and mountain steppes from 0 to 2200 m asl. Habitats can be humid and arid, but the essential prerequisite is the presence of stony and rocky sites.

Conservation status. At the workshop on IUCN assessment of Palearctic reptiles and amphibians in Antalya, Turkey in September 2008, its status was designated as LC. *G. caucasicus* deserves particular attention for its marginal distribution and rarity in the Caucasus. It is protected in Lenkoran Reserve and Hyrcanian National Park, Azerbaijan.

Subfamily True vipers – Viperinae Laurenti, 1768

The largest in this subfamily genus *Vipera* Laurenti, 1768 (sensu lato) has been acknowledged to comprise 5 genera: *Vipera* Laurenti, 1768 (sensu stricto); *Macrovipera* Reus, 1927; *Montivipera* Nilson, Tuniyev, Andrén, Orlov, Joger et Herrmann, 1999; *Pelias* Merrem, 1820 and monotypic *Daboia* Gray, 1842 [*D. russelli* (Shaw et Nodder, 1797)]. The Viperinae live in Pakistan, India, Sri Lanka, Bangladesh, Myanmar, Thailand, Cambodia, Indonesia, China and Taiwan (Joger, Stümpel, 2005). There are 4 genera in the fauna of the Caucasus. Information about the occurrence of *Pseudocerastes* Boulenger, 1896 [*P. persicus* (Dumeril, Bibron et Dumeril, 1854)] in the eastern Transcaucasus [Soganlug near Tiflis (=Tbilisi, Georgia) and the Ashtarak village in Erivan Province (=Armenia)] (Strauch, 1868, 1873; fig. 104; Nikolsky, 1913, 1916) are mistaken and attributed to individuals imported from Persia (=Iran).

While discussing the distribution of *P. persicus*, Nikolsky (1916) wrote: “It occurs in Persia and the eastern part of the Transcaucasus”, referring to the statements

by K.F. Kessler, K.A. Satunin and A.F. Laister. It should be noted that the absence of *P. persicus* in the eastern Transcaucasus has been supported by its absence also in eastern and southern Turkey. This snake is recorded only in western Pakistan, Afghanistan, Iran, northern Iraq and mountainous Oman. The second species (or subspecies) of the genus *Pseudocerastes* (*P. fieldi* Schmidt, 1930) inhabits Israel, Jordan and south-western Iran (Leviton et al., 1992) and the third species *Pseudocerastes urarachnoides* Bostanchi, Hamid, Anderson, Kami et Papenfuss, 2006 was found in western Iran's Zagros Mts. (from a description by Bostanchi et al., 2006).

The *Pelias* and *Vipera* species often co-exist in the Sarmatian sites of the northern Prichernomie (Black Sea region) what indicates their early divergence soon after the viperids appeared in geological chronicles (Zerova et al., 1987).

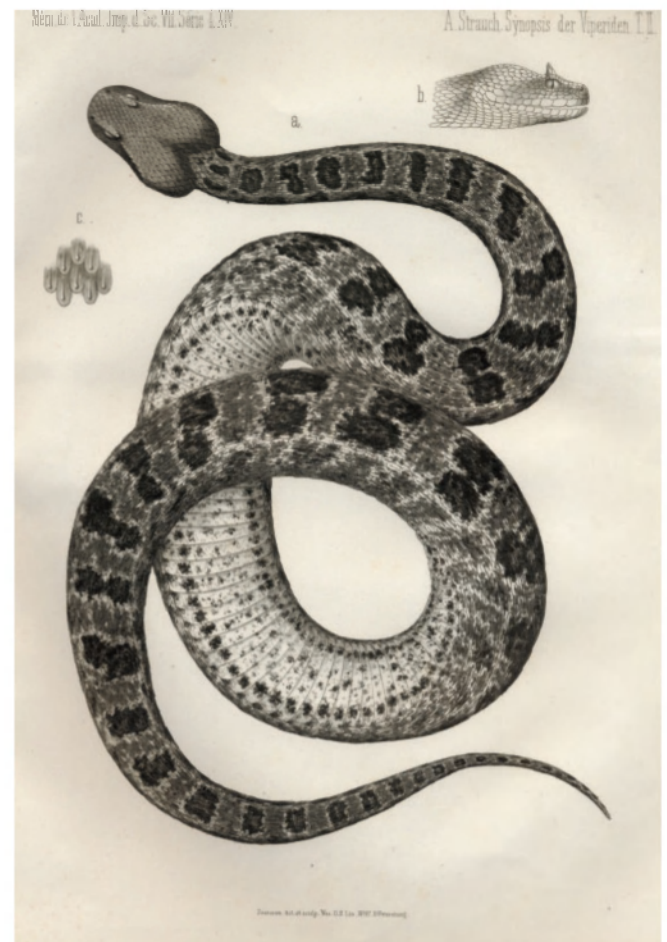


Fig. 104. A drawing of the Persian horned viper, *Vipera persica* (= *Pseudocerastes persicus*) from the book “Synopsis der Viperiden, nebst Bemerkungen über die geographische Verbreitung diese Giftschlangen Familie” by A.A. Strauch (1869).

Genus Giant vipers – *Macrovipera* Reus, 1927

Macrovipera Reus, 1927, Sechs europäische Giftschlangenattungen. Zool. Anz. Leipzig, 73(5/8): 126 (124–129).

Type species. In the original description – *Coluber lebetinus* Linnaeus, 1758 [= *Vipera lebetina* (Linnaeus, 1758)]. The valid species name is *Macrovipera lebetina* (Linnaeus, 1758).

Large snakes, sometimes exceeding 2 m in length. The head is large, well separated by the cervical interception. The body is bulky, dorso-ventrally slightly flattened and covered by keeled scales. The tail is short. The head is covered by small scales. There are no large regular-shaped scutes and even big supraorbital scutes so common in other viperid genera are absent. The scales are arranged in 23–27 rows around the midbody. The ventral scutes are 123–187 and the subcaudal scutes are 31–66 pairs in two rows. The anal scale is divided.

These snakes live in North Africa, islands of the East Mediterranean, Arabian Peninsula, Lebanon, Syria, Iraq, Turkey, Iran, Afghanistan, Pakistan, northwestern India, Central Asia, southern Kazakhstan and the Caucasus. *Macrovipera mauritanica* and *M. lebetina* are paraphyletic based on mtDNA sequences. *M. mauritanica* was referred to *Daboia* genua and renamed as *Daboia mauritanica* (Garrigues et al. 2005). There are three species in this genus: *Macrovipera lebetina* (Linnaeus, 1758), *M. razii* Oraie, Rastegar-Pouyani, Khosrovani, Moradi, Akbari, Sehhatiasbet, Shafiei, Stümpel et Joger, 2018 from central and southern parts of Iran and *M. schweizeri* (Werner, 1935) (Oraie et al., 2018). One of them (*M. lebetina*) lives in the Caucasus.

Blunt-nosed viper, Levantine Viper – *Macrovipera lebetina* (Linnaeus, 1758)

Coluber lebetinus Linnaeus, 1758, Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Tomus I. Editio decimal, Reformata. Laurenti Salvii, Holmiae: 218(824) pp.

Terra typica. Cyprus. “Oriente” [= Eastern Asia]. Restricted to Cyprus *vide* Mertens and Müller (1928 (1928: 52) (Van Wallach et al., 2014).

Type specimens. Holotype, not designated, lost *vide* Andersson (1899: 29) (Van Wallach et al., 2014).

Distribution. Levantine viper inhabit Algeria, Tunisia, Cyprus, Iraq, Turkey, Afghanistan, Syria, Lebanon, Iran, W. Pakistan, NW India, Jordan. Southern Russia (Dagestan), Armenia, Azerbaijan, Georgia, Turkmenistan, southern Kazakhstan, Tajikistan. Uzbekistan, Kirgizstan (Ananjeva et al., 1998, 2006; Bannikov et al., 1977; Muskhelishvili, 1970; Nikolsky, 1913, 1916; Terentiev, Chernov, 1949; Al-Oran et al., 1998; Baran, 1976; Baran, Atatür, 1998; Başoğlu, Baran, 1980; Böhme, 1987; Chikin, Szczerbak, 1992; David, Ineich, 1999; Demirsoy, 1996; Disi et al., 2001; Golay et al., 1993; Harding, Welch, 1980; Joger, 1984; Khan, 2002; Welch, 1983; Klemmer, 1963; Leviton et al., 1992; McDiarmid et al., 1999; Nilson, André, 1988; Nilson et al., 1988; Schleich et al., 1996; Strauch, 1869, 1873; Szczerbak, 2003; Welch, 1988; Šcerbak, Böhme, 2005; Van Wallach et al., 2014). The status of some subspecies was argued by Billing and Schatti (1986). The species comprises five subspecies: *M. l. lebetina* (S Turkey, Cyprus, N Iraq, NW Syria; Cyprus); *M. l. obtusa* (Dwigubsky, 1832) (Turkey, Iraq, western Iran, Syria, Lebanon, the Caucasus); *M. l. transmediterranea* (Nilson and André, 1988) (Morocco, Algeria, Tunisia, Lybia); *M. l. turanica* (Chernov, 1940) (southern Kazakhstan, Tajikistan, Uzbekistan) and *M. l. cernovi* (Chikin et Szczerbak, 1992) (Turkmenistan, Iran, Uzbekistan, Kyrgyzstan, Afghanistan, India (Kashmir), Pakistan).

The subspecies *M. l. obtusa* lives within the Caucasian Ecoregion in the Transcaucasus and Dagestan.

Distribution in the Caucasus. *M. l. obtusa* lives within the Caucasian Ecoregion in the Transcaucasus and Dagestan (Map 29).

Macrovipera lebetina obtusa (Dwigubsky, 1832) (Fig. 105–106)

Vipera obtusa Dwigubsky, 1832] Dwigubsky, 1832, Opyt estestvennoi istorii vsekh zhyvotnykh Rossiiskoi Imperii. Gady. Moskva, Moskovskii Imperatorskii Universitet, 30: (1–46) +(2pages) + pl. 1–12).

Terra typica. “Geok Tapa (Elizabetpol), Caucasus”, [now Gāncā (=Elizabetpol, = Kirovabad, = Gyanja, Azerbaijan)]. The neotype and *terra typica* are provided as in David et al. (1999). The type is selected from the “specimens [ZISP] collected by A.B. Shelkovich in Geok-tapa of the Elizavetpol Province” as indicated by Nikolsky (1913).

Type specimens. Neotype ZISP 8595, adult male (David et al., 1999). Golay et al. (1993) point the speci-



Map 29. Distribution map of *Macrovipera lebetina*.

men 1047 as the lectotype *Macrovipera lebetina obtusa* (Dwigubsky, 1832) which should be treated as a mistake.

The range in the Caucasus extends from the foothills of Dagestan in the north through all Azerbaijan (except for the Talysh Mts. and highlands of the Lesser Caucasus) to eastern Georgia, Armenia (aside from highlands of the Lesser Caucasus and the Armenian Highland), Nakhichevan and further to north-eastern Turkey and north-western Iran. Four new observations of *M. lebetina* in Artvin Province was made by Mebert et al., 2015. Extreme cases of colour pattern and size in Levantine Viper, *Macrovipera lebetina* (L., 1758) from the west of Euphrates River Basin (Southern Anatolia, Turkey) were observed by Mermer et al. (2012).

Habitats. Blunt-nosed vipers live in a variety of desert and mountain steppe landscapes. Most often they can be recorded in dry foothills, on scrubby slopes (usually with *Rhamnus pallasii*), in rocky canyons with small creeks and streams, pistachio and juniper sparse forests, brinks of riversides, along the irrigation canals and in orchards. In south-eastern Armenia, they can be encountered in riparian plane groves and montane broadleaf forests. In some places, they can permeate into the mid-elevation birch forests, subalpine oakeries of *Quercus macranthera* and meadows. These snakes move up to 2500 m asl. In Armenia, they live at no more than 2000 m on the Mt. Dorakh in Khosrov Forest Reserve and reach 2450 m on the Meghri Ridge.

In Azerbaijan's Gobustan Reserve, near the Mt. Chayniza blunt-nosed vipers live on a vast maritime terrace with widely scattered steep slopes interspersed with ravines and gullies and covered by *Salsola gemascens* – *S. nodulosa* desert. The sympatric reptiles are *Eremias velox*, *Ophisops elegans*, *Testudo graeca*, *Telescopus fallax*, *Xerotyphlops vermicularis*, *Eirenis collaris*, *Platyceps najadum*, *Dolichophis schmidtii*, *Natrix tessellata* and *Hemorrhois ravergieri*. In the same area, vipers occur in sand desert stretched as a narrow strip along the ephemeral creek with tamarisks, *Caragana* sp. and *Salsola ericoides*, as well as on 15-m high loess precipices, along with *Ophisops elegans*, *Cryptopodion caspius*, *Paralaudakia caucasia*, *Natrix tessellata* and *Hemorrhois ravergieri*.

In the Lachin district of Azerbaijan, in a vicinity of the Mishny village, vipers live in two-storey riparian forests growing in the narrow areas of the Aker riverside. The first storey is dominated by *Quercus macranthera*, *Salix alba* and sub-dominated by *Carpinus betulus*. The second storey comprises *Swida australis*, *Corylus* sp. and *Hyppophae rhamnoides* thickets along the river course. The other reptiles living here are *Darevskia raddei*, *D. portschinskii*, *Anguis colchicus* and *Natrix tessellata*.

On interchanging cliffy and gentle (up to 30°) slopes, blunt-nosed vipers are recorded at 600–800 m asl in *Juniperus foetidissima* and *J. polycarpus* sparse forests (see Dahl's whip snake for habitat description), living together with *Lacerta media*, *Darevskia raddei*, *Paralaudakia caucasia*, *Xerotyphlops vermicularis*, *Eirenis modestus*, *E. collaris*, *Platyceps najadum* and *Natrix tessellata*.

In Armenia's Arpa River basin, between Eghegnadzor and Areni, these snakes co-exist with *Pseudopus apodus*, *Ophisops elegans*, *Lacerta media*, *Dolichophis schmidtii*, *Natrix tessellata* and *Hemorrhois ravergieri* in the V-shaped rocky meridian canyon at 800–1000 m asl, in riparian forests growing as a narrow (20–60 m wide) strip along the Arpa. The dominant trees are *Salix australior* and *Ulmus carpinifolia*, while the subdominant trees are *Morus alba*, *Elaeagnus caspica* and *Tamarix meyeri*. Vipers can also be seen in phryganoid vegetation on the southeaster and steep (up to 40°) right bank of the Arpa River where the key plants are *Rhamnus pallasii* and *Ephedra procera*. The other reptiles living here are *Heremites septemtaeniatus*, *Xerotyphlops vermicularis*, *Eirenis punctatolineatus*, *E. collaris* and *Eryx jaculus*. In pistachio sparse forests on the plateau-

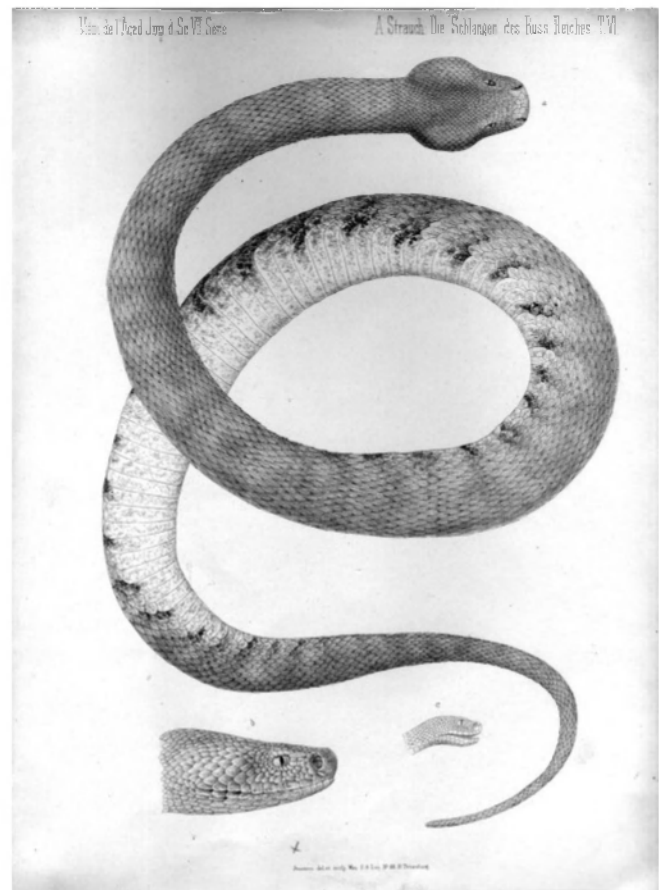


Fig. 105. A drawing of the blunt-nosed viper, *Vipera euphratica* (= *Macrovipera lebetina obtusa*) from the book “Die Schlangen des Russischen Reiches” by A.A. Strauch (1873).

like left bank of the Arpa River, blunt-nosed vipers share their habitats with *Natrix tessellata*, *Dolichophis schmidtii*, *Hemorrhois ravergieri*, *Xerotyphlops vermicularis*, *Eirenis punctatolineatus* and *E. collaris*.

In the Meghri district of southern Armenia, near the Nrnadzor village, vipers are recorded in the meridian canyon with branches covered by juniper sparse forests and numerous rocky outcrops along the ridgetops and on the northern and western slopes. The other reptiles are *Ophisops elegans*, *Eremias strauchi*, *Testudo graeca* and *Hemorrhois nummifer*. The dominant trees are *Juniperus foetidissima*, *Juniperus polycarpus* and some *Quercus infectoria* and *Celtis glabrata*. The second storey is composed of *Berberis orientalis*, *Rhamnus pallasii*, *Lonicera iberica* and *Juniperus oblonga*.

In the same area near Nrnadzor, this species is found in grass oakeries in small canyons at more than 1500 m asl on the northern and north-western slopes. Here, it co-exists with *Hemorrhois ravergieri* and *Montivipera raddei*. The oakeries are seed, well-developed,



Fig. 106. Blunt-nosed viper, *Macrovipera lebetina obtusa* – Meghri, Armenia.

with crown density up to 1.0 and two-storey stand. The first storey includes *Quercus macranthera*, *Fraxinus oxycarpa* and *Celtis glabrata* and the second one comprises *Berberis orientalis*, *Lonicera iberica* and *Padellus mahaleb*. Extra-storey vegetation is represented by large *Vitis silevstris*. The herbal cover is represented by *Melandrium boissieri*, *Dictamnus caucasicus*, *Vinca herbacea*, *Plantago lanceolata* and (near streams) *Ophrys apifera*. Levantine vipers also co-exist with *Dolichophis schmidti* near Yerevan in ravines with smooth hillsides, tuff agglomerates and breakstones along the brink edges, among ruderal vegetation of *Avena* sp., *Pyrethrum tamrutense* and *Pyrethrum* sp. and remnants of primary saltwort-wormwood semi-desert dominated by *Artemisia* sp., *Salsola gemmascens* and some *Allium* sp. and *Euphorbia* sp.

The northwestern border of its distribution range (Dagestan) passes along on the left bank of the Sulak River (mean river flow) from the villages of Inchha and Zubutl, Kazbek district, to the villages of Bavtugai and Nizhny Chiriyurt, Kizilyurt region, then the area stretches along the central foothills to the south-east and goes to neighboring Azerbaijan. The range expansion to the west is limited to the belt of beech-hornbeam forests. The eastern boundary lies at the junction of the lower foothills and the Maritime lowlands. The range of inhabited heights is 18–600 meters asl (Ismailova, 2015).

Conservation status. At the workshop on IUCN assessment of Palearctic reptiles and amphibians in Antalya, Turkey in September 2008, its status was designated as LC. As a rare species of declining population (category 2), the blunt-nosed viper is included in the Red Data Book of the Russian Federation (2001) and Dagestan (2009). It is protected in Dagestansky, Khosrov Forest, Shikahogh, Vashlovani and Turianchay Reserves and in Vashlovani National Park.

Genus Mountain vipers – *Montivipera* Nilson, Tuniyev, Andrén, Orlov, Joger et Herrmann, 1999

Montivipera Nilson, Tuniyev, Andrén, Orlov, Joger and Herrmann, 1999, Taxonomic position of the *Vipera xanthina* Complex. Kaupia, Darmstadt, 8: 101 (99–102).

Type species. *Daboia xanthina* Gray, 1849 [= *Vipera xanthina* (Gray, 1849)]. The valid species name is *Montivipera xanthina* (Gray, 1849).

Medium-sized snakes, usually no more than 1 m long, including a tail, with splendid colour patterns like zigzags, stripes and blotches of black, white and reddish-brown tints. The scales are arranged in 23 (seldom 25–27) rows around the midbody. The head is large, flat, clearly separated by the cervical interception and almost completely covered by small irregular scales,

except for the large well-developed supraorbital scutes. The nasal and prenasal scales are merged and the sub-orbital scutes form a double row. The rounded snout tip is only slightly protruding to the anterior. Two apical scales contact with the nasals. The ventral scutes are 166–193, subcaudal scutes are 25–36 pairs in females and 32–38 pairs in males, arranged in two rows. The anal scute is whole. Males are larger, brighter and more distinctly coloured than females. Ovoviviparous. These snakes live exclusively in mountains.

Nine species of *Montivipera* are distributed in the Transcaucasus, Turkey, Greece, Iran, Syria, Jordan, Israel and Lebanon. These are *M. albicornuta* (Nilson et Andrén, 1985b) (north-western Iran); *M. albizona* (Nilson, Andrén et Flärdh, 1990) (central Turkey); *M. bornmuelleri* (Werner, 1898) (Lebanon, Israel, Syria), *M. bulgardaghica* (Nilson et Andrén, 1985a) (southern Anatolia, Turkey); *M. kuhrangica* Rajabizadeh, Nilson et Kami, 2011 (Central Zagros mountains, Iran); *M. latifii* (Mertens, Darevsky et Klemmer, 1967) (Lar Valley, Alborz Ridge, Iran); *M. wagneri* (Nilson et

Andrén, 1984a) (eastern Turkey, possibly north-western Iran); *M. xanthina* (Gray, 1849) (north-eastern Greece, Aegian islands, western Turkey including its European part); *M. raddei* (Boettger, 1890) (southern Transcaucasus and adjacent parts of Turkey and Iran).

Taxonomic issues in this genus had been vigorously discussed (Nilson, Andrén, 1984a, 1985a, b, 1986a, b, 1992; Rajabizadeh, 2011a; Van Wallach et al., 2014; Stümpel et al., 2016; Behrooz et al., 2018). In general, there are 3 species of *Montivipera* occurring in the Caucasus (eastern Transcaucasus and adjacent areas of Turkey and Iran): *M. albicornuta*, *M. raddei* and *M. wagneri*.

White-horned mountain viper – *Montivipera albicornuta* (Nilson et Andrén, 1985)
(Fig. 107)

Vipera albicornuta Nilson and Andrén, 1985, Systematics of the *Vipera xanthina* complex (Reptilia: Viperidae). I. A new Iranian viper in the *raddei* species-group. Amphibia-Reptilia 6: 207 (207–214).



Fig. 107. White-horned mountain viper, *Montivipera albicornuta* – Zanjan, Iran. Photo by Khosro Rajabizadeh.



Map 30. Distribution map of *Montivipera albicornuta*.

Terra typica. In the original description – Abhar in the Zanjan valley, between Tabriz and Teheran, NW Iran” [= Abhar, Zanjan Prov., N Iran, 36°08’N, 49°13’E, elevation 1545 m]. Van Wallach et al., 2014).

Type specimens. Holotype RSI 3098.

Distribution. Southern slope of the Alborz Ridge and northern part of the Zagros Ridge in Iran.

Distribution in the Caucasus. A small part of the range extends into the Caucasus Ecoregion in north-western Iran (Map 30).

Habitats. This snake is known to live in mountain, very arid sandy and rocky habitats with sparse herbal and depressed scrubby vegetation (Nilson, Andrén, 1986a,b).

Conservation status. Information about population size is lacking, but many individuals have been kept in Iran's serpentaria (Nilson, Andrén, 1986a,b). At the workshop on IUCN assessment of Palearctic reptiles and amphibians in Antalya, Turkey in September 2008, its status was designated as VU A4d.

Armenian or Radde's viper – *Montivipera raddei* (Boettger, 1890) (Figs 108–111)

Vipera raddei Boettger, 1890, Eine neue Viper aus Armenien, Zool. Anz. 13: 62 (62–64)

Terra typica. In the original description – “Kasikoparan in Armenia” (now in Turkey); Kazikkiran (=Kazikkoparan), Tuzluca, Kars Province, N.E. Anatolia;

40°02'N, 43°26'E (Nilson et al., 1999a; Ananjeva et al., 2006; Van Wallach et al., 2014).

Type specimens. Syntypes (2), ZMT (Christoph), lost *vide* Nilson, Andrén (1986a: 5) (Van Wallach et al., 2014). “Boettger described this species from Kazikoparan in Armenia from an individual he received from G.I. Radde” (Nikolsky, 1913, 1916). Nilson and Andrén (1986a) wrote about two syntypes sent by Radde from Zoological Museum of Georgia, Tbilisi (ZMT) to Boettger and a topotype he had given to British Museum of Natural History (BMNH 6.7.96) (McDiarmid et al., 1999).

Distribution. The Armenian viper comprises two subspecies: *Montivipera raddei raddei* (Boettger, 1890) occurring in the Caucasus Ecoregion and

Montivipera raddei kurdistanica (Nilson et Andrén, 1986) living in north-western Iran from the Lake Urmia westwards to the border with Turkey. The occurrence of this subspecies is highly likely also in eastern Turkey and Iraq (Nilson et al., 1988). A local population comprising very dark individuals (males are nearly black with lateritious blotches) is found in the eastern part of southern Armenia's Meghri Ridge, at 2300–2450 m asl. It is still unclear if this variation is taxonomically relevant.

Distribution in the Caucasus. A chain of isolated habitat patches in southern Armenia and Nakhichevan (Azerbaijan) from the Mt. Aragats in the west to the Meghri Ridge inclusive in the east, as well as in adjacent areas of Turkey and Iran (Map 31).



Map 31. Distribution map of *Montivipera raddei*.



Fig. 108. A drawing of the Armenian viper *Vipera xanthina* (= *Montivipera raddei*) from the book “Synopsis der Viperiden, nebst Bemerkungen über die geographische Verbreitung dieser Giftschlangen Familie” by A.A. Strauch (1869).

Recently *Montivipera wagneri*-*M. raddei* transition zone was firstly revealed in the Arax River Valley. *M. wagneri* occurs predominantly west of Kağizman and *M. raddei* east of it with about 40 km distance between their closest officially known populations (Mebert et al., 2015, 2016).

Habitats. These snakes live at 1000–2700 m asl in mountain xerophytic oak and juniper sparse forests, on stony slopes with scanty vegetation (mainly *Spiraea crenata*) and in mountain steppes with screes. The distribution of the Radde's viper over the southern slopes of the Lesser Caucasus is mosaic in strong concordance with the patchiness of suitable habitats.

In the Meghri district of southern Armenia, vipers are recorded in the Meghri riverhead, on the southern macroslope of the Meghri Ridge in phryganoid oakeries of crown density 0.1–0.3 dominated by *Quercus macranthera*. The other reptiles living here are *Darevskia raddei*, *Lacerta media*, *L. strigata*, *Ablepharus bivittatus*, *Natrix tessellata*, *Paralaudakia caucasia*, *Platyceps najadum* and *Dolichophis schmidtii*. This species is also found, along with *Hemorrhoids ravergeri* and *Macrovipera lebetina*, near the Nrnadzor village in the Meghri district in grass oakeries growing in small lateral canyons at over 1500 m asl on the northern and



Fig. 109. Kurdistan Radde's viper, *Montivipera raddei kurdistanica* – south-eastern Turkey.



Fig. 110. Armenian Radde's viper, *Montivipera raddei raddei*, male – Shikahogh Reserve, Armenia.



Fig. 111. Armenian Radde's viper, *Montivipera raddei raddei*, female – Shikahogh Reserve, Armenia.

north-western slopes. These oakeries are seed, well developed, with crown density up to 1.0 and two-storey stand. The first storey includes *Quercus macranthera*, *Fraxinus oxycarpa* and *Celtis glabrata* and the second one comprises *Berberis orientalis*, *Lonicera iberica* and *Padellus mahaleb*. Extra-storey vegetation is represented by large *Vitis silvestris*. The herbal cover is represented by *Melandrium boissieri*, *Dictamnus caucasicus*, *Vinca herbacea*, *Plantago lanceolata* and (near streams) *Ophrys apifera*.

In Abovian suburbs, Armenian vipers live along with lizards *Lacerta media* on the gentle eastern slopes with rocky outcrops, debris and small stones in grass meadow-steppes dominated by *Rhamnus pallasii*, *Amygdalus fenzliana* and *Rosa* sp. The herbal cover is dominated by *Achillea santolina*, *Geranium* sp., *Thalictrum isopyroides* and *Trifolium alpinum*. The forbs include *Urtica dioica*, *Orobanchaceae hirsutus*, *Taraxacum montanum*, *Bryonia alba*, *Euphorbia* sp., *Heracleum* sp., *Galium* sp., *Muscari* sp., *Adonis aestivalis* and *Poa bulbosa*.

Conservation status. Population of *Montivipera r. raddei* is declining because of land use and infrastructure development on slopes, deforestation and overgrazing. It is included in the Red book of the Republic of Azerbaijan (2013) and Red book of the Republic of Armenia (2010: VU B1a+2b(ii, iii)) as a narrowly distributed endemic species. At the workshop on

IUCN assessment of Palearctic reptiles and amphibians in Antalya, Turkey in September 2008, its status was designated as NT. The Armenian viper is protected in Khosrov Forest, Arevik National Park and Shikahogh Reserve in Armenia. Populations of *V. r. kurdistanica* in northwestern Iran suffer mostly from sheep overgrazing in their habitats.

Wagner's viper – *Montivipera wagneri* (Nilson et Andrén, 1984) (Fig. 112)

Vipera wagneri Nilson and Andrén, 1984, Systematics of the *Vipera xanthina* complex (Reptilia: Viperidae). I. An overlooked viper within the *xanthina* species-group in Iran. Bonn. Zool. Beitr., 35: 178(175–184) [178 – Fig.1; 179 – Fig.2; 180] (Fig. 113).

Terra typica. In the original description – “Urmie die Armenisch-Persische Grenze”; Lake Urmia on the border between Armenia and Persia, now – the provinces West Azerbaijan and East Azerbaijan in north-western Iran.

Type specimens. Holotype ZFMK 23495.

Distribution. North-eastern Turkey, north-western Iran (Map 32). As it was written above the contact zone among parapatric species *Montivipera (wagneri, raddei)*, was revealed in northeastern Anatolia (Mebert et al., 2015, 2016).



Fig. 112. Wagner's viper, *Montivipera wagneri* – eastern Turkey.



Map 32. Distribution map of *Montivipera wagneri*.

Distribution in the Caucasus. Reliable records of this species are known from the canyons of the upper Arax River in eastern Turkey, Karakurt and Kagizman (Joger et al., 1988; Mebert et al., 2015). Possibly, Wagner's vipers also exist in the Arax riverside near the junction with the Akhurian River and in the Akhurian River basin in Armenia. An individual was found in the Euphrates River basin (upper Murat River) (B.Tuniyev et al., 2014). This is a new record on the boundary of the Caucasus Ecoregion.

Habitats. These vipers live in rather mesophilic areas of canyons with streams, lush herbal cover and numerous rocky outcrops at 1600–2000 m asl.

Conservation status. As a rare endemic in depressed condition, this species demands for urgent conservation measures. At the workshop on IUCN assess-

ment of Palearctic reptiles and amphibians in Antalya, Turkey in September 2008, its status was designated as CR A2a+4c. It is essential to search for new habitats along the Arax tributaries in Turkey and Armenia.

Genus Shield-headed vipers – *Pelias* Merrem, 1820

Pelias Merrem, 1820, Versuch eines Systems der Amphibien. Tentamen Systematis Amphibiorum. J.C. Krieger, Marburg, 145 (xv +191 pp., 1 pl.).

Type species. *Coluber berus* Linnaeus, 1758 [= *Vipera berus* (Linnaeus, 1758)] – designated by Fitzinger (1843). The valid name is *Pelias berus* (Linnaeus, 1758).

Small and medium snakes, the largest species do not exceed 900 mm in length, including a tail. The head is covered on top by small scales and large regular-shaped scutes. The frontal, paired temporal and paired supraorbital scutes are the largest. The nasal scute is separated from the intermaxillary by nasomaxillary scutes. The body scales are strongly costate. The ventral scutes are 128–157, subcaudal 21–46 pairs in two rows and the anal scute is whole. All species are ovoviviparous.

This genus comprises about 20 species living in Eurasia (Van Wallach et al., 2014; Uetz et al., 2017): Europe, Mediterranean region and boreal Asia. The number of taxa in *Pelias* is always a matter of debates. There are 3 clearly defined species groups: 1) *Pelias berus* group [*Pelias berus* (Linnaeus, 1758); *P. nikolskii* Vedmederya, Grubant et Rudayeva, 1986; *P. seoanei* (Lataste, 1879); *P. sachalinensis* (Čarevsky, 1917); *P. barani* (Böhme et Joger, 1984), *P. walseri* Ghilmi, Menegon, Marsden, Laddaga et Ursenbacher, 2016; 2) *Pelias ursinii* group [(*P. altaica* Tuniyev, Nilson et Andren, 2010; *P. anatolica* (Eiselt et Baran, 1970); *P. graeca* (Nilson et Andren, 1988), *P. ursinii* (Bonaparte, 1835); *P. renardi* (Christoph, 1861); *P. eriwanensis* (Reuss, 1933); *P. lotievi* (Nilson, Tuniyev, Orlov, Höggren et Andrén, 1995); *P. ebneri* (Knoepffler et Sochurek, 1955, *P. shemakhensis* Tuniyev, Orlov, Tuniyev et Kidov, 2013] and 3) *Pelias kaznakovi* group [*P. ka-*

znakovi (Nikolsky, 1909); *P. dinniki* (Nikolsky, 1913); *P. darevskii* (Vedmederja, Orlov et Tuniyev, 1986); *P. olguni* Tuniyev, Avci Tuniyev, Agasyan et Agasyan 2012, *P. pontica* (Billing, Nilson et Sattler, 1990); *P. orlovi* (Tuniyev et Ostrovskikh, 2001); *P. magnifica* (Tuniyev et Ostrovskikh, 2001) and *Pelias sakoi* Tuniyev, Avci, Ilgaz, Olgun, Petrova, Bodrov, Geniez et Teynié, 2018]. Relationships within this group of species are under active study (Nilson et al., 1995; Zinenko et al., 2015, 2016). The relict species *P. anatolica*, *P. darevskii*, *P. sakoi* and *P. barani* take a more distant position in their groups. Possibly, they can be considered as outgroup taxa within the genus *Pelias*. Analysis of mitochondrial DNA and more detailed morphological studies of complex of characters have confirmed this point of view (Kalyabina-Hauf et al., 2004; Murphy et al., 2007b; Geniez, Teynié, 2005; Zinenko et al., 2015, 2016). The species *P. ebneri* is morphologically close to *P. eriwanensis* and the gaps in distribution areas can be filled by new records in the Karadag Ridge in Iran.

There are intensive discussions around the taxonomic status of *P. kaznakovi*, *P. dinniki* and *P. darevskii* (Vedmederja et al., 1986) and their relationships with other shield-headed vipers (Orlov, Tuniyev, 1986, 1990) (Fig. 114); Höggren et al., 1993; Joger et al., 1992; Kalyabina-Hauf et al., 2004; Nilson et al., 1999; Tuniyev, Ostrovskikh, 2001; Orlov, Tuniyev, 2005a, b; Tuniyev et al., 2010, 2013, 2018). In 1990, a new species *Pelias pontica*, possibly belonging to the *kaznakovi* group was discovered in the lower Çoruh River basin in Turkey (Billing et al., 1990). This taxon combines the characters of *kaznakovi* group and the species *P. barani*. Joger et al. (1997) stated that *P. barani* is referred to *berus* group and phylogenetically close to *Vipera (berus) bosniensis* (= *Pelias berus bosniensis*). New findings of *P. barani* from the highlands of the Pontic Ridge allowed Baran et al. (2001) considering *P. pontica* as a junior synonym of *P. barani*. The series of individuals from the Pontic Ridge was partly similar to *P. barani* in coloration and pholidosis, and partly to *P. pontica*.

Sequencing of the fragments of mtDNA in research of phylogenetic relationships among the shield-headed vipers led Kalyabina-Hauf et al. (2004) conclude that *P. pontica* belongs to *P. barani*. Possibly, the situation with these two species is similar to that in the *kaznakovi* group species in the West Caucasus where vipers from subtropical plains and foothills are vicariants of *P. dinniki* in mountaintops. More studies are needed to elucidate this issue.

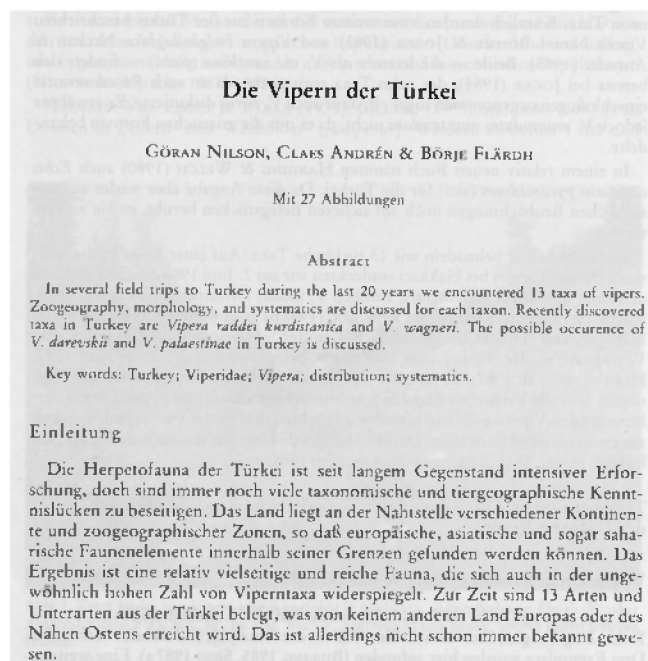


Fig. 113. Cover page of the paper “Die Vipern der Türkei” by G. Nilson, C. Andrén and B. Flärdh (1988).

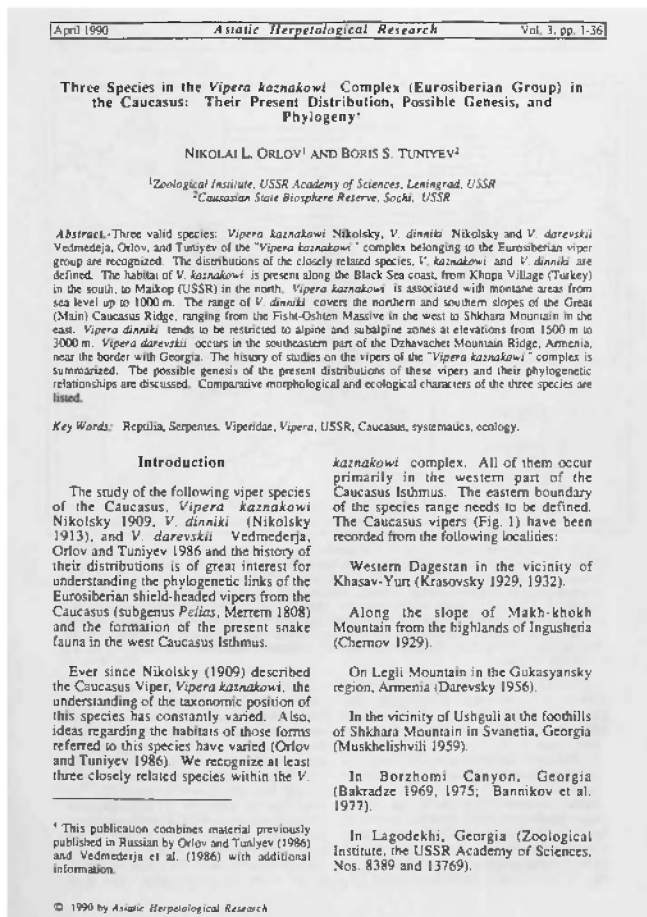


Fig. 114. Cover page of the paper "Three Species in the *Vipera kaznakovi* Complex (Eurosiberian Group) in the Caucasus: Their Present Distribution, Possible Genesis, and Phylogeny" by N.L. Orlov and B.S. Tuniyev (1990).

Important conclusions for systematics and phylogeny of the Viperinae in the Caucasus were made by Nilson et al. (1999a, b) and Tuniyev (2002) who designated the supraspecies, subgenera and genera, particularly among the shield-headed vipers.

Discussions about the relationships and taxonomic status of the *kaznakovi* group continued after another two new species were described: *Pelias orlovi* (Tuniyev, Ostrovskikh, 2001) and *P. magnifica* (Tuniyev, Ostrovskikh, 2001). In a paper on the phylogeny of the *Vipera berus* (= *Pelias berus*) group, Kalyabina-Hauf et al. (2004) provided a phylogenetic tree demonstrating the position of the *berus*, *ursini* and *kaznakovi* groups and the outgroup species *Vipera anatolica* (= *Pelias anatolica*) and *Vipera darevskii* (= *Pelias darevskii*).

Recent studies of phylogeny among the Caucasian vipers using the mitochondrial genome have produced controversial results (Kalyabina-Hauf et al., 2004; Murphy et al., 2007b; Zinenko et al., 2015). The idea of

hybrid origin was first expressed by Orlov and Tuniyev (1986) who proposed (Fig. 2, p. 113) the speciation, chorological and phylogenetic patterns within the *Vipera kaznakovi* group in the Caucasus. The *P. ursinii*, *P. orlovi*, *P. renardi* and *P. dinniki* groups turned out to be polyphyletic, implying the presence of cryptic species or hybrid origin of some Caucasian viper species. Therefore, these investigations are continued these days with the use of new markers and new study materials. The new study using genomic scale DNA markers (Zinenko et al., 2016) support the conclusion that both *V. orlovi* and *V. magnifica* had formed through a hybridization event between *V. kaznakovi* and *V. renardi*. A further study that include analyses of ecological segregation of *V. orlovi* from parental taxa and search for evolutionary consequences of hybridisation would clarify if *V. orlovi* is a distinct hybrid species (Zinenko et al., 2016).

This genus comprises many rare and narrowly distributed species. A number of them are listed on the IUCN Red List of Threatened Species and included in the Red Data Books of the USSR, post-Soviet countries and Russian federal regions. All *Pelias* species are protected in West and Central Europe by national legislations and the Bern Convention on the Conservation of European Wildlife and Natural Habitats.

Turkish viper – *Pelias barani* (Böhme et Joger, 1984) (Fig. 115)

Vipera bārani Böhme and Joger, 1984 (1983), Eine neue Art des *Vipera berus*-Komplexes aus der Türkei. Amphibia-Reptilia, 4: 267(265–271) [267 – figs. 1–2].

Terra typica. In the original description – "ca. 60 km N Adapazari, Türkei".

Type specimens. Holotype ZFMK 35444.

Distribution. "ca. 60 km N Adapazari, Turkei, 400 m N.N." [= ca. 60 km N Adapazari (40°50'N, 30°25'E), Sakarya Prov., NW Turkey (Van Wallach et al., 2014).

Distribution in the Caucasus. In the Caucasus Ecoregion, these vipers occur in the eastern part of the Pontic Ridge where it is a vicariant of *P. pontica*, unless the conspecificity of both these taxa discussed above is assumed (Joger et al., 1997; Baran et al., 2001; Kalyabina-Hauf et al., 2004) (Map 33). A record in the Ordu Province, northern Turkey looks like an intermediate link in the chain of earlier records all of which came only from the western and eastern Turkish coasts of the Black Sea (Avci et al., 2004). Seven new locations of *V. barani*



Map 33. Distribution map of *Pelias barani*.

from northwestern Turkey, including three new province records and the current southernmost locality, and one from the northeast confirms the much wider range of this viper than was known earlier (Göçmen et al., 2015). Distribution models of *Pelias barani* under current climatic conditions showed the better adaptation of this Pontic endemic species to the northwest and northeast part of Turkey (Gül, 2016). Kumultas et al. (2012) informed about new records from Kozlu, Zonguldak; Gül et al. (2016) wrote about new record from Tektaş village of Pazar, Rize, Turkey. Potential contact zone of *Vipera barani* and *V. kaznakovi* was recorded between Ardeşen and Findikli, Rize Province (Mebert et al., 2015).

Habitats. Glades with screes and stony areas along the treeline in the subalpine zone of the Pontic Ridge.

Vegetation is represented by subalpine tall grasses with typical Colchic species of plants. This species inhabits open patches of deciduous forest along the subtropical Black Sea coast (Mebert et al., 2015).

Conservation status. A poorly studied species. At the workshop on IUCN assessment of Palearctic reptiles and amphibians in Antalya, Turkey in September 2008, its status was designated as NT. Preservation of populations on the Pontic Ridge entirely depends on the conditions of landscapes and habitats of *P. barani*. Overgrazing and deforestation are the main threats to this species. There are a number of protected areas around the Kaçkar Mts. and in adjacent areas of the Pontic Ridge, which cover a part of the viper's range.



Fig. 115. Turkish viper, *Pelias barani* – Ordu, Pontic Mountains, northern Anatolia, Turkey. Photo by Göran Nilson.

Darevsky's viper – *Pelias darevskii*
(Vedmederja, Orlov et Tuniyev, 1986)
 (Figs. 116–122)

Vipera darevskii Vedmederja, Orlov et Tuniyev, 1986, Sistematika gadyuk kompleksa *Vipera kaznakowi*. Trudy Zool. inst. AN SSSR, Leningrad, 157: 58 (55–61).

Terra typica. In the original description - Mt. Legli, Mokrye gory (Wet mountains), Ghukasyan district, Armenia. Additional study showed that I. S. Darevskiy unintentionally transformed this name Mt. "Leyli" to Mt. "Legli." Thus, terra typica of *Pelias darevskii* (on an actual place of type series collecting, including holotype) it is necessary to recognize as the Mt. Sevsar, Dzhavakhetskiy (Kechutskiy) Ridge, Ashotsk (former Gukasyan) district, northwestern Armenia (Tuniev et al., 2014a).

Holotype: ZIN (=ZISP) 19934, an adult female from Legli Mountain, the Mokrye (Wet) Mountains, Gukasynsky region, Armenia. The specimen was collected in June, 1980 by I. S. Darevsky. The specimen is

preserved at the Zoological Institute, the USSR Academy of Sciences, Leningrad. Paratypes: ZIN (=ZISP) 16546 a and b. The specimens were collected in May 28, 1954; ZIN (=ZISP) 17545, the specimen was collected August 6, 1955; ZIN (=ZISP) 19935, the specimen was collected June, 1980 by I. S. Darevsky.

Distribution. Endemic of the Caucasus distributed entirely within the Ecoregion (Map 34).

Distribution in the Caucasus. Darevsky's vipers occur in the southeastern part of the Javakheti Ridge in Armenia and Turkey. I.S. Darevsky (1956) who considered it as *Vipera kaznakowi dinniki* first discovered the species. The southern boundary of the range is stretched along the south of Javakheti Ridge up to the Karagach Pass (2272 m asl) and the northern boundary extends over the subalpine zone of the south-western slopes of the Javakheti Ridge towards the border with Georgia. Recently, new record sites were found near the Saragugh village 12 km away from the earlier known sites. The entire range represents a chain of isolated patches (Aghasyan, Aghasyan, 2008). This species occurs in the territory of South Georgia in Mt. Madatapa at

Dzhavakhetskiy Ridge and Mt. Gumbati in the Erusheti Mountains and Mt. Airilanbashi in Akhaltsihe Highland near Village Tskaltiba (S.Tuniyev et al., 2014). The Darevsky's viper was found in northeastern Turkey's Artvin Province at 1970–2070 m asl 2 km to the east of the Zekeriya village and in 2005 near the Posof village of the same province, in subalpine meadows (Geniez, Teynié, 2005; Avci et al., 2010). It was recorded in Turkey, Artvin Province, the Yalnızçam Dağları Ridge, vicinity of Zekeriya Village and Ardahan Province, the Yalnızçam Dağları Ridge, vicinity of Bağdaşan Village (Tuniyev et al., 2018a).

Habitats. In Armenia, Darevsky's vipers are known only from subalpine and alpine meadows on the hillsides of the Legly and neighbouring peaks of the Javakheti Ridge. This snake is a highland species living in screes somewhere emerging from under the snowfields. Even in comparison with other mountain shield-headed vipers,

Pelias darevskii has an extremely short period of summer activity. At the upper limits of altitudinal distribution in the scree-snowfield contact zone, snakes emerge on the surface only by mid-June. Probably, females have a prolonged reproductive cycle of about two years. Habitats represent the western and south-western slopes of a dormant volcano at 1900–2800 m asl. The terrain is gentle in the foothills and steep (up to 15°) up the slopes. The landscapes comprise subalpine and alpine meadows interspersed with vast screes and bedrock outcrops. The soils are mountain-meadow, close to andesoles (mountain black earth). Vegetation consists of herbal subalpine meadows across the stony hillsides and screes with limited areas of unclosed scrublands. The scrubs are scattered *Daphne glomerata*, *Rubus buschii* and *Rosa* sp. The dominant herbs are *Cephalaria gigantea*, *Ranunculus caucasicus*, *Trifolium canescens*, *Stachys macrantha*, *Astrantia major*, *Anemonastrum fasciculatum*, *Ajuga ori-*



Fig. 116. Darevsky's viper, *Pelias d. darevskii* – Saragyukh, Ashotsk, Armenia. Photo by Khosro Rajabizadeh.



Fig. 117. Darevsky's viper, *Pelias d. darevskii* – male, Saragyukh, Ashotsk, Armenia.



Fig. 118. Darevsky's viper, *Pelias d. darevskii* – female, Saragyukh, Ashotsk, Armenia.



Fig. 119. *Pelias d. uzumorum* – vicinity of Zekeriya, Artvin, Turkey.



Fig. 120. *Pelias d. uzumorum* – vicinity of Zekeriya, Artvin, Turkey.



Fig. 121. *Pelias d. kumlutasi*, northern volcanic part of the Yalnızçam Dağları Ridge, Turkey.

entalis, *Plantago atrata*, *Primula macrocalyx*, *Ornithogalum balansae* and *Alchemilla* sp. The plants *Pedicularis schelkownikowi*, *Gentiana pontica*, *Huynhia pulchra*, *Fritillaria caucasica* and *Gallium* sp. are rare. Some clusters of *Myosotis* sp., *Muscari neglectum*, *Pulsatilla albana* and *Pulsatilla violaceae* grow on screes. Abundant flowering of *Scilla armena*, *Pushkinia scilloides*, *Corydalis emanuelii*, *Ficaria ficarioides*, with some *Gagea* sp. and *Colchicum szovitsii* can be seen on snowfields

Conservation status. An extremely rare, relict and narrowly distributed species. At the workshop on IUCN assessment of Palearctic reptiles and amphibians in Antalya, Turkey in September 2008, it was designated as CR B1ab(ii,iii)+2ab(ii,iii). It is included in Red Book of Animals of the Republic of Armenia (2010) as CR B1ab(ii, iii)+2ab (ii, iii).

Three subspecies are recognized:

***Pelias darevskii darevskii* (Vedmederja, Orlov et Tuniyev, 1986)** (Figs. 116–118)

We would like to elucidate name of the type locality of *Pelias darevskii*. In the original description (Vedmed-

erja et al., 1986), the type locality was indicated as Mt. Legli, Wet Mountains, Gukasyan District, Armenia, in accordance to the label of holotype. However, the detailed study of cartographic material, including old editions, showed that a mountain with the similar name “Legli” in the examined district is absent. However, there is a Mt. Leyli (Azeri name), also called Kechut (Armenian name), located directly on a border with Georgia, altitude 3156 m a.s.l. Southward the highest peak of Dzhavakhet-skiy Ridge — the Mt. Achkasar (= Achkala—3196 m) is located, which was also temporary identified as mountain “Legli.” Arising misunderstanding under labeling by I. S. Darevsky appears to the all subsequent publications. It is explained by the fact that one of Mt. Sevsar’s branches had the local name Leyli among Azeri people living at that time there. I. S. Darevsky unintentionally transformed this name Mt. “Leyli” to Mt. “Legli.” Thus, terra typica of *Pelias darevskii* (on an actual place of type series collecting, including Holotype) it is necessary to recognize as the Mt. Sevsar, Dzhavakheti (Kechutskiy) Ridge, Ashotsk (former Gukasyan) district, northwestern Armenia (S.Tuniyev et al., 2014).



Fig. 122. *Pelias d. kumlutasi*, northern volcanic part of the Yalnızcım Dađlari Ridge, Turkey.

Distribution. North-West Armenia and adjacent regions of southmost Georgia within Dzhavakheti Ridge and Akhaltsihe Highland.

Habitats. Flat stone talus deposits characteristic for the subspecies.

Conservation status. Critically Endangered B1ab(ii,iii)+2ab(ii,iii)

Pelias darevskii uzumorum Tunıyev, Avcı, İlğaz, Olgun Petrova, Bodrov, Geniez et Teynié, 2018 (Figs. 119–120)

Type territory. Turkey, Artvin Province, the Yalnızcım Dađlari Ridge, vicinity of Zekeriya Village, (2000 m above sea level).

Type specimens. Holotype: SNP No 904 (adult female); paratypes: SNP 908 (adult female, three new-

born females born in the terrarium); SNP No 909 (two adult females); ZDEU 99/2011 (adult female and newborn male born in terrarium); BEV.8369 and BEV.8855 (juvenile male and adult female respectively); MNHN-RA-2002.410 (adult male).

Distribution. This taxon distribution covers the southern part of the Yalnızcım Dađlari Ridge in its most warm calcareous part.

Habitats. Biotopes of *Pelias darevskii uzumorum* in vicinity of Zekeriya Village are represented by subalpine hemixerophyt meadows close on edaphically signs to meadow-like steppes with juniper lying shrubs (*Juniperus oblonga* Bieb.) on limestones in altitudinal range 1990 – 2100 m a.s.l. Along all the habitats the stony areas, small talus, acanguares and rocky outputs of limestone are located (Geniez and Teynié 2005; Tunıyev et al., 2018).



Map 34. Distribution map of *Pelias darevskii*.

Conservation status. As rare taxa, limited in a natural habitat and a number *P. d. uzumorum* needs to be included in the Red List of IUCN with the category of status of VU C1.

Pelias darevskii kumlutasi Tuniyev, Avcı, Ilgaz, Olgun Petrova, Bodrov, Geniez, Teynić, 2018 (Figs. 121–122)

Vipera erivanensis (Reuss, 1933) [part.]: Baran et al. 2005:2–3.

Type territory. Turkey, Ardahan Province, the Yalnızçam Dağları Ridge, vicinity of Bağdaşan Village.

Type specimens. Holotype: SNP No 910 (adult female); paratypes: ZDEU 145/2001 (three adult females, two juvenile females, two juvenile males).

Distribution. Distribution is restricted to arid northern part of the Yalnızçam Dağları Ridge within the limits of upper basin of Kura River from Bağdaşan Village to Ardahan pass.

Habitats. The vipers' biotopes are stony mountain steppes with *Ferula ovina*, *Papaver serigerum*, etc. under the conditions of sharply continental climate.

Conservation status. As rare taxa, limited in a natural habitat and a number *P. d. kumlutasi* needs to be included in the Red List of IUCN with the category of status of EN A3bc; B2ab(i,ii).

Dinnik's viper – *Pelias dinniki* (Nikolsky, 1913)
(Figs. 123–126)

Vipera berus dinniki Nikolsky, 1913, Presmykayuschiesia i zemnovodnye Kavkaza. Herpetologia Caucasica. Izdanie Kavkazskogo muzeya, Tiflis: 176(1–272, +3 Plates).

Terra typica. “Upper Malaya Laba at elevation 8000' (feet); Svanetia at elevation 7000' (feet)” (Nikolsky, 1913). “Upper stream of the Laba River, 8000 feet above sea level, Caucasus” (Orlov, Tuniyev, 1986, 1990).

Type specimens. Lectotype – Museum of Natural History of Kharkov State University MNKNU (=ZDKU) 26044, adult female (Coll. N.J. Dinnick, 1908) (designated by Vedmederja et al., 1986).

Distribution. The global area covers the middle and high mountain regions of both slopes of the Greater Caucasus Ridge in Russia, Abkhazia, South Ossetiya, Georgia, and probably Azerbaijan. The range extends over the northern and southern slopes of the Greater Caucasus from the Fisht-Oshten Massif in the west to eastern Georgia's Lagodekhi Reserve and Zakataly

Reserve in northwestern Azerbaijan in the east. On the northern slope of the Greater Caucasus, the range is continuously stretched from the Mt. Fisht eastwards to the Bolshaya Laba River. Further, it is split into the isolated patches in Karachaevo-Cherkessia, Kabardino-Balkaria, North Ossetia-Alania, Ingushetia, Chechen Republik, Dagestan, northern and eastern Georgia, and probably north-western Azerbaijan. Muskhelishvili's (1959) records of *Vipera kaznakowi* and *Vipera ursini renardi* in Svanetia, near Ushguli, should be attributed to *Pelias dinniki*. There are also some distant, fully isolated populations on the Lagonaksky Ridge and along the Chernomorskiy Ridge.

Distribution in the Caucasus. It fully coincides with global range of this Caucasian endemic (Map 35). The genesis of the range has clear periglacial features throughout the Greater Caucasus, with the maximum of color polymorphism in the west (Krasnodar Territory, Republic of Adygheya and Karachaevo-Cherkessian Republic) and the relative uniformity of coloration and skin patterns in the east (from Karachevo-Cherkessia to Dagestan) (Tuniyev et al., 2009). In South Ossetia, the species is known from the high valleys of the basins of



Fig. 123. Dinnik's viper, *Pelias dinniki*, orange-black morph – Mt. Fisht, Krasnodar Territory, Russian Federation.



Fig. 124. Dinnik's viper, *Pelias dinniki*, yellow-black morph – valley of the upper reaches of the Mzymta River, Krasnodar Territory, Russian Federation.

the Bolshaya and Malaya Liakhvi (= Styr and Chysyl Leuakhi) (Red Data Book of South Ossetiya, 2017). This snake here is locally numerous (in some gorges of the basin of the upper reaches of the Bolshaya Liakhvi River, up to 5 individuals per 1 km of the route can be encountered on glacial moraines). However there is a limited number of habitats, which preservation depends even on the short-lived anthropic effects (Tuniyev et al., 2017). In Abkhazia it is reliably registered on the slopes of the eastern exposure Kutikhug (Kutakheku) mountain ridge, the right bank of Audhara River. In 2017 an isolated population was found on Mount Pshahushkha (Pshegishkhva). The information of Mammadov, Bayramov (2015) about records in the foothill and mountain areas (1000–2500 m above sea level) of the Ordubad and Shahbuz regions of the autonomous republic of Nakhchivan, Azerbaijan can not be considered as reliable. New records from Mtskheta – Mtianeti Region in Georgia: Sno riverhead, Kazbegi Municipality, gorge of Kistinka (= Khde, Brolistskali), Kazbegi Municipality the vicinity of Gudani village (= Gadani), Dusheti Municipality are localted in the territory of Kazbegi National Park and complement the fragmentary data on species range in Georgia (Bekoshvili, Doronin, 2015).

Habitats. The Dinnik's viper is a generally sub-alpine species, but occurs from mid-elevations to the upper alpine zone. These snakes live in subalpine and alpine meadows, fescue-forbs communities, sub-alpine tall grasses, overgrown screes and moraines and abandoned shepherds' dwellings (atsanguar's). Rarely enough, they occur also along the treeline, in subalpine birch and pine forests, maple parks, crooked highland forests, rhododendron thickets and post-forest glades at 1500–3100 m asl. However, snakes can also move down to 1200 m asl, especially through the lava-covered areas. In the Itum-Kalinskaya Depression, Chechen Republik, vipers are quite rare in oreoxerophytic secondary, somewhere primary, Mediterranean vegetation (sibljak) dominated by *Paliurus spina-christi* and *Rhamnus pallasii*, as well as in petrophilic vegetation. In Abkhazia the population density in Kutikhug reaches 5–6 individuals for 1 km of the route. Degradation of habitats is observed due to intensive grazing in subalpine pastures (Tuniyev, 2005, 2017).

Conservation status. Intensive grazing on sub-alpine meadows and steadfast recreational development in the Caucasus lead to large-scale habitat loss and direct killings. In the western part of its range, the



Fig. 125. Dinnik's viper, *Pelias dinniki*, bronze morph – valley of the upper reaches of the Mzymta River, Krasnodar Territory, Russian Federation.



Fig. 126. Dinnik's viper, *Pelias dinniki*, melanistic morph – Mt. Fisht, Krasnodar Territory, Russian Federation.



Map 35. Distribution map of *Pelias dinniki*.

Dinnik's viper is depressed and can vanish even under insignificant additional impacts. The main threats are overgrazing, poaching and direct killings.

At the workshop on IUCN assessment of Palearctic reptiles and amphibians in Antalya, Turkey in September 2008, its status was designated as VU B1ab (iii,v). The Dinnik's viper *Vipera dinniki* (= *Pelias dinniki*) previously considered as Caucasian viper (*Pelias kaznakovi*) was included in the Red Data Books of the USSR (1984) and Georgia (1982) without IUCN categories. Georgian Red List, VU IUCN. Currently, it is listed in the Red Data Books of the Russian Federation (2001) without IUCN category, Krasnodar Territory (2017) as VU C1+2a, Kabardino-Balkariya Republic (2018) as VU A4cd; B2a; C2a(i), Republic of Adygheya (2012)

as VU B1ab(iii,v); Chechen Republic (2007), Republic of Dagestan (2009), Red Book of Karachai-Cherkessiya Republic (2013) without IUCN categories. It is indicated in the Red Data Book of Republic of South Ossetia (2017) as VU B1ab(i,v). This species is protected in Kavkazsky, Teberdinsky, Kabardino-Balkarsky, North Ossetian and Lagodekhi Reserves and in Sochi, Prielbrusie and Ritsa National Parks.

Iranian mountain-steppe viper – *Pelias ebneri* (Knoepffler et Sochurek, 1955) (Fig. 127)

Vipera ursinii ebneri Knoepffler and Sochurek, 1955, Neues über die Rassen der Wiesenotter (*Vipera ursini* Bonaparte). Burgenl. Heimatblat, 17(4): 185–188.



Map 36. Distribution map of *Pelias ebneri*.

Terra typica. “Elbursgebirge zwischen Rhema und Demawend, 2700 m, Nord-Persien”; Alborz Ridge between Rhema and Demavend, northern Iran, 2700 m asl.

Type specimens. Holotype NMW 14889.

It is considered as separate species or synonyms of *P. ursinii* fide McDiarmid et al. 1999) or *Vipera eriwanensis* (Reuss, 1933) (Uetz et al., 2017).

Distribution. Nilson and Andrén (2001) considered it as a distinct species distributed in the Talysh Mts. in southern Azerbaijan and the Alborz Mts. in northern Iran. The range covers Northern Iran (Mazandaran) and extreme southeastern Azerbaijan (Lerik) (Van Wallach et al., 2014).

Distribution in the Caucasus. The northwestern periphery of the species range extends into the

Caucasus Ecoregion within the Talysh-Zuvand area in Azerbaijan and adjacent areas of northern Iran (Map 36).

Habitats. They are similar to those of *P. eriwanensis* and represented by stony mountain steppes at 2000–2700 m asl (Wettstein, 1953; Van Wallach et al., 2014).

Conservation status. Very little is known about the population status and abundance. At the workshop on IUCN assessment of Palearctic reptiles and amphibians in Antalya, Turkey in September 2008, its status was designated as VU B2ab(iii).



Fig. 127. Iranian mountain-steppe viper, *Pelias ebneri* – Lar valley, Alborz, Iran.

Armenian steppe viper – *Pelias eriwanensis*
(Reuss, 1933) (Fig. 128)

Acridophaga renardi eriwanensis Reuss, 1933,
Fortsetzung und Schluss der Originalberichte. Nachr.-
Bl. Aquar.-u. Terr.-Ver., Berlin, 1933: 372–373.

Terra typica. “Lake Sevan above Shordzha at
2000 m a.s.l. [Yerevan], Armenia,” *fide* Krecsák (2007:
658) (Van Wallach et al., 2014).

Type specimens. Holotype, ZMB 55160, a
425 mm (Van Wallach et al., 2014).

Distribution. Armenian Highland (Map 37).



Fig. 128. Armenian steppe viper, *Pelias eriwanensis* – Kaputan, Armenia.



Map 37. Distribution map of *Pelias eriwanensis*.

Distribution in the Caucasus. The range of the Armenian Steppe Viper, *P. eriwanensis* (Reuss, 1933) encompasses the greater part of the Armenian Plateau in Armenia, northeastern Turkey and western Azerbaijan, including the Karabakh Plateau and Nakhichevan (Aleksperov, 1978; Orlov and Tuniyev, 1990; Baran et al., 2005; Tuniyev et al., 2009; Tuniyev et al., 2011; Arakelyan et al., 2011; Kukushkin et al., 2012). It was recorded in Kars and Erzurum provinces in northeastern Turkey, mountain steppes of Armenia, Nakhichevan Republic and, possibly, adjacent areas of Iran. In Turkey it was recorded above the Gelbelen village on the slope of Kysyrdag mountain inhabiting stony mountain steppe on the elevation about 2000 m asl. The presence of *P. eriwanensis* in southern Georgia was indicated in a single paper

(Vedmederja et al., 1986) and after many years these data were substantially supplemented with the records in the Georgian Akhalkalaki and Ninotsminda districts bordering with the known range of the species and situated on the Armenian Plateau (Kukushkin et al., 2012) as well as near Kartsakhi lake on the border with Turkey (S. Tuniyev, et al., 2014). The small-sized vipers, *P. davevsky* and *P. eriwanensis* inhabit rocky areas in alpine grassland in eastern Hanak District, Ardahan Province, Turkey but no contact zone or proximate populations have been reported so far, but can be expected in eastern Ardahan Province (Mebert et al. 2015).

Habitats. Mountain steppes at 1000–2400 m asl. Vipers live on xero-mesophilic mountain slopes, stony mountain steppes, dwarf juniper communities and can-

yon sides over which they descend to the lower zones to co-exist with *Montivipera r raddei* and, in some places, with *Macrovipera lebetina obtusa*. Sometimes they use crevices and caves as ibernacula.

Conservation status. At the workshop on IUCN assessment of Palearctic reptiles and amphibians in Antalya, Turkey in September 2008, its status was designated as VU B1ab(iii,v). The main threats are overgrazing, land use and infrastructure development. It is included in Red Book of Animals of the Republic of Armenia (2010) as VU B1ab(iii,v). It is protected in Sevan National Park and Khosrov Forest Reserve and Bargushat Sanctuary in Armenia.

Kaznakov's or Caucasian viper – *Pelias kaznakovi* (Nikolsky, 1909) (Figs. 129–132)

Vipera kaznakovi Nikolsky, 1909, Mitt. Kaukas. Mus. Tiflis, 4: 174 (173–174).

Terra typica. In the original description – “Tsebelda, Sukhumi district”; Abkhazia, West Caucasus.

Type specimens. **Lectotype** MGT 4408 [National Museum of Georgia, Tbilisi (former Caucasian Museum)]. Designated by Orlov and Tuniyev (1986, 1990). **Paralectotype** MNKNU 14702 (“Urjevskoje village, Tsebelda, Sukhumi Okrug”, coll. J.N. Voronov) (Vedmederya et al., 2009).

Distribution. The global area covers the foothill areas of the Krasnodar Territory, the Republic of Adygeya, Abkhazia, Western Georgia, Adzharia and the Lazistan coast of Turkey. Generally, the range comprises two fragments: Adjara-Lazistan (Turkey, Adjara) and North Colchis (western Georgia, Abkhazia, Republic of Adygeya and Krasnodar Territory of Russia). Possibly, an isolated population of the Kaznakov's viper also lives on the eastern slope of the Adjara-Imereti Ridge in the Baniskhevi Gorge (Bakradze, 1969). The range is extended along the Black Sea coast, covering the forested foothills up to 800 (sometimes 1000) m asl, from Hopa town and the Mt. Karçil of the Shavsheti Ridge (Kamili Biosphere Reserve) in Turkey (Afsar, Afsar, 2009) and the Suramo Pass through the Colchis (excluding proper Colchic Lowland) to Tuapse suburbs.

Distribution in the Caucasus. It fully coincides with the global range of this Caucasian endemic (Map 38). In the Russian Federation occurs in the foothills of the Krasnodar Territory and the Republic of Adygeya. The area covers the foothills of the Black Sea coast from

Nikolski, Herpetologia caucasica.

Tab. III.



Fig. 129. A drawing of the Caucasian viper, *Vipera (Pelias) kaznakovi* from the book “The reptiles and amphibians of the Caucasus” by A.M. Nikolsky (1913).

Tuapse to the border with Abkhazia, on the northern slope of the western Caucasus from Goryachyi Klyuch (Hot Spring) to the foothills of the Absheron district inclusive (Tuniyev, Tuniyev, 2007). In South Ossetia all known records are confined to the basin of the river Kura, mainly to the Tskhinvali district. It is the eastern periphery of the area of distribution of this relict snake, the endemic of Colchis. In South Ossetia, the species occurs in the transition zone from the foothills to the middle mountains of the Dzau, Znaur and Tskhinvali regions.

Habitats. Caucasian viper inhabits forested slopes, bottoms of the canyons, and post-forest glades, from the maritime lowlands to 1000 m asl. They are also recorded in azalea and Cotinus-Cornus oakeries,



Fig. 130. Kaznakov's or Caucasian viper, *Pelias kaznakovi*, orange-black morph, male – vicinity of Sochi, Krasnodar Territory, Russian Federation.



Fig. 131. Kaznakov's or Caucasian viper, *Pelias kaznakovi*, melanistic morph, female – vicinity of Sochi, Krasnodar Territory, Russian Federation.



Fig. 132. Kaznakov's or Caucasian viper, *Pelias kaznakovi* – vicinity of Gagra, Abkhazia.

mixed subtropical forests with evergreen understorey, in chestnut and beech forests, riparian willow thickets, alder forests, polydominant forests on fluvial terraces and large overgrown screes. At the top limit of altitudinal distribution (Achipse and Bzyb basins), this species reaches the zone of conifer forests and lives in the beech-fir-fern-forbs and spruce-fir ecotones, but do not move deep into the conifer forest. The most suitable habitats are broadleaf forest glades and margins densely covered by *Pteridium tauricum* and *Rubus anatolicus* at 50–300 m asl. It is noted on the tea plantation 5 km above the town of Hopa and in the village Esenkyuyu in Turkey. Apparently, the species can be found in the environs of the village Archavi, where magnificent Colchis cenoses still well preserved (B.Tuniyev et al., 2014). In South Ossetia, the species occurs in the transition zone from the foothills to the middle mountains of the Dzau, Znaur and Tskhinvali regions (Red Book of South Ossetiya Republic, 2017). They live there in the medium-sized forests and post-forest stations in the altitude range from 900 (near the village of Grom

and the village of Arceu) to more than 1300 m above sea level (South Ossetian Reserve). It is extremely rare everywhere in South Ossetiya. At the top limit of altitudinal distribution (Achipse and Bzyb basins), this species reaches the zone of conifer forests and lives in the beech-fir-fern-forbs and spruce-fir ecotones, but do not move deep into the conifer forest. It inhabits the forested mountain slopes, post-forest glades, stony screes of the forest belt. In the forest belt is noted in a number of forest types: azaleus and mackerel-dogwood oak forests, mixed-subtropical forests with evergreen undergrowth, chestnut trees, deadly armed birchbark, spring-willow willows, and polydominant forests on steep overgrowing talus. Vipers can survive in the transformed lands: post-forest meadows, orchards, vineyards, tea plantations, old parks, etc.

Northeastern Anatolia harbours a high diversity of viperid snakes including *P. kaznakovi*. Potential contact zone of *P. barani* and *V. kaznakovi* was registered between Ardeşen and Findikli, Rize Province, along the subtropical Black Sea coast. Another potential contact



Map 38. Distribution map of *Pelias kaznakovi*.

zone of *V. kaznakovi* and *V. davevskii* was found north of the Karçal Mountains between Camili and Maden, Artvin Province, Turkey (Mebert et al., 2015).

Conservation status. This viper is rare everywhere on the Black Sea coastline and in many places it is already gone. The populations of rather high densities have still survived in forest screes of Sochi National Park. The main threats are recreational pressure in the resort belt along the coastline, deforestation, haying on post-forest glades and in forest margins. It has disappeared from many resort areas. At the workshop on IUCN assessment of Palearctic reptiles and amphibians in Antalya, Turkey in September 2008, its status was designated as EN B2ab (ii,iii,v) (<https://www.iucn-redlist.org/species/22990/114546825>).

The Kaznakov's viper was included in the Red Data Books of the USSR (1984), Georgian SSR (1982), Georgian Red List, EN IUCN, and the Russian Federation (2001) without IUCN categories. Currently, it is listed in the Red Data Books of the Krasnodar Territory (2017) as EN A4abcd; B2ab(i,ii,iii,iv,v), Republic of Adygeya (2012) as CR A4abc; B1ab(i,ii,iii,iv,v) and Republic of South Ossetia (2017) as CR A3abc; B1ab(i,ii,iii,iv,v).

It is protected in Sochi National Park where all high-density sites are incorporated to the reserve zone, Kavkazsky Biosphere Reserve (Russia), Ritsa National Park, Pitsunda-Mussera Reserve (Abkhazia), Kintrishi Reserves and Mtirala National park (Georgia), Kamili Biosphere Reserve (Turkey), South-Ossetian Reserve (South Ossetia).

Lotiev's viper – *Pelias lotievi* (Nilson, Tuniyev, Orlov, Höggren et Andrén, 1995) (Figs. 133–134)

Vipera lotievi Nilson, Tuniyev, Orlov, Höggren and Andrén, 1995, Asiatic Herpetological Research, 6: 21 (1–26, fig. 22).

Terra typica. “Armkhi, Checheno-Ingushetia, Russia, below Mt. Stolovaya, 2000 m altitude”; Armkhi, near the foothills of the Mt. Stolovaya, 2000 m asl, Republic of Ingushetia (formerly Checheno-Ingushetia), Russia.

Type specimens. Holotype ZIN (=ZISP) 20309; paratypes ZIN (=ZISP) 20305, 20307, 20310, 20304, 20312, 20313, 18203, 18226, 11996, 20303; ZIG (GNHM) 298–306, 297.

Distribution. Mountain steppes and oreoxerophytic landscapes of the North Caucasus in Karachaevo-Cherkessia, Kabardino-Balkaria, North Ossetia-Alania, Ingushetia, Dagestan and, possibly, Lagodekhi in eastern Georgia and headwaters of the Terek River. An isolated population is known from the eastern part of the Krasnodar Territory (Map 39).

Distribution in the Caucasus. It fully coincides with global range of this Caucasian endemic. The origin of *P. lotievi* was associated with aridization of the Greater Caucasus in the Holocene and the expansion of oreoxerophytic landscapes upwards to highlands. In modern times, these trends take place mostly in the central and eastern parts of the Greater Caucasus, and in some small relict areas of the West Caucasus.



Map 39. Distribution map of *Pelias lotievi*.

P. lotievi was recorded in the gorge of Tsovatitskali River near Indurta village, Akhmeta municipality, Kakheti Region and 2 km upriver from that locality. Both localities are in the territory of Tusheti National Park (Bekoshvili, Doronin, 2017). Previously, it was assumed that *Pelias lotievi* was known in Georgia based only on a photograph taken near the small town of Kazbegi (= Stepantsminda). Along the northern macroslope of the Greater Caucasus it was predicted in the regions bordering Dagestan (Tuniyev et al., 2011). The first record of Lotiev's viper in the mountain territories within the Guba district of Azerbaijan (near the village of Khinalik, altitude 1900–2400 m above sea level) confirmed this point of view and indicates a wider distribution of this species. These territories are located on the northern sloping and steep rocky slopes of the Greater Caucasus (Iskenderov et al., 2017).

Habitats. Semi-arid slopes with oreoxerophytic East Mediterranean vegetation and mountain depressions at 1200–1800 m asl. Most often these snakes occur on screens overgrown by lichens and sparse scrubs, as well as in vole colonies, ruins and abandoned high-

land cemeteries. In Azerbaijan, they inhabit the slopes characterized by xerophytized subalpine meadows and rock outcrops (Iskenderov et al., 2017).

At higher limits of altitudinal distribution, vipers reach subalpine meadows preferring the *Festuca varia* communities. In the zones of sympatry with the Dinnik's viper (Abishir-Akhuba Ridge, upper Teberda River, slopes of the Mt. Elburs and Itum-Kalinskaya Depression), *P. lotievi* occupy semi-arid depressions and dry pine forests while mesophilic *P. dinniki* live in humid areas. Most often these two vipers act as ecological and altitudinal vicariants in mid-elevations and highlands on the northern macroslope of the Great Caucasus.

In the Itum-Kalinskaya Depression where the Dinnik's viper is rare, Lotiev's vipers are common in ecotones and stony sites among the oreoxerophytic secondary, sometimes primary, East Mediterranean sibiljak dominated by *Paliurus spina-christi* and *Rhamnus pallasii*. The co-existing reptiles are *Lacerta strigata*, *Coronella austriaca*, *Anguis colchicus*, *Platyceps najadum* and *Zamenis hohenackeri*. Lotiev's vipers occur also



Fig. 133. Lotiev's viper, *Pelias lotievi* – Dagestan, Russian Federation.



Fig. 134. Lotiev's viper, *Pelias lotievi* – Itum-Kale, Chechnya, Russian Federation.

in this depression's thickets and cushions (phrygana) which grow only on breakstones in the lower part of the left bank slope.

In the Nazran district of Ingushetia, in the basin of the Armkhi River (right tributary of the Terek River), vipers occur in oreoxerophytic vegetation in the bottom and on the southern and south-eastern slopes of the semi-arid depression. The lower parts of the depression are covered by pine-juniper forests with *Pinus kochiana* and *Juniperus hemisphaerica*. The plants *Spiraea hypericifolia*, *Rhamnus pallasii*, *Stipa* sp. and *Diphelypaea coccinea* are common. The other reptiles living here are *Darevskia caucasica*, *D. daghestanica*, *D. rudis* and *Coronella austriaciaca*. Also, this viper lives in vegetation of cliffs and screes (petrophytes and hasmophytes) in the bottom of the depression.

Conservation status. The areas of suitable habitats are substantial in the North Caucasus, but high densities of the Lotiev's viper (up to 40 individuals/ha) have been maintained only in protected areas. Outside of protected areas, vipers experience a strong pressure of overgrazing, direct killings and recreation. It is rare species of declining population and shrinking range.

Rarity of this species in the Krasnodar Territory and western Karachaevo-Cherkessia is caused by the lack of suitable climatic and habitat conditions.

At the workshop on IUCN assessment of Palearctic reptiles and amphibians in Antalya, Turkey in September 2008, its status was designated as NT. The species is included in the Red Data Books of the Krasnodar Territory (2017) as CR C2(ii), Chechen Republic (2007) and Karachai-Cherkessiya Republic (2013) without IUCN categories. It is listed in Kabardino-Balkariya Republic (2018) as VU A4cd; B2a; C2a(i).

The Lotiev's viper is protected in Kavkazsky, Teberdinsky, Kabardino-Balkarsky, North-Ossetian and Erzi Reserves and in Prielbrusie and Alania National Parks.

Magnificent (or Relic) viper – *Pelias magnifica* (Tuniyev et Ostrovskikh, 2001) (Fig. 135)

Vipera magnifica Tuniyev and Ostrovskikh, 2001, Two new species of vipers of «kaznakovi» complex (Ophidia, Viperinae) from the Western Caucasus. Russ. J. Herpetol., 8(2): 123 (117–126).



Map 40. Distribution map of *Pelias magnifica*.

Terra typica. In the original description – “Schahkghireevskoye Gorge, the Malaya Laba River, Krasnodarskii region, Russia”.

Type specimens. Holotype SD CSNBR 541 (adult male); paratypes SD CSNBR 542, 543, 544, 545 (2 males and 2 females).

Distribution. Southern slope of the Skalistyi Ridge in the Republic of Adygheya (Mt. Afonka) and the Krasnodar Territory (Malyi Bombak Ridge) (Map 40). Possibly, this species is also present in the Karachaevo-Cherkessian Republic. Six color morphs are recorded (Ostrovskikh, 2008). Results of study using genomic scale DNA markers support the conclusion that *V. magnifica* had formed through a hybridization event between *P. kaznakovi* and *P. renardi* (Zinenko et al., 2016).

Distribution in the Caucasus. It fully coincides with global range of this Caucasian endemic.

Habitats. Derivates of Colchic vegetation enriched by Mediterranean and steppe vegetation comprising the light grass oakeries, dry meadows and scrubs on rocky ledges in limestone massifs at 700–1000 m asl. These vipers succeed to live even on tiny rock overhangs in forests.

Conservation status. A depressed, relict and narrowly distributed species of very low numbers faced by high extinction risk even under slight additional pressures (Tuniyev et al., 2016). The main threats are frequent ground fires, recreation and poaching. At the workshop on IUCN assessment of Palearctic reptiles and amphibians in Antalya, Turkey in September 2008,



Fig. 135. Magnificent (or Relic) viper, *Pelias magnifica* (holotype) – Malaya Laba River, Krasnodar Territory, Russian Federation.



Fig. 136. Magnificent (or Relic) viper, *Pelias magnifica* (male) – Malaya Laba River, Krasnodar Territory, Russian Federation.



Fig. 137. Magnificent (or Relic) viper, *Pelias magnifica* (female) – Malaya Laba River, Krasnodar Territory, Russian Federation.

its status was designated as EN B1ab(ii,iii,v), C2a(i). The magnificent viper is included in the Red Data Books of the Krasnodar Territory (2017) as EN A2abc; B2ac(iv), Republic of Adygheya (2012) as CR A4abc; B2ab(i,ii,iii,v)c(iv).

A part of the population has been protected in Kavkazsky Biosphere Reserve. Incorporation of the Malyi Bombak Ridge to this reserve would be a very efficient protection measure.

***Pelias olguni* Tuniyev S., Avcı A, Tuniyev B., Agasian A. et Agasian L., 2012 (Figs. 138–139)**

Type territory. Turkey, Ardahan Province, Town Posof, Mt. Ilgar-Dağ, (2020 m a.s.l.).

Type specimens. Holotype: herpetological collection of the Sochi National Park, Sochi, SNP No. 866 (adult female); paratypes: fifteen specimens: 13 specimens, SNP No. 874 (1 adult female and 2 new-born females), No. 875 (1 adult female, 1 new-born female and 1 newborn male), No. 876 (1 new-born male and 2 new-born females), No. 877 (adult male), No. 878

(adult female), No. 879 (adult female), No. 880 (adult male); Zoology Department Ege University, Zoology Lab. of the Department of Biology at Buca Education Faculty, Turkey, 2 specimens, ZDEU No. 270_2005 (adult male and female).

Distribution. Modern distribution of species is limited by vicinities of town Posof in the borderline district of Turkey with Georgia, from where this species is known within Türkgözü Plateau and slopes of mountain Ilgar-Dağ in the left-bank basin of upper flow Kura River and from mountain Gumbati in Georgia (S. Tuniyev et al., 2012, 2014) (Map 41).

Habitats. The first two specimens were found on moist humid zone with short alpine meadows and numerous piles of stone, above the upper altitudinal limit of the forest at elevation of approximately 2050 m on Türkgözü Plateau (Avcı et al., 2010). Biotopes of vipers on Mt. Ilgar-Dağ is presented by subalpine middle grass meadows with bushes, extending from the upper edge of the forest and subalpine elfin-woodland (*Betula litwinowii*) by subalpine glades with moraines among subalpine light forest (*Acer trautvetteri*, *Betula*



Map 41. Distribution map of *Pelias olguni*.

litwinowii, *Salix caprea*, *Sorbus aucuparia*) in a altitudinal range from 2020 up to 2100 m a.s.l. In biotopes of vipers occur the single undersized trees and bushes, including *Pinus kochiana*, *Cerasus avium*, *Malus orientalis*, *Corylus avellana*, *Rosa spinosissima*, *Viburnum lantana*, *Rubus buschii*, *Lonicera orientalis*, *Ribes caucasicum*, *Ribes alpinum*. Subalpine glades, transiting more high to subalpine meadows are presented by graminea-mixtoherbosum associations with such species as *Grossheimia macrocephala*, *Delphinium speciosum*, *Lapsana intermedia*, *Lilium szowitsianum*, *Achillea* sp., *Silene* sp., *Geranium psilostemon*, *Chaerophyllum roseum*, *Stachys macrantha*, *Stachys balansae*, *Campanula latifolia*, *Campanula collina*, *Rhinanthus colchicus*, *Astrantia maxima*, *Origanum vulgare*, *Vicia*

balansae, *Ranunculus caucasicus*, *Briza* sp., *Rumex acetosa*, *Veratrum lobelianum*, *Heracleum apiifolium*, *Pyrethrum roseum*, *Lotus caucasicus*, *Securigera varia*, *Hymnadenia conopsea*, *Hypericum montanum*, on moraines — *Trifolium alpestre*, *Trifolium canescens*, *Alchemilla* sp., *Sibbaldia semiglabra*. Biotopes on Mt. Gumbati are also represented by the slopes of quiet volcano of east and south exposure. Here, steppe-like short-grass subalpine meadow is also developed with obvious tracks of overgrazing and presence of ruderal species of plants, such as *Urtica dioica*. Below, on a slope in a canyon, the narrow-leaved forests are developed with such species as *Betula litwinowii*, *Salix caprea*, *Sorbus aucuparia* and other. The area of viper habitats is extensive and proceeds on territory of Turkey. In Georgia,



Fig. 138. Olgun's viper, *Pelias olguni* – Turkey, Ardahan Province, Posof, Mt. Ilgar-Dag, black morph, female.



Fig. 139. Olgun's viper, *Pelias olguni* – Turkey, Ardahan Province, Posof, Mt. Ilgar-Dag, brown morph, female.

vipers were found at altitudes from 2200 to 2600 m a.s.l. In the vegetation bushes of *Rosa pimpinellifolia* is marked; such grassy species were identified as *Seseli libanotis*, *Stachys macrantha*, *Lotus caucasicus*, *Trifolium canescens*, *T. montanum*, *Pedicularis armena*, *Centaurea nigrofimbria*, *Campanula hohenackeri*, *Myosotis alpestris*, *Anthemis caucasica*, *Polygala alpicola*, *Thymus nummularius*, *Anemone fasciculata*, *Dactylorhiza euxina* and other, i.e., in the predominant majority species characteristic of subalpine meadows.

Conservation status. As rare taxa, limited in a natural habitat and a number *Pelias olguni* needs to be included in the Red List of IUCN with the category of status of VU B2ab(iii).

Orlov's viper – *Pelias orlovi* (Tuniyev et Ostrovskikh, 2001) (Fig. 140)

Vipera orlovi Tuniyev and Ostrovskikh, 2001, Two new species of vipers of «*kaznakovi*» complex (Ophidia, Viperinae) from the Western Caucasus. Russ. J. Herpetol., 8(2): 117 (117–126).

Terra typica. In the original description – “Papai Mountain Krasnodarskii region, Russia”.

Type specimens. Holotype SD CSNBR 528 (adult male); paratypes SD CSNBR 524, 529, 530, 531, 532, 533, 534, 535, 536, 537, 538, 539 and 540 (6 males and 7 females).

Distribution. A chain of patches in the Krasnodar Territory on both slopes of the lowest north-western part of the Greater Caucasus. It includes Mt. Papai, Ubin and Praskoveevka villages, Mikhailovsky Pass, Mt. Oblego and Mt. Bolshoi Pseushkho. Some isolated populations can be present near Gelenjik.

Distribution in the Caucasus. It fully coincides with global range of this Caucasian endemic (Map 42). Results of study using genomic scale DNA markers support the conclusion that both *P. orlovi* and *P. magnifica* had formed through a hybridization event between *P. kaznakovi* and *P. renardi*. The average admixture proportion in individuals was low (6.39 %) in the case of *P. magnifica*, but was higher in *P. orlovi* (19.02 %). Further studies include analyses of ecological segregation of *P. orlovi* from parental taxa and search for evolutionary consequences of hybridisation (Zinenko et al., 2016).

Habitats. The range lies completely within the zone of Mediterranean climate and xero-mesophilic



Fig. 140. Orlov's viper, *Pelias orlovi* (topotype) – Mt. Papay, Krasnodar Territory, Russian Federation.



Map 42. Distribution map of *Pelias orlovi*.

landscapes. Orlov's vipers live in Mediterranean and sub-Mediterranean landscapes from intrazonal riparian glades to steppe-meadows and ecotones of juniper sparse forests. Elevations of viper occurrence sites vary from 450 to 950 m asl.

Conservation status. A narrowly distributed relict species living on the edge of extinction in a series of micropopulations. The main threat is poaching. The Orlov's viper is included in the IUCN Red List of Threatened Species as CR B1ab(i,v); C2a(i) and the Red Data Book of the Krasnodar Territory (2017) as EN A2abcd. It is formally protected on Mt. Papai. It is essential to establish Novorossiysk Reserve, the Mt. Papai inclusive, and to adjoin the entire massif of the Mt. Bolshoi Pseuskho to Sochi National Park.

Black Sea viper – *Pelias pontica* (Billing, Nilson et Sattler, 1990) (Fig. 141)

Vipera pontica Billing, Nilson, Sattler, 1990, *Vipera pontica* sp.n., a new viper species in the *kaznakovi* group from northeastern Turkey and adjacent Transcaucasia. Zool. Scripta, 19(2): 228 (227–231, figs. 1–4).

Terra typica. In the original description – “Çoruh valley, Province Artvin, northeastern Turkey”.

Type specimens. Holotype NHMG 5021.

Distribution. This viper is known from its type locality in the lower Çoruh River basin downstream from Artvin, not far from the Turkish-Georgian border. Supposedly, it also exists in the Kura River basin near Gori (Georgia) and in the vicinity of Ke-

murlu in the Çoruh basin (Erzurum Province, Turkey) (Map 43).

Distribution in the Caucasus. It fully coincides with global range of this Caucasian endemic. vicariant of *P. barani*, The conspecificity of this taxon with *P. barani* is assumed (Joger et al., 1997; Baran et al., 2001; Kalyabina-Hauf et al., 2004; Uetz et al., 2017).

Habitats. Canyons covered by stony hornbeam siblijak and tree stands taking an intermediate position between the humid Colchic polydominant forests in the lower Çoruh in Adjara, East Mediterranean maquis (*Arbutus andrachne*, *Cistus tauricus* and *C. salviifolius*) and the *Pinus pinea* forests in the Artvin Depression. The suburbs of Gori comprise the hornbeam siblijak on

steep stony hillsides, thus indicating the possible existence of *P. pontica*. Due to the recent record of *Pelias kaznakovi* near Borçka (Afsar, Afsar, 2009), this can be another area of co-existence between the *Pelias* species in the Caucasus Ecoregion.

Conservation status. A narrowly distributed, relict and depressed species in demand of urgent conservation. At the workshop on IUCN assessment of Palearctic reptiles and amphibians in Antalya, Turkey in September 2008, its status was designated as EN B1ab(i,iii,v), C1. It is strongly recommended to set aside a protected area in the lower Çoruh downstream Artvin or to declare it a natural monument like it happened with the pine forest near Artvin.



Map 43. Distribution map of *Pelias pontica*.



Fig. 141. Black Sea viper, *Pelias pontica* – Borchka, Artvin, Turkey.

Steppe Viper – *Pelias renardi* Christoph, 1861
(Figs. 142–145)

Vipera renardi renardi Christoph, 1861, Bull. Soc. Imp. Nat. Moscou, 34: 599–606.

Terra typica. “Sarepta allenthalben in der Steppe, südlichen Russland” [= Krasnoarmeysky Rayon, Volgogradskaya Distr., SW Russia, 48°31’N, 44°31’E (Van Wallach et al., 2014); “Sarepta” – a German colony on the Lower Volga, Russia. Nilson and Andrén (2001) designate the *terra typica* as “Sarepta, lower Volga, Russia”].

Type specimens. Syntypes not preserved. The individual illustrated in Boulenger (1893: plate LXIV, Fig. 109) as the type is actually irrelevant to the type series and can only be considered as the topotype (Nilson, Andrén, 2001).

Distribution. Steppes, forest-steppes and semi-deserts of South and South-East Europe, including the steppes of Crimea, southern Ukraine, Ciscaucasus and foothills of the Greater Caucasus eastwards to north-western and north-eastern Central Asia, Kazakhstan and South Siberia (Nilson, Andrén, 2001) (Map 44). The range reaches the Volga-Kama region to the north

and the Altai Mts. and Dzungaria to the east. The species comprises three subspecies: nominate *P. r. renardi* (most of the range, except for Central Asia); *P. r. tien-shanica* (Nilson et Andrén, 2001) (Kyrgyzstan, eastern Uzbekistan, northern Tajikistan and south-eastern Kazakhstan); and *P. r. parursinii* (Nilson et Andrén, 2001) (northern parts of Xinjiang in China). The taxonomic status of distant populations from the Kazakh Altai remains unclear. Possibly, an isolated geographical form exists in the southern foothills of the East Caucasus.

Distribution in the Caucasus. The range covers all Ciscaucasus (aside from the Nogayskaya Steppe and arid Caspian semi-deserts) from where vipers permeate into the foothills of the West Caucasus (Raevskaya, Apshe-ronsk and Khadyshensk villages, Gerpegem Ridge) along the riversides (Psekups, Pshish, Belaya, Malaya Laba). The population living in the Krasnodar Territory is marked by high occurrence of melanistic individuals which is taxonomically irrelevant (Ostrovskikh, 2006). Snakes of the *P. renardi* and *P. kaznakovi* complexes living in lowland or dry mountain grasslands which have expanded their range in Northern Caucasus through natural or artificial corridors resulting in a zone of contact between these two groups what can lead to

to historical and/or ongoing hybridization between these snakes (Zinenko et al., 2016). Melanism is also recorded in the lower Volga region.

Habitats. Fescue-forbs, wormwood and beard grass steppes, forest-steppes, riparian meadows with oakeries, seldom foothill oakeries. Vipers also occur on the steep coastal slopes and sand spits of the Azov Sea. Affected by ploughing, snakes disappear and survive only in gullies, roadsides, forest remnants and coastal brinks. In the Caucasus, they move up to 600–800 m asl.

Conservation status. Population is declining because of large-scale land use and infrastructure development. In many areas, this viper has vanished. At the workshop on IUCN assessment of Palearctic rep-

tiles and amphibians in Antalya, Turkey in September 2008, its status was designated as VU A1c+2c. The steppe viper is listed on the Annotated list of taxa and populations in want of special attention to their environmental status (Annex to the Red Data Book of the Russian Federation, 2001) and included in the Red Data Books of the Krasnodar Territory (2017) as VU A4cd; B1ab(i,ii,iii,iv), Kabardino-Balkariya Republic (2018) as EN A4cd; B1ab(ii,iii,iv,v) + 2ab(ii,iii,iv,v); C2a(i), Republic of Adygheya (2012) as VU A4cd, B1ab(i,ii,iii,iv,v); Red Data Books of Chechen Republic (2007), Republic of Dagestan (2009), Karachai-Cherkessiya Republic (2013), Stavropol Territory (2014) and Rostov Region (2014) without IUCN categories.



Map 44. Distribution map of *Pelias renardi*.



Fig. 142. Steppe Viper, *Pelias renardi* (typical morph) – northern Dagestan, Russian Federation.



Fig. 143. Steppe Viper, *Pelias renardi* (melanistic morph) – western Ciscaucasus, Russian Federation, female.



Fig. 144. Steppe Viper, *Pelias renardi* (red morph) – western Ciscaucasus, Russian Federation.

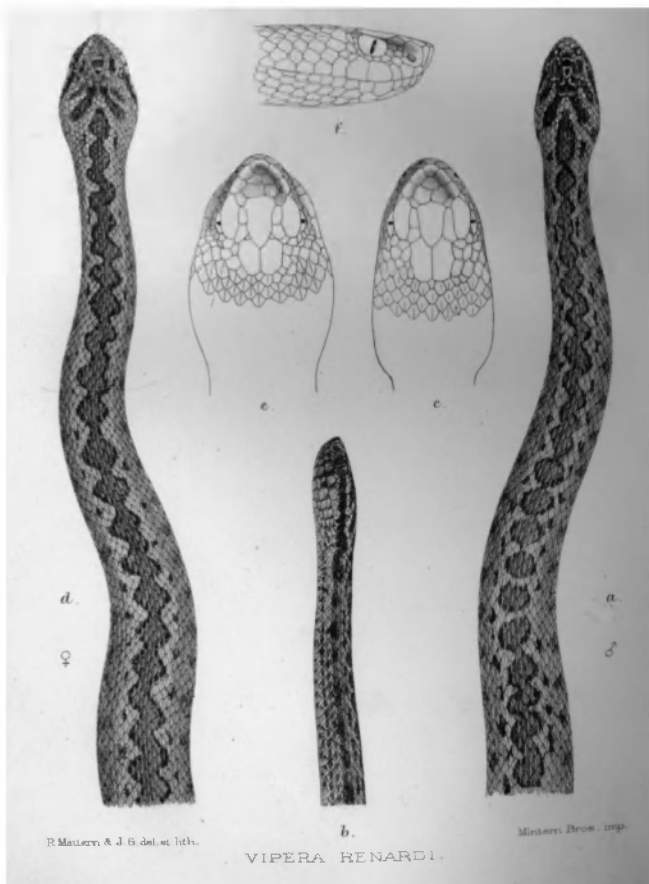


Fig. 145. A drawing of the steppe viper from the paper “On a little-known European viper, *Vipera ursinii* Bonap.” by G. Boulenger (1893, plate LXIV).

Only insignificant part of the distribution area is covered by protected areas. The steppe viper is quite common in Rostovsky Reserve, but disappeared in Chernye Zemli Reserve and the Kizliar district of Dagestansky Reserve for the transgression of the Caspian Sea and terrain inundation. Small population is protected in Utrish Reserve.

***Pelias shemakhensis* Tuniyev, Orlov, Tuniyev et Kidov, 2013 (Figs. 146–147)**

Vipera ursinii renardi (Christoph, 1861) (Muskhelishvili, 1968; Alekperov, 1978) (part.).

Pelias renardi Christoph, 1861 (Nilson and Andren, 2001; Ananjeva et al., 2006; Tuniyev et al., 2009) (part.).

Vipera (Pelias) eriwanensis (Reuss, 1933) (Vedmederya et al., 2007; Kukushkin et al., 2012) (part.).

Type territory. Vicinity of Shemakhan (= Shemakha, north-eastern Azerbaijan). From original description.

Type specimens. Holotype: Herpetological collection of Zoological Institute of Russian Academy of Sciences in St. Petersburg, ZISP, No 21720 (subadult male).

Distribution. Recent distribution of species is limited by the Shemakha District of Azerbaijan, from here it is known from vicinity of Shemakha town, village Demirchi; Gobustan District — village



Fig. 146. Shemakha viper, *Pelias sh. shemakhensis* – Shemakha, north-eastern Azerbaijan.



Fig. 147. Shemakha viper, *Pelias sh. kakhetiensis* – Dedoplistskaro, Fortress Khornabudji, Shirak Plateau (Kakhetia, East Georgia), male.



Map 45. Distribution map of *Pelias schemakhensis*.

Maraza (Map 45). Aliev (1973) noted finds of steppe vipers in the north Azerbaijan in Shemakha District (villages Khankend, Ortabulag, Eddi, Krumbez, and others) and in Sheki District (Villages Akhmedbeli, Gazakend). Alekperov (1978) specified finds in town Shemakha, between Shemakha and village Angekharan, between Shemakha and village Khynysly, at the foot of Mt. Pirdirechidag, on the slopes of Mt. Gyzkalasy. Alekperov also specified on specimens, stored in State Museum of Georgia (Tbilisi) from village Karatala and city Nukhi (= Sheki), now located in Azerbaijan.

Habitats. The biotopes of species are presented by shibliaks of *Paliurus spina-christy* and ecotones of dry *Andropogon* steppes and derivatives of

the broad-leaved forests on the stony slopes of foothills. By other words, vipers are pushed now from steppes habitats into unusual for them biotopes, quite recently presenting areas of the broad-leaved for ests the extreme variant of which degradation is a *Paliurus shibliak*.

Conservation status. Species became very rare in northeastern Azerbaijan. As rare taxa, limited in a natural habitat and a number *Pelias schemakhensis* needs to be included in the Red List of IUCN and Red Data Book of Azerbaijan with the category of status of CR Blab (i, ii, iii, iv, v). For today the species is indicated in the the Red Book of Republic Azerbaijan (2013) as VU as *Pelias renardii*.

***Pelias shemakhensis kakhetiensis* Tuniyev, Iremashvili, Petrova et Kravchenko, 2018** (Fig. 147)

Type territory. Vicinity of village Dedoplistskaro, Fortress Khornabudji, Shirak Plateau (Kakhetia, East Georgia). From original description.

Type specimens. Holotype: Herpetological collection of the Sochi National Park, Sochi, SNP No 1059 (adult male); paratypes: 6 specimens, SNP No 1052 (4 juv.), No 1053 (2 specimens, adult male and adult female).

Distribution. Distribution of the species in Georgia covers the peripheral areas Shirak Plateau in two neighboring regions – vicinity of village Chinkani and village Zemo Kedi; in vicinity of village Dedoplistskaro near Khornabudji Fortress, also known as the Fortress of Queen Tamar; at north foot of mountain Artsivis Kheoba. In the collection of the State Museum of Georgia, there is specimen from vicinity of village Norio (No. 125, year 1933, unnamed collector), which represents the western limit of the distribution of the species in Georgia.

Both surviving fragment of its former distribution area in Georgia and Azerbaijan are clearly the relic.

Habitats. As well in Azerbaijan, the biotopes of species are presented by shibliaks of *Paliurus spinachristy* and ecotones of dry *Andropogon* steppes and derivatives of the broad-leaved forests on the stony slopes of foothills of Shirak Plateau in East Georgia, since the entire central part of Shirak Plateau are opened and used for the cultivation of crops. By other words, in East Georgia the vipers penetrated now from steppes habitats into the biotopes unusual for them or to areas of the broad-leaved forests. Extreme variant of their degradation is a *Paliurus shibliak*. In addition to ploughing of Shirak Plateau, it should be indicated a high anthropogenic press from grazing on the edge parts of not ploughing area of the Plateau.

Conservation status. We require status category CR B1ab (i, ii, iii, iv, v) for inclusion in the Red List of IUCN.

Genus True vipers – *Vipera* Laurenti, 1768

Vipera Laurenti, 1768, Specimen Medicum, Exhibens Synopsis Reptilium Emendatam cum Experimentis circa Venena et Antidota Reptilium Austriacorum, quod Autoritate et Consensu. Viennae, Joan. Thom. Trattner: 99(1–214).

Type species. *Vipera francisci redi* Laurenti, 1768 (= *Coluber aspis* Linnaeus, 1758) (designated by Fitzinger, 1843). The valid name is *Vipera aspis* (Linnaeus, 1758) [*Vipera aspis francisciredi* (Laurenti, 1768)].

Middle-sized snakes of body length up to 1300 mm, including a tail. The head is covered on top by plicate scales. Only large supraorbital scutes are notable. The nasal and naso-intermaxillary scales are divided. The snout tip is bent upwards and, in some species, protruded as a soft protuberance covered by small scales. There are two rows of scales between an eye and the supralabial scales. The ventral scales are 131–165, subcaudal scales 22–42 pairs, supralabial 9–10. The anal scute is whole. There are 21–23 scales around the middle of the body.

The genus *Vipera* sensu stricto comprises 5 species known from North Africa and South Europe: *Vipera ammodytes* (Linnaeus, 1758) – north-eastern Italy, southern Slovakia, western Hungary, Slovenia, Croatia, Bosnia and Herzegovina, Serbia, Montenegro, Albania, Greece (including Macedonia and the Kiklady Archipelago), Romania, Bulgaria, Turkey and Syria; *V. aspis* (Linnaeus, 1758) – France, Andorra, north-eastern Spain, south-western Germany, Switzerland, Monaco, Elba and Montecristo islands, Italy with Sicily, San Marino and Slovenia; *V. transcaucasiana* (Boulenger, 1913) – north-eastern Anatolia and the Transcaucasus; *V. latastei* Bosca, 1878 – south-western Europe (France, Portugal and Spain) and North-West Africa (Morocco, Algeria and Tunisia); *V. monticola* Saint-Girons, 1954 – Atlas Mts. (Ananjeva et al., 2006; Brodmann, 1987; David, Ineich, 1999; Golay et al., 1993 Heckes et al., 2005; Joger, 1984; Joger, Stümpel, 2005; Klemmer, 1963; McDiarmid et al., 1999; Nilson et al., 1999b; Welch, 1983). Fossil remains are known from the Upper Sarmat in eastern Georgia [(Rustavi (=Yagljudja)] (Zerova et al., 1987).

The Caucasus is inhabited by one species of the genus, *Vipera transcaucasiana*, which was formerly considered as the subspecies *Vipera ammodytes transcaucasiana* (Linnaeus, 1758).

Transcaucasian long-nosed viper – *Vipera transcaucasiana* (Boulenger, 1913) (Fig. 148)

Vipera ammodytes transcaucasiana Boulenger, 1913, On the geographical races of *Vipera ammodytes*. Ann. Mag. Nat. Hist., 8: 284, pl. 5 (283–287).

Terra typica. “Borzom, in the district Gori, Province Tiflis” [Borzom, Georgia].



Map 46. Distribution map of *Vipera transcaucasiana*.

Type specimens. Three syntypes – BMNH 1913.10.30.1; MGT (National Museum of Georgia, Tbilisi, former Caucasian Museum – two syntypes lost).

Distribution. This viper occurs in the Lesser Caucasus in Turkey and Georgia along the Black Sea: from the Bosphorus in Istanbul in the west to the Georgian border in Artvin in the east. From the coastal provinces Düzce, Sinop, Giresun, Trabzon and Rize no records are known. Inland the species occurs southwards at least as far as 39°54'N in the province of Sivas. In Georgia it inhabits Meskhedsky and Trialetsky mountain ranges and the ravine of the upper current of Kura River up to the vicinity of the town Akhalkalaki in the south-west. Other southern records are from the provinces of Bursa and Ankara. Turkey. Information about species distribution

to the Bosphorus Strait in the west and the Konya Province in the south needs verification (Nilson et al., 1988). Given the photograph of *V. transcaucasiana* provided in Tok and Kumlutas (1996), these individuals from Pershembe (Ordu Province, Black Sea coast, northern Turkey) differ from typical Transcaucasian long-nosed vipers by their coloration patterns. Until recently, *V. transcaucasiana* had been considered as *Vipera amodytes* (Linnaeus, 1758) with 5 subspecies.

Distribution in the Caucasus. In Georgia, vipers live in the Meskheti and Trialeti Ridges, eastern parts of the Adjara-Imereti Ridge and the canyon in the upper Kura River south-eastwards to Akhalkalaki (Map 46). Collections of Zoological Institute, RAS contain three individuals from western Azerbaijan (northern slopes of



Fig. 148. Transcaucasian long-nosed viper, *Vipera transcaucasiana* – Kojori, Georgia.

the Lesser Caucasus, near Gyanja). Armenia is sometimes indicated as included within the distribution, but no convincing proof is known. Supposedly Azerbaijan-originated records of specimens stored in Zoological Institute, Russian Academy of Sciences (Ananjeva et al., 2006) need confirmation (Tuniyev et al., 2009; Mulder, 2017). This species is also known from the Artvin Province in Turkey (Artvin, Ardanuç, Borçka).

Habitats. Vipers live in xerophytic montane forests, preferring the stony slopes covered by oakeries, *Ostrya* sp., *Pinus kochiana* and *Carpinus orientalis*. They often occur in forest glades, screes covered by lichens and rocky outcrops in riversides. They move up to 1700 m asl. The vipers were noted in the fir-spruce belt of the valley of the Chorokh River with Ormanly-Koy (Artvin hollow), in the oak forest among the large boulders in the lower part of the gorge of the Murgul River, in the tract of Dereichi with Karshiky (vicin-

ity of Muratly Villege) and in the gorge of the Harshit River in the vicinity of Gyumushkhane town. All findings are associated with the forest biotopes and their derivatives on the spurs of the Pontic and Shavsetian mountain ranges (Tuniyev et al., 2014).

Conservation status. At the workshop on IUCN assessment of Palearctic reptiles and amphibians in Antalya, Turkey in September 2008, its status was designated as NT. According to the Red Data Book of the USSR (1984), total population size was estimated around 10000 individuals. The main threat is agricultural use of viper habitats. The species was included in the Red Data Books of the Georgian SSR (1982) without IUCN categories.

The Transcaucasian long-nosed viper is protected in Bojomi-Kharagauli National Park. The establishment of protected areas in high-density areas on the Meskheta and Trialeti ridges is pending.

Chapter 4.

TAXONOMIC DIVERSITY OF SNAKES IN THE CAUCASUS

Changing views on the number of snake species living in the Caucasus

We have analyzed the changes in the ideas on the taxonomic diversity of snake species in the Caucasus during the past 100 years, beginning from the first monograph by A.M. Nikolsky (1913) dedicated to the Caucasus. The field guides by Terentjev and Chernov (1949) and Bannikov et al. (1977) with extractions about the Caucasian snakes (within the USSR), the latest monographs by Szczerbak (2003), Ananjeva et al. (2006), Tuniyev et al. (2009) and information provided in this book were used as the input for subsequent comparative analysis (Table 1).

A.M. Nikolsky (1913) described 29 species of snakes from materials of the Caucasian Museum. He considered the Caucasus in its broadest geographical meaning, including the Aralykh Steppes, and indicated also the questionable species such as *Coluber leopardinus*, *Zamenis ventrimaculatus* and *Pseudocerastes persicus*. So, Nikolsky's list of snakes comprised the following species (their modern names are given in parentheses): *Typhlops vermicularis* (*Xerotyphlops vermicularis*), *Eryx jaculus*, *Eryx miliaris*, *Tropidonotus* (= *Natrix*) *natrix*, *Tropidonotus tessellatus* (= *Natrix tessellata*), *Zamenis gemonensis* (= *Dolichophis caspius*), *Zamenis dahli* (= *Platyceps najadum*), *Zamenis ventrimaculatus* (= *Platyceps ventromaculatus*), *Zamenis* (= *Hemorrhoids*) *ravergieri*, *Coluber* (= *Elaphe*) *dione*, *Coluber quatuorlineatus* (= *Elaphe sauromates*), *Coluber* (= *Zamenis*) *hohenackeri*, *Coluber leopardinus* (= *Zamenis situla*), *Coluber longissimus* (= *Zamenis longissimus*), *Coronella austriaca*, *Contia* (= *Eirenis*) *collaris*, *Contia* (= *Eirenis*) *modesta*, *Contia schelkovnikovi* (= *Eirenis punctatolineatus*), *Contia satunini* (= *Rhynchocalamus satunini*), *Tarbophis iberus* (= *Telescopus fallax iberus*), *Coelepeltes monspessulana* (= *Malpolon insignitus*), *Vipera renardi* (= *Pelias*

renardi), *Vipera berus dinniki* (= *Pelias dinniki*), *Vipera* (= *Pelias*) *kaznakovi*, *Vipera ammodytes* (= *Vipera transcaucasiana*), *Vipera* (= *Montivipera*) *raddei*, *Vipera* (= *Macrovipera*) *lebetina*, *Pseudocerastes persicus* and *Ancistrodon halys* (= *Gloydus caucasicus*).

The field guide published by P.V. Terentjev and S.A. Chernov (1949) provided information about 27 species of snakes: *Typhlops vermiculatus* (= *Xerotyphlops vermiculatus*), *Eryx jaculus*, *Eryx miliaris*, *Natrix natrix*, *Natrix tessellata*, *Coluber jugularis* (= *Dolichophis caspius*), *Coluber* (= *Platyceps*) *najadum*, *Coluber* (= *Hemorrhoids*) *ravergieri*, *Elaphe* (= *Zamenis*) *situla*, *Elaphe* (= *Zamenis*) *hohenackeri*, *Elaphe longissima* (= *Zamenis longissimus*), *Elaphe quatuorlineata* (= *E. sauromates*), *Elaphe dione*, *Coronella austriaca*, *Oligodon* (= *Rhynchocalamus*) *melanocephalus* (= *R. satunini*), *Contia* (= *Eirenis*) *collaris*, *Contia* (= *Eirenis*) *punctatolineatus*, *Contia* (= *Eirenis*) *modestus*, *Tarbophis* (= *Telescopus*) *fallax*, *Malpolon monspessulamus* (= *M. insignitus*), *Vipera ursinii* (= *Pelias renardi*), *Vipera* (= *Pelias*) *kaznakovi* (*kaznakovi*), *Vipera ammodytes* (= *Vipera transcaucasiana*), *Vipera* (= *Montivipera*) *raddei*, *Vipera* (= *Macrovipera*) *lebetina* and *Ancistrodon halys* (= *Gloydus caucasicus*). The Persian horned viper (*Pseudocerastes persicus*) was pointed out as definitely absent in the USSR and western Turkey.

The field guide by Bannikov et al. (1977) which was published more than 30 years later listed 27 species of snakes occurring in the Caucasian part of the USSR: *Typhlops vermiculatus* (= *Xerotyphlops vermiculatus*), *Eryx jaculus*, *Eryx miliaris*, *Natrix natrix*, *Natrix tessellata*, *Coluber* (= *Platyceps*) *najadum*, *Coluber jugularis* (= *Dolichophis caspius*), *Coluber* (= *Hemorrhoids*) *ravergieri*, *Elaphe* (= *Zamenis*) *situla*, *Elaphe* (= *Zamenis*) *hohenackeri*, *Elaphe longissima* (= *Zamenis longissimus*), *Elaphe quatuorlineata* (= *E. sauromates*), *Elaphe dione*, *Eirenis collaris*, *Eirenis punctatolineatus*, *Eirenis modestus*, *Coronella austriaca*, *Rhynchocalamus melanocephalus* (= *R. satunini*), *Telescopus fallax*, *Psammophis lineolatum*, *Malpolon*

monspeulamus (= *M. insignitus*), *Vipera ursinii* (= *Pelias renardi*), *Vipera* (= *Pelias*) *kaznakovi* (= *kaznakovi*), *Vipera ammodytes* (= *Vipera transcaucasiana*), *Vipera xanthina* (= *Montivipera raddei*), *Vipera* (= *Macrovipera*) *lebetina* and *Agkistrodon halys* (= *Gloydus caucasicus*). Compared to Terentjev and Chernov (1949), the authors added one genus and species *Psammophis lineolatum* (Darevsky, 1959) and removed the disputable Persian horned viper (*Pseudocerastes persicus*).

In the beginning of the 21st century, several reviews of the herpetofauna of the East Palearctic (Szczerbak, 2003) and Northern Eurasia (Ananjeva et al., 2006) were published which summarized the results of the long-term research of reptiles of the Soviet Union, including the Caucasus. According to Szczerbak (2003), 33 snake species belonging to 14 genera occur in the Caucasus. Ananjeva et al. (2006) consider 37 species and 16 genera in the Caucasus (Table 1, Fig. 149).

Table 1. Number of genera and species of the snakes of the Caucasus (species number in brackets) at different stages of the Caucasian herpetological research

Nikolsky, 1913	Terentyev and Chernov, 1949	Bannikov et al., 1977	Szczerbak, 2003	Ananjeva et al., 2006	Tuniyev et al., 2009	Present monograph
Typhlopidae						
<i>Typhlops</i> (1)	<i>Typhlops</i> (1)	<i>Typhlops</i> (1)	<i>Typhlops</i> (1)	<i>Typhlops</i> (1)	<i>Typhlops</i> (1)	<i>Xerotyphlops</i> (1)
Boidae						
<i>Eryx</i> (2)	<i>Eryx</i> (2)	<i>Eryx</i> (2)	<i>Eryx</i> (2)	<i>Eryx</i> (2)	<i>Eryx</i> (2)	<i>Eryx</i> (2)
Colubridae						
<i>Tropidonotus</i> (2) <i>Zamenis</i> (4) <i>Coluber</i> (5) <i>Coronella</i> (1) <i>Contia</i> (4) <i>Tarbophis</i> (1) <i>Coeleptelis</i> (1)	<i>Natrix</i> (2) <i>Coluber</i> (3) <i>Elaphe</i> (5) <i>Coronella</i> (1) <i>Oligodon</i> (1) <i>Contia</i> (3) <i>Tarbophis</i> (1) <i>Malpolon</i> (1)	<i>Natrix</i> (2) <i>Coluber</i> (3) <i>Elaphe</i> (5) <i>Coronella</i> (1) <i>Rhynchocalamus</i> (1) <i>Eirenis</i> (3) <i>Telescopus</i> (1) <i>Pseudocyclophis</i> (1) <i>Psammophis</i> (1) <i>Malpolon</i> (1)	<i>Natrix</i> (3) <i>Coluber</i> (5) <i>Elaphe</i> (5) <i>Coronella</i> (1) <i>Rhynchocalamus</i> (1) <i>Eirenis</i> (3) <i>Telescopus</i> (1) <i>Pseudocyclophis</i> (1) <i>Psammophis</i> (1) <i>Malpolon</i> (1)	<i>Natrix</i> (3) <i>Coluber</i> (3) <i>Coronella</i> (1) <i>Eirenis</i> (3) <i>Elaphe</i> (5) <i>Hierophis</i> (2) <i>Malpolon</i> (1) <i>Psammophis</i> (1) <i>Pseudocyclophis</i> (1) <i>Rhynchocalamus</i> (1) <i>Telescopus</i> (1)	<i>Natrix</i> (3) <i>Hemorrois</i> (2) <i>Hierophis</i> (2) <i>Platyceps</i> (1) <i>Coronella</i> (1) <i>Eirenis</i> (3) <i>Elaphe</i> (2) <i>Zamenis</i> (4) <i>Malpolon</i> (1) <i>Psammophis</i> (1) <i>Pseudocyclophis</i> (1) <i>Rhynchocalamus</i> (1) <i>Telescopus</i> (1)	<i>Natrix</i> (3) <i>Dolichophis</i> (2) <i>Hemorrois</i> (2) <i>Platyceps</i> (1) <i>Coronella</i> (1) <i>Eirenis</i> (4) <i>Elaphe</i> (2) <i>Zamenis</i> (3) <i>Rhynchocalamus</i> (1) <i>Telescopus</i> (1)
Number of genera (species) 7 (18)	Number of genera (species) 8 (17)	Number of genera (species) 9 (18)	Number of genera (species) 10 (22)	Number of genera (species) 11 (22)	Number of genera (species) 13 (23)	Number of genera (species) 10 (20)
Lamprophiidae						
----	----	----	----	----	----	<i>Malpolon</i> (1) <i>Psammophis</i> (1)
						Number of genera (species) 2 (2)
Viperidae						
<i>Vipera</i> (6) <i>Pseudocerastes</i> (1) <i>Ancistrodon</i> (1)	<i>Vipera</i> (5) <i>Pseudocerastes</i> (1) <i>Ancistrodon</i> -1	<i>Vipera</i> (5) <i>Ancistrodon</i> (1)	<i>Vipera</i> (7) <i>Agkistrodon</i> (1)	<i>Vipera</i> (10) <i>Macrovipera</i> (1) <i>Gloydus</i> (1)	<i>Macrovipera</i> (1) <i>Montivipera</i> (3) <i>Pelias</i> (11) <i>Vipera</i> (1) <i>Gloydus</i> (1)	<i>Macrovipera</i> (1) <i>Montivipera</i> (3) <i>Pelias</i> (13) <i>Vipera</i> (1) <i>Gloydus</i> (1)
Number of genera (species) 3 (8)	Number of genera (species) 3 (7)	Number of genera (species) 2 (6)	Number of genera (species) 2 (8)	Number of genera (species) 3 (12)	Number of genera (species) 5 (17)	Number of genera (species) 5 (19)
Total number of genera (species) of snakes of the Caucasian Ecoregion						
12 (29)	13 (27)	13 (27)	14 (33)	16 (37)	20 (43)	19 (44)

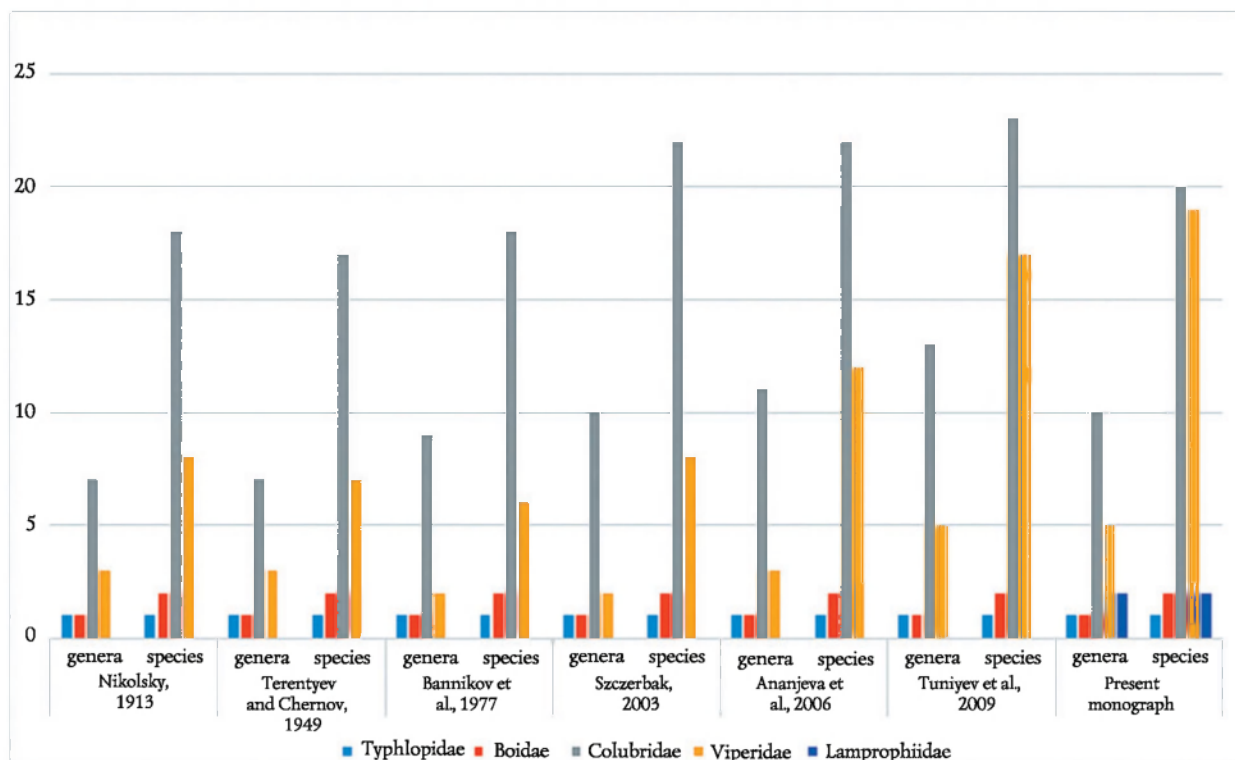


Fig. 149. Changes in the knowledge on taxonomic diversity of the Caucasian snakes in the past 100 years.

The monograph specially devoted to the snakes of the Caucasus (Tuniyev et al., 2009) includes 43 species, 20 genera and 4 families. The present book incorporates information about 44 species of snakes from 19 genera and 5 families.

Taxonomic diversity of the ophidiofauna of the Caucasus

The analysis of taxonomic diversity of the Caucasian snakes shows that new records, phylogenetic studies and taxonomic revisions have led to a significant change in the numbers of genera and species over the past 100 years. All snake species occurring in the Caucasus were related to the four families: Typhlopidae, Boidae, Colubridae and Viperidae until the new results of study of the phylogeny of advanced snakes (Colubroidea) (Pyron et al., 2010) with resurrection of one more family Lamprophiidae Fitzinger, 1843 in particular with genera *Malpolon* and *Psammophis* for the Caucasian herpetofauna.

Some authors earlier considered the genus *Gloydus* (= *Agkistrodon*) as part of the separate family Crotalidae (Terentyev, Chernov, 1949; Bannikov et al., 1977; Szc-

zerbak, 2003) but now most of sources assigned it to the subfamily Crotalinae within the family Viperidae (Nikolsky, 1913; Ananjeva et al., 2006; Tuniyev et al., 2009; Arakelyan et al., 2010; Sindaco et al., 2013; Van Wallach et al., 2014; Uetz et al. 2017). The latter point of view was confirmed by recent phylogenetic research (Vidal, Hedges, 2002, 2005; Kelly et al., 2003; Vidal et al., 2007) and accepted in basic reviews of snake fauna and evolution (Greene, 1997; McDiarmid et al., 1999; Uetz et al. 2017).

Taxonomic changes affected the snake families in different ways. In all revisions provided above, the numbers of species and genera of blind snakes and boids remained unchanged. Information by Nikolsky (1913), Terentyev and Chernov (1949) and Bannikov et al. (1977) differs very insignificantly (Table 1) because of various views on species diversity and composition of colubrid genera (*Coluber*, *Zamenis* and *Elaphe*), clarification of distribution ranges and removal of debatable species from the list of the Caucasian herpetofauna. For instance, Nikolsky (1913, p. 142) mentioned *Zamenis ventrimaculatus* (= *Platyceps ventrimaculatus*) only from a letter of R.G. Schmidt about a specimen collected near the Arus village, Lenkoran district. Thenceforth, it was never indicated. The species

Pseudocerastes persicus (Dumeril et Bibron, 1854) recorded by Nikolsky (1913, p. 188–189) from the eastern Transcaucasus on the basis of data provided by K.A. Satunin, K.F. Kessler and A.F. Laister had been considered by Terentjev and Chernov (1949, p. 276) as a species definitely unknown in the USSR.

Thereafter, new important records of the steppe ribbon racer (*Psammophis lineolatum*) (Darevsky, 1969; Doronin, 2016) and the Persian dwarf snake (*Eirenis persicus*) (Aghasyan, 1987) have enriched the lists of the Caucasian ophidiofauna and led to quantitative changes in the numbers of species and genera in later reviews (Bannikov et al., 1977; Szczerbak, 2003; Ananjeva et al., 2006; Tuniyev et al., 2009). Due to the disputable record of *Zamenis situla* (Linnaeus, 1758) which never was confirmed this species is removed now from the list of snakes of the Caucasian Ecoregion.

Later on, taxonomic changes were primarily caused by new records and the progress of new ideas on intra-family/intra-generic relationships and on species status of some colubrids and viperids (Nilson et al., 1999a, b; Helfenberger, 2001; Nagi et al., 2003, 2004; Utiger et al., 2002, 2005) which led to nomenclatural changes and increased the number of species and genera in the Caucasian ophidiofauna. For example, the number of colubrid genera and species increased from 7 to 10 and from 17 to 20, respectively (Fig. 149; table 1) due to faunistic records, description of new species in the genera *Natrix* and *Platyceps* and identification of monophyletic lineages within such “collective” genera as *Coluber* and *Elaphe* (Helfenberger, 2001; Utiger et al., 2005). Within the superfamily Colubroidea new families are distinguished (Pyron et al., 2010, Pyron et al., 2013). According these changes the ophidiofauna of the Caucasian herpetofauna includes also the fifth family Lamprophiidae with the subfamily Psammophiinae, to which according to the latest results of the phylogenetic analysis, the genera *Malpolon* and *Psammophis* are referred (Vidal et al., 2007, 2008; Kelly et al., 2008, 2011; Uetz et al., 2017).

The number of viperid genera increased in the past 100 years from 3 to 5 and the number of species soared from 7 to 19, of which 13 are vipers of the genus *Pelias*. The Caucasus has been characterized by an extreme diversity of vipers *Vipera sensu lato* (14 out of approximately 24 species of this genus occur here) and represents the node of taxonomic diversity of the *Pelias* species (13 of 20 known species). Cryptic speciation plays a significant role in the formation of this group.

Tracking the history of research of the *Pelias* vipers in the Caucasus in the past 100 years one can find a trend in description of cryptic species from the Caucasus vipers of *P. kaznakovi*–*Prenardii* species groups (Vedmederja et al., 1986; Orlov, Tuniyev, 1986; Nilson et al., 1995; Tuniyev, Ostrovskikh, 2001; Tuniyev et al., 2012, 2013, 2018a,b). The results of recent phylogenetic research of the Caucasian vipers based on the mitochondrial genome (cytochrome *b*, ND2, 16S) (Kalyabina-Hauf et al., 2004; Murphy et al., 2007; Zinenko et al., 2015, 2016) have demonstrated the polyphyly of the evolutionary lineages of *P. ursinii*, *P. orlovi*, *P. renardi* and *P. dinniki*, making the existence of complexes of cryptic species and/or the hybrid origin of some species quite possible.

The confirmation of the hypothesis about the hybrid origin of *Vipera darevskii* (= *Pelias darevskii*) supposed by N.L. Orlov and B.S. Tuniyev (1986) requires a continuous search for new markers capable of identifying new species of this genus what led to the first interesting results (Zinenko et al., 2016). The fundamental role of hybridization leading to active speciation was demonstrated by I.S. Darevsky (1967) in his classic research of rock lizards, later named after him as genus *Darevskia*. Two groups (*Darevskia* lizards and *Pelias* vipers) are particularly diverse and prone to speciation in the Caucasus Ecoregion due to the process of range insularization in mountain regions (Brown and Lamolino, 1998) where hydrological network and heterogeneity of climate and vegetation patterns create a great patchiness of habitats and contribute to insular speciation. As many species living in the Caucasus Ecoregion have disjunctive ranges, their distribution can be considered as a result of relict insularization. The discovery of a high level of diversity of *Pelias* vipers in the Caucasus has important implications for the assessment of conservation status of rare and narrowly distributed species many of which are recorded on the IUCN Red List of Threatened Species (Table 8).

In the future, we should expect changes in the taxonomic composition of the ophidiofauna because of new records, discovery of new cryptic taxa of vipers and new revisions of taxonomically complicated genera of colubrids and viperids.

Knowledge about biodiversity remains inadequate because most species living on Earth were still not formally described (the Linnean shortfall) and because geographical distributions of most species are poorly understood and usually contain many gaps (the Wallacean shortfall) (Bini et al., 2006).

Chapter 5.

HISTORICAL BIOGEOGRAPHY OF THE CAUCASIAN HERPETOFAUNA

The herpetofauna of the Caucasus is diverse in specific composition and distribution of different zoogeographical groups, largely because of various ages and origin patterns of species ranges. Autochthonous and endemic taxa co-exist with widely distributed species occurring mostly in the European part of the former Soviet Union, Central Asia and the East Mediterranean. In the meantime, a number of Colchic species occur also beyond the western Transcaucasus or, forming the biodiversity hotspot in the Lesser Caucasus, permeate further into Asia Minor. In this context, it is essential to understand the *Colchic*, *Mediterranean*, *Turanian* and *Asia Minor* herpetofaunas and their place in the amphibian and reptile fauna of the Caucasus as a whole.

History of views

Zoogeographical works related to the Caucasus began to appear in the second half of the 19th century. A. Wallace (1876) and later R. Gaake (1896) divided the Caucasian isthmus across the Greater Caucasus and assigned the Ciscaucasus to the European sub-region and the Transcaucasus to the Mediterranean. N.A. Severtsov (1877) considered the whole Greater Caucasus, western Ciscaucasus and western Transcaucasus as parts of the Mediterranean and attributed other parts of the Transcaucasus to the Central Asian region. In practice, this zoning was very close to today's views and confirmed the diversity of the Caucasian fauna.

The most comprehensive description of the heterogenic origin of the Caucasian fauna was made by K.A. Satunin (1906, 1910, 1912, 1916). In 1910, he wrote: *"I still can say very little about the origin of the fauna of the western Transcaucasus. With its evergreen vegetation and poor fauna, this region appeared to me as a part of the Mediterranean per se. There are some endemic species or forms occurring here, but not a single vertebrate not represented along the Mediterranean*

coasts, sometimes even by the same species. Did this fauna arrive from the west or it is a vestige of the fauna which was once distributed throughout the Black Sea region? Current knowledge does not allow answering this question. But even now I can confidently state that this fauna has nothing common with the faunas of other parts of the Caucasus" (p. 142).

In 1912, K.A. Satunin divided the Caucasian isthmus into 5 sub-regions and 11 districts. This work was the first to accurately identify the Colchic area bounded by the Glavnyi (Main) Ridge with the Tuapse River basin in the north, Arsian Ridge in the east and Pontic Ridge in the south. The Rioni riverside and the adjacent slopes of the Glavnyi Ridge were indicated as the kernel of this area. K.A. Satunin noted the poverty of the reptile and amphibian faunas, but stressed the occurrence of some regionally endemic species (*Pelias kaznakovi*, *Bufo verrucosissimus*).

A.M. Nikolsky (1913) viewed all the Caucasus, except for the eastern Transcaucasus, as part of the Mediterranean, but for the lack of information he did not differentiate the forest and alpine belts of the Greater Caucasus.

M.A. Menzbir (1934) put the Caucasus and the Transcaucasus into the Caucasus Sub-Province of the East Mediterranean Province of the Mediterranean Sub-Region of the Palearctic. According to Menzbir, the Caucasus is affected by the Mediterranean and Central Asian faunogenic centres.

I.I. Puzanov (1938) attributed all the Transcaucasus, Greek Archipelago, Asia Minor and mountainous Crimea to the East Mediterranean Province. Northern slopes of the Alborz and Talysh Mts. were set aside as the Hyrcanian Province.

Numerous subsequent works published in the 1940–1960s were based mainly on mammal and bird distribution zoning which placed the Caucasus either in the Mediterranean (Kuznetsov, 1949) or in European broadleaf forests (Rustamov, 1945; Kuznetsov, 1950; Bobrinsky, 1951).

A special emphasis should be made on a classical work "Mammals of the Caucasus" by a great expert in the Caucasian fauna N.K. Vereschagin (1959). Criticising the authors who underestimated the importance of the Mediterranean (which also comprised the Caucasus, as to Vereschagin), he wrote: "*The Mediterranean always had more opportunities for animal and plant colonizations than Sahara or Karakum desert, but its value as an independent and ancient centre of speciation cannot be underestimated. A correct interpretation of the notion "Mediterranean" and, hence, of "Mediterranean fauna" can be achieved only under the complex analysis of natural transformations which took place in the Kainozoic Era within the Mediterranean geosyncline. In the Pliocene and Pleistocene times, the Sarmat Sea extending from Gibraltar to the Caspian Sea broke down repeatedly into the chain of isolated basins which were interconnected during transgressions. The coastlines of the Aral Sea and the northern part of the Caspian Sea dried out early and were excluded from the Mediterranean zonation. Nonetheless, other areas of the coastlines of these Kainozoic basins had inherited some primeval landscapes originated in the Miocene. Therefore, taking into account its paleogeographical background the Mediterranean should be understood as a region spanned between southern Europe (including the south of Ukraine and Crimea), North Africa, Asia Minor, the Caucasus (excluding the Manych Depression and its vicinity), Talysh and Alborz Mts.*" (p. 462).

The interpretation of the term "Mediterranean" by N.K. Vereschagin generally coincided with the boundaries of the floristic Mediterranean delineated by N. Rikli (1946, p. 86), but botanists still continued to argue the biogeographical position of the Caucasus. Earlier, P. Boissie (1867) in his book "Flora Orientalis" attributed the Caucasian forests, northern Anatolia's broadleaf and coniferous forests as well as some parts of European Turkey to the region of Middle Europe. According to him, the Mediterranean region comprises the geographically Mediterranean countries and the southern Crimea.

V.V. Alekhin (1938) and E.V. Wulf (1944) considered the mountainous Crimea and all the Caucasus as parts of the Mediterranean Sub-Region/Province of the former USSR. Close relationships between the Caucasian and Mediterranean communities of the maquis, garigue and phrygana were noted by A.A. Grossheim (1948) and V.P. Maleev (1938, 1941, 1946). T.I. Isachenko and E.M. Lavrenko (1980) did not

agree with this opinion and assigned the Caucasus to the European Broadleaf Forest and Afro-Asian Desert botano-geographical provinces. E.M. Lavrenko (1958, 1965) thought that phytogeographically the Caucasian forests are closely related to the broadleaf forests of Europe, but not of the Mediterranean. Having critically analyzed numerous literature sources, A.L. Takhtajyan (1978) concluded that the Mediterranean Province comprises the foothills of the West Caucasus located between the towns of Anapa, Krasnodar and Tuapse. Other parts of the Caucasus belong to the Euxine and Caucasian provinces of the Boreal Sub-Kingdom and to the Armeno-Iranian, Hyrcanian and Turanian provinces of the Irano-Turanian Region.

K.V. Stanyukovich (1973) assigned the North Caucasus and Transcaucasus to the zone of subtropical mountains. N.K. Vereschagin (1959) surmised that similarity and close relationships between the mammalian complexes of the western Mediterranean and the Caucasus (eastwards to the Talysh Mts. and Alborz Mts.) could be caused by the same period of the origin and formation of highland landscapes. As A.P. Ilyinsky (1937) correctly pointed out, biogeographers often imagine Mediterranean landscapes as those of today's Spain, Sicily or Palestine. Actually, the western and eastern parts of the Mediterranean contain not only xerophytic landscapes of the garigue, phrygana and mountain grasslands, but also relict Tertiary coniferous and broadleaf forests, mesophytic meadows of subalpine and alpine types.

To understand the properties of the herpetofauna of the mesophilic Colchis Lowland and its derivatives, it is necessary to clarify and define Colchic phytolandscapes and the types of vegetation called "Colchic".

Vegetation landscapes of the Colchis were first vividly described by N.M. Albov (1895) who discovered a rare for Russia region of autochthonous limestone flora within a distinct refugium with numerous endemic and relict species and even genera (Fig.150). A.A. Kolakovskiy (1961, 1980) thought that the flora of the Colchis is mainly forest and alpine meadow and its main phytolandscapes exist since ancient times, changing only in composition of edificators and through the extinction of subtropical evergreen forests in foothill zones. Owing to insignificant changes in climate, the Tertiary relict forest mesophilic flora and vegetation are most evident (Kuznetsov, 1891). The Tertiary relict forests of the Colchis have been characterized by an extraordinary abundance and diversity of arboreal and shrub species, lack of dominating species and clear lay-



Fig. 150. Peaks Zhitnaya and Nagoy-Chuk in the Fisht-Oshtensky massif, border of Adygeya and Krasnodar Territory, Russian Federation. Habitats of *Pelias dinniki* and *Coronella austriaca*.

erage (like in tropical forests). From above, the canopy looks scalloped (alike tropical forests) with a very high density of trees, vines and epiphytes and the nearly absent grass cover. These features make the Colchic forest similar to the humid tropical forest (Pavlov, 1948). According to E.N. Sinskaya (1933), forests of the Colchis developed through the main three stages: tropical forest, more diverse and vastly distributed Colchic-like forest, and modern Colchic forest.

The Colchic vegetation encompasses a number of plant communities varying in complexity, composition and ecological features. It can be mixed (polydominant) or presented by a community of only 1–2 species, but the most general and essential property of all Colchic communities is their saturation with Tertiary mesophilic relicts. The area covered by the Colchic vegetation is thermally more or less uniform and corresponding to subtropical climate, but its soils are diverse (Gulisashvili et al., 1975).

I.S. Darevsky (1957a) considered 7 different in their origin groups of species and subspecies in the her-

petofauna of the Transcaucasus, including the Iranian (*Paralaudakia caucasica*, *Trapelus ruderatus*, *Eremias strauchi*, *E. pleskei*, *Trachylepis (Heremites) septemtaeniatus*, *Eumeces schneideri*, *Ablepharus bivittatus*, *Hemorrhois ravergieri*, *Eirenis collaris*, *E. punctatolineatus*, *Rhynchocalamus satunini*, *Macrovipera lebetina*), Asia Minor (*Parvolacerta parva*, *Lacerta strigata*, *Eirenis modestus*, *Zamenis hohenackeri*), European or boreal (*Emys orbicularis*, *Anguis fragilis*, *Coronella austriaca*, *Elaphe sauromates*, *Natrix natrix*), Mediterranean (*Tes-tudo graeca*, *Malpolon insignitus*, *Natrix tessellata*), East Mediterranean (*Mauremys caspica*, *Pseudopus apodus*, *Ophisops elegans*, *Xerotyphlops vermicularis*, *Eryx jaculus*, *Platyceps najadum*, *Natrix natrix persa*), Turanian (*Cyrtopodion caspius*, *Phrynocephalus helioscopus*, *Eremias arguta*, *E. velox*, *Psammophis lineolatus*, *Gloydus caucasicus*) and autochthonous (*Darevskia saxicola*, *D. praticola*, *D. chlorogaster*, *D. derjugini*, *Iranolacerta brandti*, *Lacerta media*, *L. agilis brevicaudata*, *Ablepharus chernovi*, *Hemorrhois nummifer*, *Telescopus fallax iberus*, *Montivipera raddei*, *Vipera transcaucasiana*).

N.N. Scherbak (1984) indicated both xerophytic and mesophilic species of amphibians and reptiles for different speciation centres in the Mediterranean. Their occurrence is possibly linked with the development of altitudinal and ecological zonation of the Mediterranean mountains which, in its turn, differentiated the structure of the Mediterranean fauna. For the Caucasian centre, he pointed out 12 endemic species with 22 taxa of the *Darevskia saxicola* complex, as well as *Mertensiella caucasica*, *Pelodytes caucasicus* and *Pelias kaznakovi*.

Surely, the Caucasus with its several speciation centres belongs to the Mediterranean. Apart from over 25 taxa of the *Darevskia saxicola* complex, here live 5 taxa of *D. derjugini*, 7 taxa of *Lacerta agilis* and many other lacertids (Orlowa, Bischoff, 1984; Bischoff, 1988). Moreover, it holds a significant number of endemic species of amphibians and reptiles. The mesophilic Colchic speciation centre with three small refugia beyond its boundaries is described earlier (Tuniyev, 1990). The presence of the xerophytic faunistic kernel in the Caucasus, which is general for all the East Mediterranean, is particularly important for understanding the modern patterns in amphibian and reptile distribution in the region. This complex has been divided sometimes into the Mediterranean and East Mediterranean groups, depending on the structure of species distribution (Darevsky, 1957a). Composition of the Mediterranean group varies between the authors (Sobolevsky, 1929; Bodenheimer, 1944; Darevsky, 1957a; Anderson, 1968; Alekperov, 1978; Kireev, 1987; Tertyshnikov, 1992 and others). Generally, the following species living in the Caucasus are considered as pertaining to the Mediterranean fauna: *Triturus karelinii*, *Pelophylax ridibundus*, *Mauremys caspica*, *Testudo graeca*, *Ophisops elegans*, *Pseudopus apodus*, *Xerotyphlops vermicularis*, *Eryx jaculus familiaris*, *Natrix natrix persa*, *N. tessellata*, *Platyceps najadum*, *Telescopus fallax iberus* and *Malpolon insignitus*.

Zoogeographical groups of the Herpetofauna of the Caucasus

The amphibian and reptile distribution areas or ranges in the Caucasus have different contours. Investigations and assessment of species distribution, phytolandscape conditions and their anthropogenic

changes have allowed designating the zoogeographical groups of the herpetofauna (Table 2).

Earlier, considering the herpetofauna of the western Transcaucasus (Tuniyev, 1990) we included the species *Triturus karelinii*, *Testudo graeca*, *Lacerta media*, *L. strigata*, *Darevskia praticola*, *Pseudopus apodus*, *Natrix tessellata* and *Platyceps najadum* in the East Mediterranean group. We suggest that *Pelobates syriacus*, *Hyla savignyi*, *Mauremys caspica*, *Ophisops elegans*, *Ablepharus chernovi*, *Cyrtopodion cotschii colchicus*, *Darevskia pontica*, *D. szczyrbaki*, *D. brauneri myuserica*, *D. bithynica tristis*, *D. rudis rudis*, *Xerotyphlops vermicularis*, *Eryx jaculus*, *Natrix natrix persa*, *Zamenis hohenackeri*, *Elaphe sauromates*, *Dolichophis caspius*, *Eirenis modestus*, *Telescopus fallax*, *Malpolon insignitus*, *Macrovipera lebetina*, *Vipera transcaucasiana* and *Pelias orlovi* should also be considered as the Mediterranean species. Despite the wide Ponto-Caspian distribution of *Dolichophis caspius* and *Elaphe sauromates* and the location of range centres of *Zamenis hohenackeri* and *Macrovipera lebetina* in Asia Minor, we think that their inclusion in the Mediterranean group is no less justified than that of *Pseudopus apodus*, *Natrix tessellata* and *Lacerta strigata*. Similarly, *Pelias orlovi* (Tuniyev, Ostroskikh, 2001) described in the north-western Caucasus have the Colchic origin, but ran through the genesis in Mediterranean and Submediterranean landscapes (Fig. 151). The North Anatolian species - *Darevskia bithynica tristis*, *D. rudis rudis*, are also common in the Mediterranean and sub-Mediterranean landscapes (Fig. 151) of the Black Sea coast of Turkey, without going westwards beyond Arhavi city, i.e. without penetrating into Colchis.

The general chorology of the Mediterranean amphibians and reptiles reveals their dispersal routes along the coastlines of the Mediterranean Sea, Balkan Peninsula, southern Crimea and some, predominantly xerophilic, regions of the Caucasus.

Our opinion is that the Colchic group comprises the following taxa: *Ommatotriton ophryticus*, *Lissotriton lantzi*, *Mertensiella caucasica*, *Bufo verrucosissimus*, *Pelodytes caucasicus*, *Darevskia derjugini*, *D. brauneri brauneri*, *D. mixta*, *D. parvula*, *D. adjarica*, *D. clarkorum*, *D. dryada*, *D. rudis bischoffi*, *D. rudis mirabilis*, *D. rudis obscura*, *Lacerta agilis grusinica*, *Natrix megalcephala*, *Zamenis longissimus*, *Pelias kaznakovi*, *P. magnifica*, *P. pontica*, *P. barani*. Below, we describe the arguments towards the designation of this zoogeographical group.

The Hyrcanian group is genetically close to the Colchic one, but its development was shaped

Table 2. Zoogeographical groups of the Caucasian snakes

№	Species	Zoogeographical groups							
		1	2	3	4	5	6	7	8
1	<i>Xerotyphlops vermicularis</i>	+							
2	<i>Eryx jaculus</i>	+							
3	<i>Eryx miliaris</i>							+	
4/5	<i>Platyceps najadum najadum</i> <i>Platyceps najadum albitemporalis</i>	+		+					
6	<i>Hemorrhois nummifer</i>					+			
7	<i>Hemorrhois ravergieri</i>					+			
8	<i>Dolichophis caspius</i>	+							
9	<i>Dolichophis schmidtii</i>					+			
10	<i>Coronella austriaca</i>						+		
11	<i>Eirenis collaris</i>					+			
12	<i>Eirenis modestus</i>	+							
13	<i>Eirenis persicus</i>					+			
14	<i>Eirenis punctatolineatus</i>					+			
15	<i>Elaphe dione</i>								+
16	<i>Elaphe sauromates</i>	+							
17	<i>Zamenis hohenackeri</i>	+							
18	<i>Zamenis longissimus</i>		+						
19	<i>Zamenis persicus</i>			+					
20	<i>Malpolon insignitus</i>	+							
21	<i>Natrix megalcephala</i>		+						
22/23	<i>Natrix natrix persa</i> <i>Natrix natrix scutata</i>	+					+		
24	<i>Natrix tessellata</i>	+							
25	<i>Psammophis lineolatus</i>							+	
26	<i>Rhynchocalamus satunini</i>					+			
27	<i>Telescopus fallax iberus</i>	+							
28	<i>Gloydus caucasicus</i>			+					
29	<i>Macrovipera lebetina</i>	+							
30	<i>Montivipera albicornuta</i>					+			
31	<i>Montivipera raddei</i>					+			
32	<i>Montivipera wagneri</i>					+			
33	<i>Pelias barani</i>		+						
34/35/ 36	<i>Pelias darevskii darevskii</i> <i>Pelias darevskii uzumorum</i> <i>Pelias darevskii kumlutasi</i>				+				
37	<i>Pelias dimniki</i>				+				
38	<i>Pelias ebneri</i>					+			
39	<i>Pelias eriwanensis</i>				+				
40	<i>Pelias kaznakovi</i>		+						
41	<i>Pelias lotievi</i>				+				
42	<i>Pelias magnifica</i>		+						
43	<i>Pelias olguni</i>				+				
44	<i>Pelias orlovi</i>	+							
45	<i>Pelias pontica</i>		+						
46	<i>Pelias renardi</i>						+		
47/48	<i>Pelias shemakhensis shemakhensis</i> <i>Pelias shemakhensis kakhetiensis</i>				+				
49	<i>Vipera transcaucasiana</i>	+							
	Total	14	6	3	6	11	3	2	1

Notes: 1 — East-Mediterranean species; 2 — Colchic species; 3 — Hyrcanian species; 4 — Caucasian species; 5 — Asia Minor species; 6 — European species; 7 — Turanian species; 8 — Palearctic species

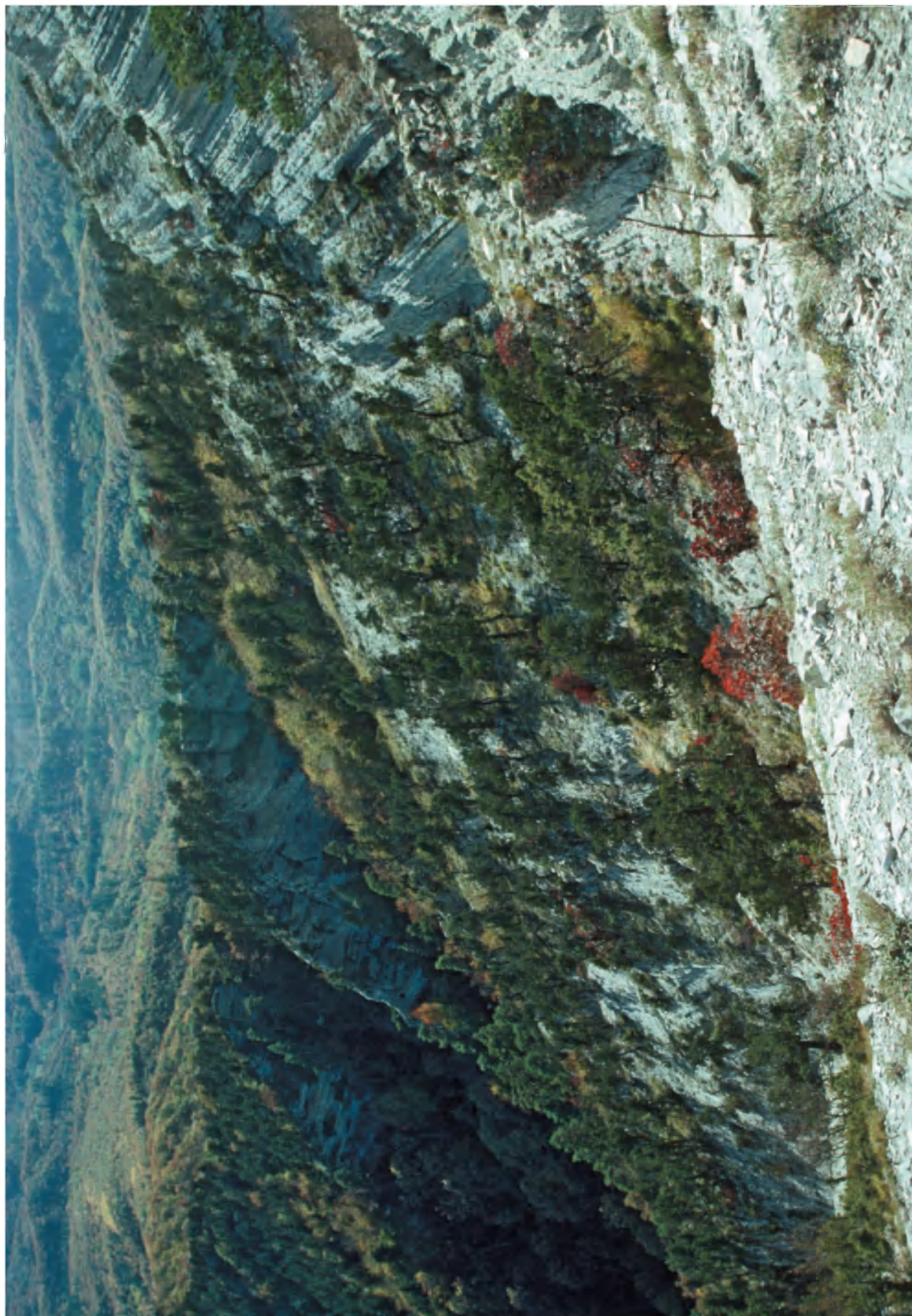


Fig. 151. Mt. Papay, Krasnodar Territory, Russian Federation. Type territory of *Pelias orlovi*.

under the strong influence of more xeromorphic conditions of the Talysh and Alborz Mts. and generally of East Asia. In the Hyrcanian group, we include the species *Bufo eichwaldi*, *Rana macrocnemis pseudodalmatina*, *Darevskia chlorogaster*, *D. praticola hyrcanica*, *Zamenis persicus*, *Platyceps najadum albitemporalis*, *Gloydus caucasicus* and the Iranian species *Batrachuperus persicus* and *B. gorganensis*. Distribution of these species is associated with mesophilic Tertiary relict forests of the northern slopes of the Alborz Mts., with further impoverishment of specific compositions in the Talysh Mts. and the eastern Alborz (Figs. 152, 153).

A number of species geographically confined to the Greater Caucasus (with some irradiations in the Transcaucasus) (Figs. 154, 155) are lumped by us into the Caucasian zoogeographical group (*Rana macrocnemis*, *Hyla orientalis*, *Darevskia saxicola*, *D. alpina*, *D. caucasica*, *D. daghestanica*, *D. rudis chechenica*,

D. rudis svanetica, *Lacerta agilis boemica*, *L. a. iorensis*, *L.a.mzymtensis*, *Pelias dinniki*, *P lotievi*, *P shemakhenisis*). These taxa can be split into two sub-groups: mesophilic West Caucasian and hemixerophilic East Caucasian (*Darevskia daghestanica*, *Lacerta agilis boemica*, *L. a. iorensis*, *Pelias lotievi*, *Pelias shemakhenisis*). The latter sub-group is closely linked with the Asia Minor mountain steppe group represented by *Lacerta agilis brevicaudata*, *Darevskia armeniaca*, *D. unisexualis*, *D. valentini*, *D. praticola loriensis*, *Pelias darevskii*, *P eriwanensis*, *P olguni*, *Rana camerani* and the Lesser Caucasus group of forest species (*D. dahli*, *D. rudis macromaculata*, *D. portschinskii*, *D. rostombekovi*).

The Asia Minor group of species is quite representative in the Caucasus. It is diverse and divided by us into four sub-groups in relation to distribution patterns and altitudinal aspects. Representatives of two sub-groups occur in the Caucasus Ecoregion.



Fig. 152. Talysh Mountains, Hyrcanic forest, Azerbaijan. Habitats of *Zamenis persicus* and *Coronella austriaca*. Photo by Artem Kidov.



Fig. 153. Talysh Mountains, broad-leaved forest, Azerbaijan. Habitats of *Gloydus caucasicus*, *Zamenis persicus*, *Coronella austriaca*. Photo by Artem Kidov.

The species of the Iranian sub-group originated from the mountains of Asia Minor and are currently distributed from eastern Anatolia and the Armenian Highland to the Iranian Highland, with some irradiations into the arid and semiarid regions of the Middle East, eastern Transcaucasus and Dagestan in the north (Figs. 156, 157). This sub-group encompasses such species as *Paralaudakia caucasia*, *Phrynocephalus persicus*, *Eumeces schneideri*, *Heremites septemtaeniatus*, *Eremias strauchi*, *Darevskia raddei chaldorandensis*, *Hemorrhoids ravergeri*, *Montivipera albicornuta* and *Eirenis persicus*.

The Armenian Highland sub-group is composed of *Phrynocephalus horvathi*, *Eremias pleskei*, *Iranolacerta brandti*, *Darevskia raddei*, *D. nairensis*, *D. uzzelli*, *Parvolacerta parva*, *Ablepharus bivittatus*, *Hemorrhoids nummifer*, *Eirenis collaris*, *E. punctatolineatus*, *Rhynchocalamus satunini* and *Montivipera raddei*. In the Irano-Turkish part they are joined by *Neurergus crocatus*, *N. microspilotus*, *Salamandra salamandra semenovi* and *Montivipera wagneri*.

The proper Turanian group includes *Phrynocephalus mystaceus*, *Ph. guttatus*, *Trapelus sanguinolentus*, *Cyrtopodion caspius*, *C. russowi*, *Ablepharus pannonicus*, *Eremias velox*, *E. arguta*, *Eryx miliaris* and *Psammophis lineolatum*.

Only one polymorphic species, *Elaphe dione*, which is widespread from southern Ukraine to the Far East is assigned to the East Palearctic group.

The so called "European" zoogeographical group is possibly the most factitious set of species. We have provisionally put *Bifotes viridis*, *Pelophylax ridibundus*, *Emys orbicularis*, *Anguis fragilis*, *Lacerta agilis exigua*, *Natrix natrix scutata*, *Coronella austriaca* and *Pelias renardi* into this group. This composition includes both mesophilic species widespread in Europe (*P. ridibundus*, *E. orbicularis*, *A. fragilis*, *C. austriaca*) and steppe-dwelling species. Some authors assign *Pelophylax ridibundus* and *Emys orbicularis* to the Mediterranean or Euro-Mediterranean group. On the other hand, the Caucasus has been considered as the region of the origin and, then, the main Pleistocene refugium for *Lacerta agilis*,



Fig. 154. Lake Bezmolviya (Lake of Silence), Karachay-Cherkessya, Russian Federation. The upper limit of the distribution of *Coronella austriaca*.



Fig. 155. Adyl-Su Gorge, Elbrus region, Kabardino-Balkaria, Russian Federation. Habitats of *Pelias lotievi*, *P. dinniki*, *Coronella austriaca*.



Fig. 156. Wormwood steppe in the vicinity of Kayakent, Dagestan, Russian Federation. Habitats of *Eirenis collaris*, *Telescopus fallax*, *Xerotyphlops vermicularis*.



Fig. 157. View of the Khosrov Reserve; in the foreground is the Horovansky Sands, Armenia. Habitats of *Eryx jaculus*, *Malpolon insignitus*, *Hemorrhois nummifer*, *Macrovipera lebetina*.

Pelias renardi, *Anguis fragilis* and *Coronella austriaca*. Wide modern distribution of the last two reptiles in the Caucasian isthmus possibly proves the correctness of their inclusion in the Caucasian (or Euro-Caucasian) group. Moreover, extant fossil records indicate the long-term persistence of *Pelophylax ridibundus* and *Emys orbicularis* in the Caucasus, likely because of their autochthonous nature in the region.

Geographical variation leading to the development of a big number of subspecies is most common in representatives of the Colchic and Caucasian groups. These are the classical examples of lizards: *Darevskia saxicola s.l.*, *D. derjugini*, *D. rudis* and others. In the meantime, members of the Mediterranean group have low variability and, apart from a few exceptions, they do not form discrete geographical subspecies.

This review of the zoogeographical groups of the herpetofauna of the Caucasus would be incomplete without a consideration of the altitudinal distribution of species. As generally known, in mountains and particularly in the Caucasus some altitudinal and ecologi-

cal zones can permeate, interchange or be absent depending upon the factors of slope declivity, exposure, lithologic composition or other features. Ignoring these exceptions, we can present the general patterns. In the West Caucasus, the lowest gradient (up to 200–400 m above sea level) (Fig. 158) is inhabited by species of the Mediterranean group, then at higher elevations they are substituted by Colchic and Caucasian species. There is a single representative of the European group living in each altitudinal gradient (Fig. 159). In the central Caucasus, the lowest gradient (up to 800 m asl) (Fig. 160) is occupied by members of the European group and then, at upper heights, by Caucasian species. Colchic species are almost absent. In the East Caucasus, Mediterranean species with some additions of Asia Minor and Turanian species live in the lowest gradients. Caucasian species appear at higher elevations (Fig. 161), but then are replaced by the impoverished Mediterranean group. The upper zones of the East Caucasus (Fig. 162) are inhabited by representatives of the Caucasian and European groups.



Fig. 158. Cape Bolshoy Utrish, Krasnodar Territory, Russian Federation. Habitats of *Dolichophis caspius*, *Zamenis longissimus*, *Platyceps najadum*, *Elaphe sauromates*, *Natrix tessellata*, *Natrix natrix*.



Fig. 159. Sofia Falls, Karachay-Cherkessia, Russian Federation. Habitats of *Pelias dinniki*, *Coronella austriaca*.



Fig. 160. Sand dune in the Chervlenye Buruny, Dagestan, Russian Federation. Habitats of *Eryx miliaris nogaiorum*, *Dolichophis caspius*.



Fig. 161. Avar-Koisu River valley, Dagestan, Russian Federation. Habitats of *Eirenis modestus*, *Natrix natrix*, *Pelias lotievi*, *Platyceps najadum*.



Fig. 162. Gunib Plateau, Dagestan, Russian Federation. Habitats of *Coronella austriaca*, *Natrix natrix persa*, *Pelias lotievi*.



Fig.163. Zuvand, Azerbaijan. Potential habitat of *Pelias ebneri*. Photo by Artem Kidov.

In the eastern Transcaucasus, plains and foothills are significantly enriched by Turanian species which are substituted by Mediterranean and Asia Minor species at higher elevations. Middle heights and mountain tops are inhabited by Asia Minor and Armenian Highland species.

In the Talysh Mts. local herpetofauna is composed by Hyrcanian species in the foothills and Asia Minor and Mediterranean species at middle elevations (Fig. 163).

Mesophilic Refugia of the Caucasus

Mesophilic refugia of the Caucasus have been comprehensively described in botanical literature, but are mentioned by zoologists only in relation to the Pleistocene events. I.S. Daversky (1957a) did not designate the Colchis as a speciation centre. N.N. Scherbak (1981) included the Colchis in the Caucasian district of

the Mediterranean Province and did not specify it as an independent kernel of herpetofauna origin.

The herpetofauna of the Colchis is surprisingly poor in spite of its uniqueness and is marked by differences between the south-eastern and north-western parts of the Colchis. For example, the western slopes of the Adjaro-Imereti, Shavsheti and Lazistan (Pontic) ridges are inhabited by *Mertensiella caucasica*, *Darevskia clarkorum*, *D. parvula* (incl. *D. adjarica*), *D. mixta*, *D. dryada*, *Pelias pontica*, *P. barani* and *P. davevskii* which are associated with forests and subalpine meadows growing on acidic soils underlain by volcanic rocks (Tuniyev, 1990). Alike the floristic endemics of this part of the Colchis (*Rhododendron unguernii*, *R. smirnowi*, *Osmanthus decorus*, *Betula medwedewii*, *Epigaea gaultherioides* and others), these amphibians and reptiles have been the Adjaro-Lazistan endemics with some slight irradiations into the adjoining areas, but are not the proper Colchic endemics per se. The lizards *Darevskia brauneri* and *Lacerta agilis grusinica* are widespread in the northwestern Colchis



Fig. 164. The Kamennyi Klad Ridge, Abkhazia. Habitats of *Pelias dinniki* and *Coronella austriaca*.

(Fig. 164) but are absent in its central and southeastern parts. These reptiles and floristic endemics (*Allium candolleianum*, *Campanula mirabilis*, *C. bzybica*, *C. calcarea*, *C. jadvigae*, *Genista abchasica*, *Gentiana paradoxa*, *Omphalodes kusnetzovii* and others) have been the north Colchic endemics. Out of 450 plant taxa endemic for the Colchis, 83 (i.e. 25%) are north Colchic endemics (Adzinba, 1980).

The proper Colchic endemics are *Ommatotriton ophryticus*, *Lissotriton lantzi*, *Bufo verrucosissimus*, *Pelodytes caucasicus*, *Darevskia derjugini*, *Lacerta agilis grusinica*, *Natrix megalcephala*, *Zamenis longissimus* and several *Pelias* species: *P. barani*, *P. kaznakovi*, *P. darevskii darevskii*, *P. d. uzumorum*, *P. magnifica*, *P. olguni*, *P. pontica*.

The distribution area of *Natrix megalcephala* is similar to that of other Colchic species, ranging from the vicinity of Gelenjik town in the west to the Malaya (Lesser) Laba River in the north-east and to the south-east across all the Colchis to the Borjomi Canyon and the Lazistan Ridge in the Artvin Province. It also occurs in isolation in the Lagodekhi-Zakataly area. In the Colchis, it reaches subalpine meadows (Fig. 165) but does not cross the 1000 m elevation in other parts of the range.

Zamenis longissimus occurs from the suburbs of Novorossiysk along all the western Transcaucasus, including low wetlands, middle elevations and mountaintops. Its isolated populations are also present in the Borjomi Canyon, Lagodekhi-Zakataly area and the Belaya (White) River basin on the northern slope of the West Caucasus.

Pelias kaznakovi lives from the south of Tuapse town throughout all the Colchis up to 1000 m asl. On the northern slopes of the West Caucasus, it is known from the Belaya River basin. Possibly, it also lives in isolation in the Borjomi Canyon and South Ossetia.

A comparison of ranges of the endemic Colchic species associated with the Colchic-type forests and meadows leads to the designation of another three areas of the Caucasian isthmus with high representativeness of the Colchic herpetofauna, apart from the proper Colchis of the western Transcaucasus. These are the Belo-Labinsky area on the northern slopes of the West Caucasus, Kakheti area (Lagodekhi-Zakataly) on the southern slopes of the East Caucasus and the Borjomi area in the eastern Transcaucasus. The herpetofauna of these refugia is presented in table 3.

As shown in table 3, the highest differences are recorded between the Colchic and Kakheti refugia and

Table 3. Distribution of Colchis species of amphibians and reptiles in the main mesophilic refugia of the Caucasus

Species	Refugia			
	Colchis refugium	Belo-Labinsky refugium	Kakheti refugium	Borjomi refugium
<i>Ommatotriton ophryticus</i>	+	+	+	+
<i>Lissotriton lantzi</i>	+	+	+	+
<i>Mertensiella caucasica</i>	+	-	-	+
<i>Bufo verrucosissimus</i>	+	+	+	+
<i>Pelodytes caucasicus</i>	+	+	+	+
<i>Lacerta agilis grusinica</i>	+	-	-	-
<i>Darevskia dryada</i>	+	-	-	-
<i>Darevskia braueri</i>	+	+	-	-
<i>Darevskia derjugini</i>	+	+	+	+
<i>Darevskia mixta</i>	+	-	-	+
<i>Darevskia parvula</i>	+	-	-	+
<i>Darevskia clarkorum</i>	+	-	-	-
<i>Natrix megalcephala</i>	+	+	+	+
<i>Zamenis longissimus</i>	+	+	+	+
<i>Pelias kaznakovi</i>	+	+	+	+
<i>P. barani</i>	+	-	-	-
<i>Pelias magnifica</i>	-	+	-	-
<i>Pelias pontica</i>	+	-	-	-
Total	17	10	8	11



Fig. 165. Mt. Chugush - the border of the Krasnodar Territory and the Republic of Adygheya. Russian Federation. Habitats of *Pelias dinniki* and *Coronella austriaca*.

the lowest ones are observed between the Colchic, Borjomi and Belo-Labinsky areas. This differentiation is even lower if the species distribution within the Colchic refugium itself is taken into account. In this case, we deal with three smaller and poorer refugia of the Colchic herpetofauna that has survived outside of the main territory of the Colchis.

Belo-Labinsky refugium

This refugium is provisionally separated from the Colchis by the Greater Caucasus Ridge. Except for *L. a. grusinica*, all north Colchic species are present on the northern slope of the West Caucasus between the Belaya and Malaya Laba Rivers. This uniformity is caused by permeability of typical Colchic plants and vegetation into the northern slope of the Greater Caucasus Ridge along the Belaya (Pshekha, Kurjips, Tsitse) and Malaya Laba riversides. They are continuously spanned from the north of the watershed ridge (Fig. 166) to the limestone Skalistyi (Rocky) Ridge. V.P. Maleev (1941) noted that a part of the Maikop dis-

trict is saturated with the Colchic flora and is inseparable from the Colchis. The viper *Pelias magnifica* is endemic for this refugium.

Borjomi refugium

The Borjomi refugium is also conditionally separated from the Colchis by the Adjaro-Imereti Ridge. The flora and vegetation of the Baniskhevi and Lika canyons, upper zone of the Mt. Lomis-Mta and the vicinity of Bakuriani town are indistinguishable from those of the Colchis.

Kakheti refugium

The Kakheti refugium is distant and isolated, but owing to its humid and warm climate it has retained a substantial part of the ancient Tertiary vegetation (Gulisashvili et al., 1975).

Summarising a basic review of the Colchic species of the herpetofauna and their main refugia, here we should mention the principal traits of these species.



Fig. 166. Shakhgireyevskoe Gorge, Krasnodar Territory, Russian Federation. Type territory of *Pelias magnifica*.

The Colchic species are ancient (preserved since the Tertiary times), autochthonous, highly variable, depressed among some taxa (*Pelias kaznakovi*, *P. magnifica*, *P. pontica*, *Darevskia clarkorum*, *D. dryada*, *Lacerta agilis grusinica*) and marked by the presence of the limestone north Colchic and the volcanic south Colchic speciation centres for narrowly endemic species. Reptiles tend to be melanistic and amphibians are disposed to low-temperature breeding thresholds as a result of glacial adaptations. The up-to-date distribution of Colchic species, with a few exceptions, does not go beyond the refugia of the Colchic vegetation or its derivatives. Altitudinal distribution is the highest in the core area (Colchis) where it reaches 1800 m, but does not exceed 1000 m in other refugia. The very existence of four refugia of the Colchic herpetofauna in the Caucasus is determined by only slight post-Pleistocene changes in local humid subtropical climate (January isotherm -3°C , precipitation isoline 800 mm).

A relatively small Hyrcanian centre of mesophilic herpetofauna covers the extreme south-east of the Caucasian isthmus in the forests and lowlands of the Talysh Mts. Most of this refugium is located on the Caspian slope of the Alborz Ridge in Iran. Its existence has been determined by the same factors as in the Colchic refugia.

Xerophilic Refugia of the Caucasus

The Caucasus has been inhabited by the three large xerophilic groups: Turanian, Asia Minor and Mediterranean. The first group is represented exclusively by colonizers. The Asia Minor and Mediterranean groups exist here for a long period of time and their taxa had survived the dramatic Pleistocene events in the xerophilic refugia of the Caucasus.

Mediterranean species of the herpetofauna are absolutely absent in the highlands of the axial part of the Greater Caucasus Ridge (over 2000 m asl) and in the highest parts of the Lesser Caucasus and are poorly presented in the western Ciscaucasus, Colchic Lowland and the upper zones of the Greater and Lesser Caucasus. In the meantime, the Caucasian isthmus has several areas with high representativeness of Mediterranean species. The largest of them encompasses the foothills and middle heights of the eastern Transcauca-

sus (Figs. 167, 168) concentrated around the Kura-Arax Plain and extending to the Talysh foothills (including the Zuvand), southern slopes of the Lesser Caucasus and, along the Arax riverside, the Armenian Highland. This area excludes proper Ararat Valley and other lowland areas along the Arax River.

The second area is located on the Caspian coastline of Dagestan's foothills (Fig. 169). A series of areas on the northern slopes of the East Caucasus is sharply contrasting against most of the territory by its diversity of Mediterranean species. These areas include the semiarid mid-elevation depressions between the Bokovoy (Lateral) and Skalistyi ridges (Gunibskaya, Botlikhskaya, Itumkalinskaya, Targimskaya, Armkhiyskaya, Sadono-Unalskaya and others (Fig. 170). A similar Mediterranean-rich area is extended as a maritime strip between Anapa and Sukhumi towns on the Black Sea coast. Mediterranean species are quite well represented in the canyon of the Kura headwaters. Two more areas deserve a particular attention within the Caucasus Ecoregion: Artvin Depression (lower basin of the Çoruh River, south-western Transcaucasus) (Fig. 171) and a narrow coastal strip extending from Gonio in Adjara to Trabzon town in Turkey.

Before considering the amphibian and reptile fauna of these areas, it is worthwhile to analyze their phytolandscape conditions since the prochoresis (slow changes in distribution of organisms over time) has been carried out mainly by communities and not by individual species (Chkhikvadze, 1991).

Vast foothills and middle elevations of the Greater and Lesser Caucasus fringe the Kura-Arax plain and the Ararat valley are covered by arid sparse pistachio, juniper, pistachio-juniper forests and by sibiljak (willow-leaved pear, Fenzl's almond, Pallas's buckthorn and others) (Fig. 172). The Oriental plane (*Platanus orientalis*) groves and wingnut (*Pterocarya pterocarpa*) stands have survived along the riversides and the fig trees (*Ficus carica*) grow near the groundwater springs in the southern part of this refugium. At lower elevations these sparse forests transform into the subtropical steppe (Fig. 173) and at higher altitudes they are replaced by phrygana and tomillares. In general, vegetation of this refugium has been a derivative of the East Mediterranean and Asia Minor regions (Fig. 174).

Notably, the proper Kura-Arax lowland and the Arax riverside located to the south of the refugium are characterized by semi-desert and desert, mainly halophilic, vegetation which is closer to the Irano-Turanian



Fig. 167. Egegiz Gorge, Armenia. Habitats of *Eryx jaculus*, *Telescopus fallax*, *Hemorrhois ravergieri*, *Dolichophis schmidtii*, *Platyceps najadum*, *Eirenis modestus*.



Fig. 168. Meghri Ridge, Armenia. Habitats of *Coronella austriaca*, *Dolichophis schmidtii*, *Hemorrhois ravergieri*, *Elaphe sauromates*, *Zamenis hohenackeri*, *Montivipera raddei*, *Macrovipera lebetina*.



Fig. 169. Rubas River Valley, Dagestan, Russian Federation. Habitats of *Xerotyphlops vermicularis*, *Telescopus fallax*, *Eirenis collaris*, *Hemorrhoids ravergeri*, *Dolichophis schmidtii*.



Fig. 170. Panorama of the Erzi State Nature Reserve, Ingushetia, Russian Federation. Habitats of *Natrix tessellata*, *Natrix natrix*, *Coronella austriaca*, *Pelias lotievi*.



Fig. 171. Tortum, Turkey. Habitats of *Zamenis hohenackeri*, *Eirenis modestus*, *Hemorrhais ravergieri*, *Hemorrhais nummifer*.



Fig. 172. Khosrov Reserve, Armenia. Habitats of *Xerotyphlops vermicularis*, *Eirenis modestus*, *Coronella austriaca*, *Dolichophis schmidtii*, *Zamenis hohenackeri*, *Elaphe sauromates*, *Natrix tessellata*, *Platyceps najadum*, *Montivipera raddei*.



Fig. 173. Vicinity of the Yeghegnadzor, Armenia. Habitats of *Xerotyphlops vermicularis*, *Eirenis modestus*, *Coronella austriaca*, *Hemorrhoids ravergieri*, *Hemorrhoids nummifer*, *Dolichophis schmidtii*, *Zamenis hohenackeri*, *Elaphe sauromates*, *Natrix tessellata*, *Natrix natrix*, *Montivipera raddei*.



Fig. 174. Noravank Gorge, Armenia. Habitats of *Montivipera raddei*, *Hemorrhoids ravergieri*, *Hemorrhoids nummifer*, *Dolichophis schmidtii*, *Platyceps najadum*, *Elaphe sauromates*, *Telescopus fallax*, *Eirenis modestus*, *Eryx jaculus*.



Fig. 175. Akhuryan River, the border of Armenia and Turkey. Habitats of *Natrix natrix*, *Natrix tessellata*, *Coronella austriaca*, *Dolichophis schmidtii*, *Eirenis punctatolineatus*, *Eirenis collaris*, *Eryx jaculus*, *Platycephalus najadum*, *Macrovipera lebetina*.



Fig. 176. Kumlakh, Azerbaijan, the Arax River and the Karadag Mountain Range in northern Iran. Habitats of *Eryx jaculus*, *Macrovipera lebetina*, *Rhynchocalamus satunini*, *Eirenis collaris*, *Xerotyphlops vermicularis*, *Natrix tessellata*, *Natrix natrix*, *Malpolon insignitus*.

desert vegetation than to vegetation of other parts of the Caucasus (Figs. 175, 176).

A.A. Grossheim in his famous work "Flora of the Caucasus" (1939) attributed the Kura-Arax Plain to the Turanian Province along with the eastern Transcaucasus and the Apsheron Peninsula. Later, E.M. Lavrenko (1965) included these deserts (without the eastern Transcaucasus) in the separate Kura-Arax Province of the Irano-Turanian Sub-Region of the Afro-Asian (Sahara-Gobi) Desert Region (Figs. 177, 178).

The Caspian coast of Dagestan representing the branches of the eastern part of the Greater Caucasus Ridge is covered by primary and secondary sibiljak, sessile oak and downy oak communities intermixed with juniper sparse forests, Jerusalem thorn scrubs and xerophytic bushes. The Samur River mouth gives home to the northernmost derivate of the Hyrcanian forest which is composed of the vine forest with the wingnut, Pastukhov's ivy, silk vine and other plants.

The East Caucasian refugia of oreoxerophytes, including the sibiljak and phrygana, are stretched along the Jurassic shale depression on the northern slope of the Greater Caucasus, between the Bokovoy and Skalistyi ridges. This is a series of semiarid depressions aligned from inner Dagestan (Gunibskoe Plateau) to the Kuban headwaters. Vegetation comprises the junipers, Jerusalem thorn, cherry, bladder senna, barberry, tragacanth astragals and many other species. There is no consensus about the age of this vegetation, but most authors adhere to its Pliocene origin (Krasnov, 1894; Grossheim, 1948 and others). According to Galushko (1974), semiarid depressions of Chechnya and Ingushetia are younger than depressions of Kabardino-Balkaria in the west and those of Dagestan in the east and are dated no older than Holocene. The vestiges of the xerophytic vegetation on ridgetops that separate the depressions prove the existence of a single vast Mediterranean refugium from the Mt. Elburs to Dagestan which split apart in the Pleistocene into a number of variously preserved microrefugia.

It should be noted that the traces of a xerothermic period were found also in the West Caucasus near the peaks Yatyrgvarta and Magisho (Althukhov, 1967), but local xerophytic vegetation was always narrowly distributed because of climatic conditions and the strong impact of the Colchis.

The Black Sea refugium comprising the westernmost fringe of the Greater Caucasus near Anapa, Gelenjik and Djubga and several enclaves from Tuapse to

Sukhumi represents the Crimea-Novorossiysk Province of the Mediterranean. In the west, the refugium is covered by pistachio and juniper sparse forests, patches of tomillares and downy oak-coniferous mixed forests. In the east, its flora includes the French broom, pomegranate, Greek strawberry tree, tree heath, bay laurel and rockroses. The Turkish pine, Jerusalem thorn, elm-leaved sumach, Eurasian smoketree, Turkish bladder senna, vitex, bush jasmine and others are very common throughout the refugium.

The Çoruh riverside near Artvin town represents a dry and hot depression surrounded by the circle of high ridges (Pontic, Shavshet, Arsian) and receives only 500–600 mm of precipitation annually with short summer downpours (Menitsky, 1984). Describing the changes in vegetation from the lower Çoruh to Artvin, Yu.V. Voronov (1908) noted that the Borçka dry slopes are covered "by sparse forests of the crooked Georgian oak, Oriental hornbeam, pine and tree juniper groves, and xerophytic scrubs... In the driest places, such as the Orçuh, Ardanuç and somewhere in the Imerkhev Canyon the arboreal vegetation is almost absent and bare cliffs are covered by distantly scattered trees of pomegranates, Pallas's buckthorns, junipers and other species, or by thorny astragals" (p. 3).

Interestingly, the herbarium materials of a typical Mediterranean oak species *Quercus infectoria* ssp. *infectoria* were collected in this region (Menitsky, 1984) and the groves of a typical Mediterranean pine *Pinus pinea* also grow here (Nasimovich, 1979).

In the Caucasus, relict types of vegetation and their refugia of different origin and ages can be located close to each other within a limited area. This rule applicable to all regions of the Caucasus reflects the multiple altitudinal movements of vegetation in the Pliocene and especially in the Pleistocene-Holocene period. In the Holocene alone, such movements were 11 (Kvavadze, Rukhadze, 1989), so the general pattern of distribution of the Mediterranean vegetation is valid, but in many places it appears to be tentative because of fragmentary and mosaic structure of landscapes. This is particularly true for the Black Sea coastline of the Caucasus, semiarid depressions of the East Caucasus, Karabakh region, Kura headwaters and the vicinity of Artvin.

For instance, in the Black Sea coastline the Mediterranean vegetation is distributed continuously only in the extreme north-west, from Anapa to Gelenjik. Further south-eastwards, it turns into the series of patches inside the Colchic vegetation confined to the steep



Fig. 177. Vicinity of the Julfa, Nakhichevan, Azerbaijan. Habitats of *Eirenis collaris*, *Hemorrhhois nummifer*, *Macrovipera lebetina*, *Psammophis lineolatus*, *Xerotyphlops vermicularis*. Photo by Daniel Melnikov.



Fig. 178. Vicinity of the Julfa, Nakhichevan, Azerbaijan. Habitats of *Eirenis collaris*, *Hemorrhhois nummifer*, *Macrovipera lebetina*, *Psammophis lineolatus*. Photo by Daniel Melnikov.

maritime hills, southerly and easterly exposed slopes. The maritime Mediterranean vegetation is preserved only in the littoral zone (Kolakovsky, 1980–1984). In semiarid depressions of the East Caucasus, the oreoxerophytic vegetation grows on the steep easterly slopes and mesophilic forests cover the westerly slopes. For example, four local disjunctions were recorded in one refugium in the Itum-Kalinskaya Depression (Chechnya): 1 – steppe species; 2 – oreoxerophytes; 3 – sibiljak; 4 – broadleaf forest (Galushko, 1974).

In Nagorno Karabakh, the relicts of the Mediterranean sibiljak and arid sparse forest (*Pistacia mutica*, *Padellus mahaleb*, *Pyrus salicifolia*, *Cotinus coggygia*, *Punica granatum*, *Rhus coriaria*, *Paliurus spina-christy* and others) co-exist with the Colchic and Hyrcanian relicts (*Zelkova carpinifolia*, *Castanea sativa*, *Taxus baccata* and others) (Arushatyan, 1973). In the Kura headwaters, vegetation undergoes transformations from Colchic (Baniskhevi and Lika canyons; with intermediate variations – Chitakhevi and Kvabiskhevi canyons) to Mediterranean in the Zoreti Canyon. Along the Çoruh River, side canyons and middle elevations are covered by lush Colchi-Lazistan vegetation dominated by *Quercus dshorochensis*, *Picea orientalis*, *Carpinus betulus* and many other trees (Menitsky, 1984) near the dry Artvin Depression.

The patchiness of the Caucasian vegetation makes regional herpetological grouping quite complicated, but the groups' faunistic kernels are always clear-cut whether the vegetation is xerophilic or mesophilic.

Kura-Arax refugium

The species widely spread throughout this refugium (Table 4) include *Pelobates syriacus*, *Testudo graeca*, *Mauremys caspica*, *Lacerta media*, *L. strigata*, *Pseudopus apodus*, *Ophisops elegans*, *Natrix tessellata*, *N. natrix persa*, *Platyceps najadum*, *Dolichophis caspius*, *Xerotyphlops vermicularis*, *Eryx jaculus*, *Zamenis hohenackeri*, *Elaphe sauromates*, *Telescopus fallax iberus*, *Eirenis modestus*, *Malpolon insignitus* and *Macrovipera lebetina obtusa*. In the northern parts of the refugium (southern foothills of the East Caucasus and the Kura River basin) these species occur at relatively low altitudes, up to 600–700 m. In the south, e.g. in the Arax riverside, they move up to higher elevations, in some sites reaching 2000 m asl. (Figs. 179, 180). The lowest areas of the Kura-Arax Plain lying beyond this refugium are inhabited by Turanian species,

such as *Eremias velox*, *E. arguta*, *Cyrtopodion caspius* and *Ablepharus pannonicus*. The Arax riverside gives home to *Psammophis lineolatus* and to other species associated with semi-deserts and deserts of the Armenian Highland and the western part of the Iranian Highland: *Eremias trauchi*, *E. pleskei*, *Heremites septemtaeniatatus*, *Ablepharus bivittatus*, *Eirenis punctatolineata*, *Rhynchocalamus satunini* and *Hemorrhois nummifer*.

It would be incorrect to consider all these species as the late Pleistocene migrants in the Caucasus. The Asia Minor xerophilic complex of flora and fauna is much better adapted to arid conditions and is directly linked with the ancient Mediterranean complex. This hypothesis can indicate the long-term co-existence of Mediterranean and Asia Minor communities in the Caucasus. In other words, the species like *Paralaudakia caucasia*, *Phrynocephalus horvathi*, *Eumeces schneideri*, *Eirenis collaris*, *Hemorrhois ravergieri* and species of the Armenian Highland could inhabit this region (Figs. 181–182) already in the Pliocene.

At the highest limits of their distribution, Mediterranean species live together with Caucasian and Asia Minor species (*Rana macrocnemis*, *R. camerani*, *Darevskia* spp., *Pelias eriwanensis*) and representatives of the mid-elevation Armenian Highland (*Montivipera raddei*, *Parvolacerta parva*).

Mediterranean species having limited distribution in the Kura-Arax refugium are represented by *Triturus karelinii* (Greater Caucasus foothills in the north and the Talysh Mts. in the south), *Cyrtopodion colchicus kotschyi* (Turkish part of the Ararat Valley), *Darevskia praticola* (northern part of the refugium), *Ablepharus chernovi* (Hrazdan Canyon in Armenia) and *Vipera transcaucasiana* (vicinity of Gyanja in Azerbaijan). Almost all these species occupy the most mesophilic habitats in generally xerophilic landscapes of the Kura-Arax refugium.

Dagestan foothill refugium

This impoverished refugium (Table 4) contains a significant number of Iranian species (*Paralaudakia caucasia*, *Eumeces schneideri*, *Hemorrhois ravergieri*, *Eirenis collaris*), but none of Armenian Highland species which are so common in the Arax part of the Kura-Arax refugium. The sand dune Sarykum near the northern boundary of the refugium is inhabited by a common Turanian species *Phrynocephalus mystaceus*.

Table 4. Distribution of Mediterranean species of amphibians and reptiles in the main xerophilic refugia of the Caucasus

№	Species	Refugia					
		1	2	3	4	5	6
1	<i>Triturus karelinii</i>	+	+	+	+	+	+
2	<i>Pelobates syriacus</i>	+	+	-	-	+	?
3	<i>Hyla savignyi</i>	+	-	-	+	-	-
4	<i>Testudo graeca</i>	+	+	-	+	-	-
5	<i>Mauremys caspica</i>	+	+	-	-	-	-
6	<i>Cyrtopodion kotschy colchicus</i>	-	-	-	-	-	+
7	<i>Lacerta media</i>	+	+	+	+	+	+
8	<i>Lacerta strigata</i>	+	+	+	+	-	+
9	<i>Darevskia pontica</i>	-	-	-	+	?	?
10	<i>Darevskia praticola</i>	+	+	+	-	-	-
11	<i>Darevskia brauneri myusserica</i>	-	-	-	+	-	-
12	<i>Darevskia szczyrbaki</i>	-	-	-	+	-	-
13	<i>Pseudopus apodus</i>	+	+	-	+	+	?
14	<i>Ophisops elegans</i>	+	+	-	-	-	+
15	<i>Ablepharus chernovi</i>	+	-	-	-	-	-
16	<i>Natrix tessellata</i>	+	+	+	+	+	+
17	<i>Natrix natrix persa</i>	+	+	+	+	+	+
18	<i>Platyceps najadum</i>	+	+	+	+	+	+
19	<i>Dolichophis caspius</i>	+	+	-	+	-	+
20	<i>Zamenis hohenackeri</i>	+	+	+	-	+	+
21	<i>Elaphe sauromates</i>	+	+	+	+	-	-
22	<i>Telescopus fallax iberus</i>	+	+	-	-	+	?
23	<i>Malpolon insignitus</i>	+	-	-	-	-	-
24	<i>Eirenis modestus</i>	+	+	+	-	+	+
25	<i>Eryx jaculus</i>	+	+	+	-	-	+
26	<i>Xerotyphlops vermicularis</i>	+	+	-	-	-	-
27	<i>Vipera transcaucasiana</i>	+	-	-	-	+	+
28	<i>Macrovipera lebetina obtusa</i>	+	+	-	-	-	+
29	<i>Pelias orlovi</i>	-	-	-	+	-	-
	Total:	24	20	11	15	11	14

Note: 1 — Kura-Arax refugium; 2 — Dagestan foothill refugium; 3 — North-East Caucasian refugium; 4 — Black Sea refugium; 5 — Upper Kura refugium; 6 — Artvin refugium.

North-East Caucasian refugium

This is the poorest of all refugia considered herein. Meantime, very unusual specific composition and the presence of flora and fauna common for more southern latitudes let this refugium be considered as a derivate of Mediterranean landscapes. Mediterranean species are present in each depression of the East Caucasus, but in different combinations. For example, *Eirenis modestus* and *Lacerta strigata* are known from the eastern part of the refugium, but the other species occur in a majority of semiarid depressions. Of Iranian species, *Hemorrhhois ravergieri* has survived in the east of the refugium. Notably, almost all depressions contain species identical or very

close to Asia Minor species, such as *Rana camerani* and *Pelias lotievi*.

The Caucasian species (*Pelias dinniki*, *Rana macrocnemis*, *Darevskia daghestanica*, *D. caucasica*) occur along the top limits of this refugium (Fig. 183). The forest-dwelling Caucasian species (*Lacerta agilis boemica*, *Rana macrocnemis*) together with the European species (*Coronella austriaca*, *Anguis fragilis*) are characteristic for the western exposures of the depressions where another typical Caucasian species, *Darevskia rudis*, lives. In the sibiljak, phrygana and steppe meadows of the Itumkalinskaya Depression, only *Coronella austriaca* (co-existing here with *Zamenis hohenackeri*) joins a local set of Mediterranean species. All other species occur along the ecotones of the Mediterranean and



Fig. 179. Meghri Ridge, Armenia. Habitats of *Coronella austriaca*, *Dolichophis schmidtii*, *Hemorrhois ravergieri*, *Elaphe sauromates*, *Telescopus fallax*, *Zamenis hohenackeri*, *Montivipera raddei*, *Macrovipera lebetina*.



Fig. 180. Kasakh River Gorge, Armenia. Habitats of *Eirenis modestus*, *Coronella austriaca*, *Elaphe sauromates*, *Natrix tessellata*, *Natrix natrix*, *Telescopus fallax*, *Montivipera raddei*, *Pelias eriwanensis*.



181. Khosrov Reserve, Armenia. Habitats of *Xerotyphlops vermicularis*, *Eirenis modestus*, *Coronella austriaca*, *Dolichophis schmidtii*, *Zamenis hohenackeri*, *Elaphe sauromates*, *Natrix tessellata*, *Platyceps najadum*, *Montivipera raddei*.



Fig. 182. Vicinity of the Ijevan, Armenia. Habitats of *Coronella austriaca*, *Platyceps najadum*, *Eirenis modestus*, *Natrix natrix*.



Fig. 183. Samursky Ridge, Dagestan, Russian Federation. Habitats of *Coronella austriaca*, *Pelias lotievi*.

Caucasian mountain forest and mountain meadow communities, but do not permeate into the Mediterranean phytolandscapes.

Black Sea refugium

The species of this refugium are described earlier (Tuniyev, 1990). Their distribution along the Black Sea coast of the Caucasus is confined to the narrow maritime strip from Anapa in the north-west to Sukhumi in the south-east. The strong correlation between the distribution of the Mediterranean herpetofauna and phytolandscapes is lacking because of the long-term transformations caused by human activities. In some places, species permeate deep into the Colchis through the treeless areas and co-exist there with typical representatives of the Colchic zoogeographical group. The richest in species diversity areas have preserved in the pristine landscapes around the Novorossiysk city and Pitsunda town. Currently, the Black Sea refugium is waning because of the high levels of humidity and precipitation preventing from the expansion of Mediterranean species.

In agreement with the disjunctive distribution of local species, *Elaphe sauromates* is known only from the north-western part and *Lacerta strigata* only from the south-eastern part of the refugium. The ranges of Mediterranean species of plants are also fragmentary, illustrating once again the common trends in the development, maturation and fadeaway of communities. The European steppe species *Bufo viridis* and *Pelias renardi* are quite common in the north-west which also retains the unique species *Bufo verrucosissimus circassicus* and *Pelias orlovi*. Towards the south, these species disappear, being substituted by the Colchic species *Bufo v. verrucosissimus*, *Darevskia brauneri*, *Pelias kaznakovi* and others.

Upper Kura refugium

This rather small area adjoins the Borjomi refugium of the Colchic herpetofauna and represents an example of complicated co-existence of genetically diverse groups that we mentioned while describing the vegetation of these two refugia. The Upper Kura refugium comprises the most mesophilic representatives of Mediterranean species with the complete absence of xerophilic taxa. The species like *Triturus karelinii*, *Lacerta media*, *Natrix tessellata*, *Natrix natrix persa* and *Vipera transcaucasiana* are quite common and

even expanding their range beyond the boundary of the refugium, but *Pelobates syriacus*, *Pseudopus apodus*, *Platyceps najadum*, *Telescopus fallax* and *Eirenis modestus* are rare and occurring only in some sites. The Turanian taxa are absent and the only Asia Minor species is *Paralaudakia caucasia*. Generally, the Upper Kura refugium is adjacent to the Colchic speciation centre, Asia Minor highland speciation centre (*Darevskia* spp., *Pelias darevskii* and others) and the Kura-Arax refugium of Mediterranean species, but in the Upper Kura Mediterranean species are distributed locally in the lower part of the Kura gorge.

Artvin refugium

The species indicated in table 4 demonstrate the presence of diverse Mediterranean habitats in the Artvin Depression, from very dry and warm areas giving home to *Cyrtopodion kotschyi*, *Lacerta strigata*, *Ophisops elegans* and *Macrovipera lebetina* to xeromesophilic and even mesophilic ranges of Colchic-Lazistan species. The vegetation diversity of the Çoruh River basin from the Borçka to Artvin and Ardanuç was described above. It can be speculated that certain species (*Pelobates syriacus*, *Darevskia praticola*, *Pseudopus apodus*, *Telescopus fallax*) can be found here. On the other hand, the Pontic viper *Pelias pontica* recorded in this area by Billing et al. (1990) shows that local climatic conditions were historically different from those of the Black Sea's Lazistan, thus ensuring the survival of stenotopic *P. pontica* in comparison to *P. kaznakovi* which is widespread in Adjara and Lazistan.

Not delving into the details of biogeographical zoning of the Caucasus, we nonetheless find the locations of some refugia quite interesting. From the sectoral multilayer approach to biogeographical analysis of mountains, it is clear that Mediterranean landscapes move up to higher elevations from west to east because of increasing aridization and solar radiation in the eastward and southward directions.

In this regard, it becomes evident that the landscapes occupied by Mediterranean species at the lower elevations of 0–600 m asl correspond to the Black Sea and Dagestan foothill refugia. Most likely, these territories should be considered as enclaves of the East Mediterranean Province. The rest of the refugia are located at higher elevations, being substituted or enriched at lower heights by Asia Minor or Turanian species. The position of the Kura-Arax, North-east Caucasian, Up-

per Kura and Artvin refugia in the Asia Minor, Mediterranean or other regions needs more research and careful evaluation.

Mediterranean species living in the Caucasus are autochthonous, ancient and relict what makes the inclusion of some refugia in the East Mediterranean (*sensu stricto*) and of most of the Caucasus in the Mediterranean (*sensu lato*) warranted.

History of the Herpetofauna origin and its main Refugia in the Caucasus

Understanding of the causes and relationships of recent distribution of different zoogeographical groups in the Caucasian isthmus demands for the analysis of fossil records. Available paleontological findings are limited, but essential in elucidating the general trends in the development of the herpetofauna of the Caucasus. Having quite full information on fossil mammals of the Caucasus (Vereschagin, 1959) and paleobotanical chronicles, we will try to reconstruct the processes of development of the region's herpetofauna.

The pre-Miocene history of the Caucasus has been described by many authors (Vereschagin, 1959; Darevsky, 1967; Alekperov, 1978 and others) as the history of a tropical montane island with lush moisture-loving vegetation in the Tethys Ocean. Mountains always have locally dry sites (e.g., on cliffs and steep slopes) where arid plants, or xerophytes, grow. Such local changes are not enough for the development of xerophilic vegetation which demands for overall climate aridization. Therefore, it is quite possible that before the Miocene the Caucasus was more humid than mountainous lands located to the south and spread from Afghanistan through central Iran, Asia Minor and Balkans to the Alps. In this belt of mountains, arid climate with respective subtropical hemixerophilic phytolandscapes existed continuously from the Cretaceous onward (Krishtofovich, 1954; Kolakovsky, 1974a, b). The fossil herpetofauna of the pre-Miocene Caucasus is represented by the mid-Jurassic sea crocodile *Stenosaurus* sp. from mountainous Dagestan (Bakradze, Chkhikvadze, 1988), dinosaur tracks on the Lower Cretaceous limestones of the Sataplia, western Georgia (Gabunia, 1951), *Mosasaurus* sp. from the late Cretaceous in Azerbaijan (Gabunia, 1958) and the Oligocene to Lower

Miocene records from the Benar in southern Georgia where *Palaeochelys gabunii* (Emydidae), *Ergilemys meschethica* (Testudinidae) and *Trionyx* sp. (Trionychiidae) were found (Bakradze, Chkhikvadze, 1988).

From the mid-Sarmat, the Caucasus became a peninsula of Asia Minor (Vereschagin, 1959; Darevsky, 1963; Menitsky, 1984) which was also adjoined by Anatolia and the Balkans. A.A. Kolakovsky (1974a) surmised that floristic exchanges between Europe, Caucasus and East Asia occurred up to the Upper Miocene. During these processes, the Greater Caucasus was surrounded from three sides by the seas, but the increasingly landlocked southern areas underwent the strong development of semiarid habitats inside the humid landscapes. Such a scenario of climatic and landscape development can explain the existence of *Cheilonia caucasica* in the Chernaya rechka (Black River, North Caucasus) and a giant tortoise like *Ergilemys meschethica* in the Akhaltsikhe (Bakradze, Chkhikvadze, 1988).

The processes of "borealization" in the Miocene covered almost all the Caucasus. In eastern Georgia, up to 70% of tree species from the mid-Sarmat times were already deciduous (Palibin, 1935). A.A. Grossheim (1936) compared this flora with the Upper Miocene flora of Asia Minor and noted their striking similarity marked by the same assortment of the boreal and subtropical species. As in the Sarmat, the Caucasus was colonized by representatives of the hipparion fauna. N.K. Vereschagin (1959) indicated nascent "borealization" as an important stage for understanding of future evolution of the fauna.

The Mt. Sehend near Meraghe in Iran is of particular interest for reconstruction of the Miocene landscapes and faunistic relationships between Asia Minor and the Caucasus. The reptilian fossils include only one tortoise (Bakradze, Chkhikvadze, 1988), but there are 40 mammalian species (Primates, Carnivora, Tubulidentata, Proboscidea, Perissodactyla, Artiodactyla) and also some birds (*Struthio* sp., *Urmiornis maraghamus*) recorded there (Vereschagin, 1959). A clear dominance of open space species over subtropical forest-dwelling ones allows speculating the existence of mixed savanna-rainforest landscapes in the Miocene in the northern parts of today's Iranian Highland. In Asia Minor, the Upper Miocene mammals found near Istanbul, Upper Gediz and Muğla, in Galatia and Cappadocia are identical to the fossils on the Samos Island and in the Pikerimi near Athens on the Balkans (Vereschagin, 1959).

N.K. Vereschagin supposed that the Meraghe-like faunistic complex was common for all Asia Minor. Generally, the Upper Miocene fauna of Asia Minor, Caucasus, Crimea and the Balkans is similar.

Interestingly, A.A. Grossheim (1936) considered the Meotis as a period of large-scale permeation of southern xerophilic vegetation into the Caucasus. The eastern Transcaucasus already had many recent species of reptiles or their relatives. A.M. Alekperov (1978) indicated *Testudo eldarica* for the late Sarmat period in western Azerbaijan and the species *Testudo burtschaki*, *Chelydropsis* sp., *Trionyx* sp., *Emydoidea taraschuki* and *Mauremys sarmatica* were found in the adjacent parts of eastern Georgia (Eldari, Pantishare, Iori) (Bakradze, Chkhikvadze, 1984, 1988). The large *Vipera* sp. dated the late Sarmat was recorded by G.A. Zerova and V.M. Chkhikvadze (1984) and later identified as the blunt-nosed viper *Vipera* cf. *lebetina* (Bakradze, Chkhikvadze, 1988). The Meotis-aged species *Mauremys* sp., *Ergilemys* sp. and *Testudo* sp. were recorded near the Udabno village in the Garedji Steppe, watershed of the Kura and Iori Rivers (Bakradze, Chkhikvadze, 1988).

The warm subtropical climate contributed to the thriving expansion of predecessors of the warmth- and moisture-loving taxa in the Caucasus (*Ommatotriton ophryticus*, *Lissotriton lantzi*, *Pelodytes caucasicus*, *Bufo verrucosissimus*, *Darevskia braueri*, *D. derjugini*, *Natrix megalcephala*, *Zamenis longissimus*, *Pelias kaznakovi*, as well as more eurybiont species *Rana macrocnemis*, *Hyla orientalis*, *Darevskia rudis* and *Lacerta agilis* - complex). The fossil remains of mammals (*Mesocricetus*, *Prometheomys*, *Sorex*, *Talpa*) (Vereschagin, 1959) and insects (Orthoptera, Hemiptera, Blattoidea, Coleoptera) (Rodendorf, 1939) indicate the adequate food base for amphibians and reptiles in the Miocene. Also, in the Miocene a majority of these species reached the eastern parts of the Caucasus over the southern slopes of the Greater Caucasus Ridge from where they dispersed through the Karabakh Bridge to the Talysh Mts. and reached the contact with the East Asian species. The historical connectedness of the Colchic and Hyrcanian vegetations was also noted by N.I. Kuznetsov (1909), I.V. Safarov (1966) and others. Even now the floristic composition of the Kakheti area and Karabakh has much in common with forests of the Colchis and Talysh Mts. (Arushanyan, 1973; Sokolov et al., 1977; Takhtajyan, 1978; Gadjeiev et al., 1985).

On the northern slope of the Greater Caucasus, the Miocene herpetofauna comprised both mesophilic and

xerophilic species peculiar for today's Mediterranean Europe. The mid-Miocene *Trionyx* sp.? *Ergilemys* sp.? *Protestudo* sp., *Lacerta* sp. and Colubridae gen. indet. were described from the Belomechetskaya village (Chkhikvadze, Lungu, 1984). The mid-Sarmat amphibians and reptiles *Trionyx khosatzkyi*, Emydidae gen. indet., *Mioproteus caucasicus*, *Triturus* cf. *marmoratus*, *Lacerta* sp., Ranidae gen. indet., Discoglossidae gen. indet. were found in the lacustrine sediments of the Belaya River in Maikop (Estes, Darevsky, 1977; Chkhikvadze, Lungu, 1984). The local remains of *Lacerta* skulls were later analyzed by I.S. Darevsky (1990) who assigned them to a representative of the subgenus *Lacerta* s. str., possibly belonging to one of the recent species (*L. media*, *L. strigata*, *L. agilis*) or to an extinct ancestor taxon. According to Darevsky, the mid-Miocene *Lacerta* from the Belomechetskaya could also be the same species. As Darevsky wrote, these lizard records could indicate the permeation of lacertids from Europe to the Caucasus via Asia Minor which was separated from the Balkans by sea straits only in the post-Sarmat times. L.Ya. Borkin (1987) expressed the same idea on a basis of records of *Triturus* cf. *marmoratus* and *Mioproteus caucasicus* related to the recent relict.

In the Lower Pliocene, the Caucasus was still a peninsula and only by the end of the Pontic Age the sea retreating from the Ciscaucasus had turned the Caucasus into the isthmus (Vereschagin, 1959; Alekperov, 1978). By that time, the landscapes of the western and eastern parts of the Caucasus were already different. The Colchis and adjacent lands remained to be the humid subtropics and (in the Cimmerian age) even the tropics, whereas in the eastern part dry Hyrcanian forests were continuously stretched along the west Caspian coast and its Kura and Samur bays northwards to the Yergeni's. The inner lands of the East Caucasus had been affected by further expansion of arid and semiarid spaces.

An unrivaled beauty of the Cimmerian flora of the western Transcaucasus was granted by the extraordinary diversity of ferns comparable only with that of the Cretaceous (Mchedlishvili, 1963). The flora of the Colchis, apart from various ferns, was extremely rich in subtropical gymnosperms (*Ginkgo adiantoides*, *Podocarpus*, *Cedrus*, *Tsuga*, *Abies*, *Clyptostrobus*, *Sequoia*, *Cryptomeria* and others) and angiosperms, whereas the lack of edificators made it look like an ancient tropical forest, with some resemblance of the Oligocene flora. As found out by spore and pollen analyses, the region's vegetation comprised the dark coniferous, broadleaf,

wetland, leafed, evergreen, riparian and hygrophilous communities (Mchedlishvili, 1963).

The Tertiary relicts of the West Caucasus that have survived until today are very diverse but, according to V.P. Maleev (1938), closely tied with hemixerophilic and mesophilic vegetations of the Mediterranean. The complex of hemixerophilic species derives from the ancient subtropical Poltava-type flora with a significant admixture of Asia Minor species. The mesophilic complex has been a slightly changed derivate of the Angarid or Turgay flora. As to A.A. Grossheim (1936), the vast centre of xerophilic vegetation began its development in the Mediterranean in the second half of the Tertiary, but at present it is confined only to the maquis on the Black Sea coast and the sibiljak in the centre and east of the isthmus. In the meantime, the xerophilic flora of the Caucasus is closely related to Asia Minor from where ancient xerophytes permeated to the Transcaucasus and even the northern slope of the Greater Caucasus Ridge in Dagestan (A.A. Grossheim). N.I. Kuznetsov (1909) also wrote about the development of two xerophytic centres in Armenia and mountainous Dagestan. The main route of permeation of the Mediterranean species into the Caucasus was stretched across the Manych in the north and the main surge took place quite recently, before the glacial period (Grossheim, 1936).

The floristic differences in the western parts of the Ciscaucasus and the Transcaucasus were recorded already in the Cimmerian age. In the western Ciscaucasus, vegetation continued to lose its ferns, subtropical gymnosperms and angiosperms and to become enriched in herbal species. The spore-pollen spectra reflect the historical existence of the forest-steppe vegetation in this region (Mchedlishvili, 1963). On the northern slope of the Greater Caucasus, the Pliocene fossils of reptiles belonged to the Moldavian complex which was widespread in the northern parts of the Black Sea region. For example, the Kosyakinsky pit (North Caucasus) yielded the records of *Lacerta* sp., *Bufo* sp., *Rana* sp. (Vereschagin, 1959), *Melanochelys pidoplickoi*, *Sakya riabinini*, *Testudo černovi černovi* (Bakradze, Chkhikvadze, 1988; Chkhikvadze, 1989a, b). The species *Andrias* sp., *Mioproteus* sp., *Latonina* cf. *seymfriedii*, *Ophisarus* sp., *Varanus* sp., *Vipera* cf. *lebetina*, *Chelydropsis nopcsai*, *Melanochelys pidoplickoi*, *Sakya riabinini*, *Testudo černovi černovi* and *Emys orbicularis antiqua* are known from the northern Black Sea region (Ukraine, Moldova) (Bakradze, Chkhikvadze, 1988; Redkozubov, Shushpanov, 1985). The last of these spe-

cies was found and described in the Pliocene deposits near Stavropol town (North Caucasus). Also, fossils of several *Testudo* species were recorded in the Pliocene layers in Ust-Labinsk (Krasnodar Krai) and near Grozny, Chechnya (Aleksperov, 1978).

For most Mediterranean species, the Upper Pliocene was the last period of wide distribution in the northern Black Sea region, including the Ciscaucasus. It was also the last period for most of Europe, as the Sarmat-dated forests similar to today's Mediterranean grew even in Hungary (Andreánzsky, 1963). These forests were dominated by such trees as *Quercus ilex*, *Pistacia lentiscoides*, *Rhus palaeocotinus*, *Rh. cf. coriaria*, *Acer decipiens*, *A. cf. monspessulanum*, *Phillyrea cf. latifolia* and *Viburnum tinus*.

A.A. Kolakovsky (1964) found a unique kind of hard-leafed oak paleocommunity with the dominance of *Quercus sosnowskyi* in the Pontic layer of the Kodor River, Abkhazia. This evergreen species has been an extinct link between the Himalayan-Chinese *Q. semicarpifolia* and the Mediterranean *Q. alnifolia* and *Q. suber* (Menitsky, 1984). Despite its hard leaves, *Q. sosnowskyi* was considered by A.A. Kolakovsky a more moisture-loving species than its recent Mediterranean descendants because its communities included mesophilic deciduous species *Carpinus cuspidens*, *C. uniserrata* and only few taxa of modern Mediterranean flora (*Arbutus elegans*, *Laurus nobilis* foss., *Myrtus rarinervis*, *Pistacia miochinensis*, *Celtis magnifica*, *Cotinus coggygria-fossilis*). *Sakya riabinini* known from these fossils (Bakradze, Chkhikvadze, 1988) has been a typical component of the Moldavian faunistic complex, i.e. Mediterranean animal species were present in the Black Sea coast of the Caucasus since the Pliocene times.

In the East Caucasus, the deciduous and warmth-loving vegetation of *Corylus fossilis*, *Alnus incana*, *Quercus* sp., *Castanea* sp., *Parrotia persica* and *Aralia-acea* sp. described by V.I. Baranov (1952) from Yernegi's moved along the Caspian coast and then the Balakhan basin. The species *Parrotia persica* that has survived now only in the Talysh and Alborz Mts. has been a good indicator of warm climate (Vereschagin, 1959). The xerophilic Mediterranean and Asia Minor vegetation developed coherently with the Hyrcanian one. A convincing evidence is the Upper- to Mid-Pleistocene *Testudo* sp. the size of recent *Testudo graeca* which was found in Yernegi's (Aleksperov, 1978).

N.K. Vereschagin (1959) described the independent Asia Minor speciation centre of the mountain-steppe

and mountain-desert subtypes of the Pliocene-aged mammalian fauna. The isolation of these two subtypes was caused by rough terrain and climatic differences in the mountains. Mountain deserts were formed in wide intermontane valleys and narrow canyons while mountain steppes and even meadow steppes covered the adjacent high plateaus and ridgetops (Vereschagin, 1959). The influence of southern species upon the Caucasus was divided into several phases, the strongest of which was the Miocene-Pliocene phase. In the East Caucasus, the Asia Minor species (mountain steppe – *Paralaudakia caucasica*, *Hemorrhhois ravergieri* and others; mountain desert – *Heremites septemtaeniata*, *Hemorrhhois nummifer*) were apparently widespread no less than Mediterranean species.

The Pliocene fossils from the East Caucasus foothills generally belong to the tortoises: *Testudo černovi transcaucasica* from Kvabebi, Kumuros-Khevi (eastern Georgia), *Testudo bosporica* from Bazaleti, *Mauremys cf. caspica* from Enikend (Azerbaijan) and *Nurnus* (Armenia) (Chkhikvadze, 1977; Bakradze, Chkhikvadze, 1984, 1988). The species *Rana macrocnemis angeloi* is known from Ksatibi, southern Georgia (Bogachev, 1927). These findings demonstrate the development of semiarid landscapes with warm shallow water bodies of open lands in the foothills and mesophilic habitats of the mountains.

The primary breakup of the ranges of Colchic species began in the Middle to Upper Pliocene when the Greater and Lesser Caucasus ridges were affected by intense glaciation (Gvozdetsky, 1954, 1958; Markov et al., 1965).

Fossilization patterns and specific composition of the Upper Pliocene mammals of the Transcaucasus were determined by temperate and mild climate in the Apsheron Age (upper Pliocene), impetuous volcanic activity and arid/semiarid conditions (Fig. 184) in the eastern and southern parts of the Caucasus (Vereschagin, 1959). The primary breakup of hemixerophilic landscapes of the Caucasus likely happened in the Pliocene which led to their separation into the Transcaucasian and Ciscaucasian landscapes due to continuous orogenesis and transgressions of the Caspian Sea. The large-scale inundation of the Balakhan, Akchagyl and Apsheron lowlands, Apsheron Peninsula and the lower Terek during all three transgressions of the Caspian Sea was an important factor affecting the survival of modern Mediterranean refugia. Dagestan foothills remained a terrain because of their connectivity in the Pleistocene

with recent refugia of the North Caucasus. During the same period, the Artvin Depression underwent aridization and separation from humid Lazistan due to orogenesis and the shadow effect in the depression surrounded by the Pontic, Shavsheti and Arsian ridges. Semiarid conditions alike those of the Artvin could also advance on the Akhaltsikhe Highland to the north of today's Upper Kura refugium. The Black Sea coast was dominated in the Pliocene by humid landscapes and only some taxa of xerophilic flora and fauna succeeded to permeate to the steep maritime slopes with locally arid conditions.

So, all recent reptile families in the Caucasus existed in the Paleogenic times (Bakradze, Chkhikvadze, 1988) and its herpetofauna was represented by mesophilic and diverse xerophilic taxa identical or related to many recent species. I.S. Darevsky (1963) thought that by the end of the Pliocene the Caucasus already had the primary centre of its herpetofauna with such genera as *Agama* (= *Paralaudakia*), *Lacerta* (s.l.), *Ophisaurus* (= *Pseudopus*), *Anguis*, *Typhlops* (*Xerotyphlops*), *Malpolon* and *Vipera* (s.l.).

The Pleistocene history of the Caucasus is, first of all, the glacial impact along the axis of the Greater Caucasus Ridge and in the highest parts of the Lesser Caucasus and the Armenian Highland. This history was marked by glacial and pluvial periods of pulsations of the Black Sea and especially the Caspian Sea basins, as well as indirectly affected by European glaciers.

In the Greater Caucasus (Figs. 185, 186), glaciation was much stronger in the western and central parts than in the east. For this reason, the forest zone moved down to the foothills on the northern slopes and to 100–1200 m on the southern slopes of the western and central parts of the Greater Caucasus, even in the warmest and most protected Abkhazia (Kvavadze, Rukhadze, 1989). The pollen analysis has shown that the lowest forest zones changed very insignificantly (extinction of the most warmth-loving species) and the most dramatic changes occurred in the upper forest and subalpine zones. The humid and relatively warm Colchis had become the main refugium for the mesophilic flora (Fig. 187) and fauna in the Pleistocene (Vereschagin, 1959; Adamiants, 1971).

Along with the Colchis, smaller refugia sporadically survived along the Black Sea coast and on the northern slope of the Greater Caucasus Ridge (between the Pshékha and Malaya Laba Rivers) as it is shown by modern distribution of the Tertiary relict Colchic vegetation in the West Caucasus (Kharadze, 1974;



Fig. 184. Pambak Ridge, Armenia. Habitats of *Pelias eriwanensis* and *Coronella austriaca*.



Fig. 185. Zakan Peak, Karachay-Cherkessia, Russian Federation. Habitats of *Pelias dinniki* and *Coronella austriaca*.



Fig. 186. Azgek River, Teberdinsky Nature Reserve, Karachay-Cherkessia, Russian Federation. Habitats of *Coronella austriaca*, *Pelias dinniki*.



Fig. 187. Boxwood in the valley of the Mzymta River, Krasnodar Territory, Russian Federation. Habitats of *Natrix megalcephala*, *Natrix tessellata*, *Zamenis longissimus*, *Coronella austriaca*, *Pelias kaznakovi*.

Pecherin, Lozovoy, 1980; Kholiavko et al., 1978; Adamiants, 1971; Koval, Litvinskaya, 1986). Representatives of the Colchic group survived in the narrow moist canyons with quite stable thermal conditions. Some isolated populations could also survive in the middle elevations as it happened with the Colchic refugia in the Fisht-Oshten site, Lagonaki Plateau and even in the central Caucasus (Kholiavko et al., 1978; Dolukhanov, 1974). Most likely, some small Colchic refugia were preserved also on the southern slope of the eastern part of the Greater Caucasus and in the Kura headwaters. I.S. Darevsky (1967) indicated such refugia for *Archaeolacerta* (= *Darevskia*).

Doubtless, most of the mountain populations of Colchic species vanished during the glacial period and the taxa that survived in the refugia accumulated their original characters to form geographical varieties (subspecies) on different slopes of the Greater Caucasus Ridge and the Adjara-Imereti Ridge. Information provided by A.L. Tahtajyan (1946) and L.I. Maruashvili (1956) prove this, showing that in the glacial times the mean annual air temperature decreased by no more than 1.5–2°C, but precipitation remained abundant at 1500–2000 mm per annum. I.S. Darevsky (1967) considered this fact as a strong argument in favour of the possible survival of reptile refugia

in the seaward foothills of the Gagra and Bzyb ridges (Fig. 188) and in other areas in spite of fundamental post-glaciation range transformations.

For instance, the Pleistocene fossils of *Bufo verrucosissimus* are known from different sites in the Colchis: Kholodnyi Grot (Cold grotto) in Abkhazia and the Belaya Peschera (White cave) in Guria (Chkhikvadze, 1984). Of great interest are the remains of amphibians (*Rana* sp., *Bufo* sp.) from the Kudaro-1 cave in South Ossetia (Darevsky, 1980; Röcek, 1993). In that period of time, xerophytic Mediterranean communities of the West Caucasus survived only in the extreme north-west, in the vicinity of Novorossiysk city, but were strongly ousted by Colchic landscapes that moved downwards. In the Pleistocene, the mesophilic species such as *Ommatotriton ophryticus*, *Bufo verrucosissimus*, *Rana macrocnemis*, *Darevskia brauneri* and *Pelias kaznakovi* reached the western fringes of the Greater Caucasus, along with the mesophytes like *Fagus orientalis*, *Carpinus betulus* and some others which still occurred here in relict microhabitats. Possibly, a small area of Mediterranean habitats was also preserved on the Kavkluk Upland in Abkhazia.

Further development of the Black Sea refugium of the Mediterranean herpetofauna is associated with the

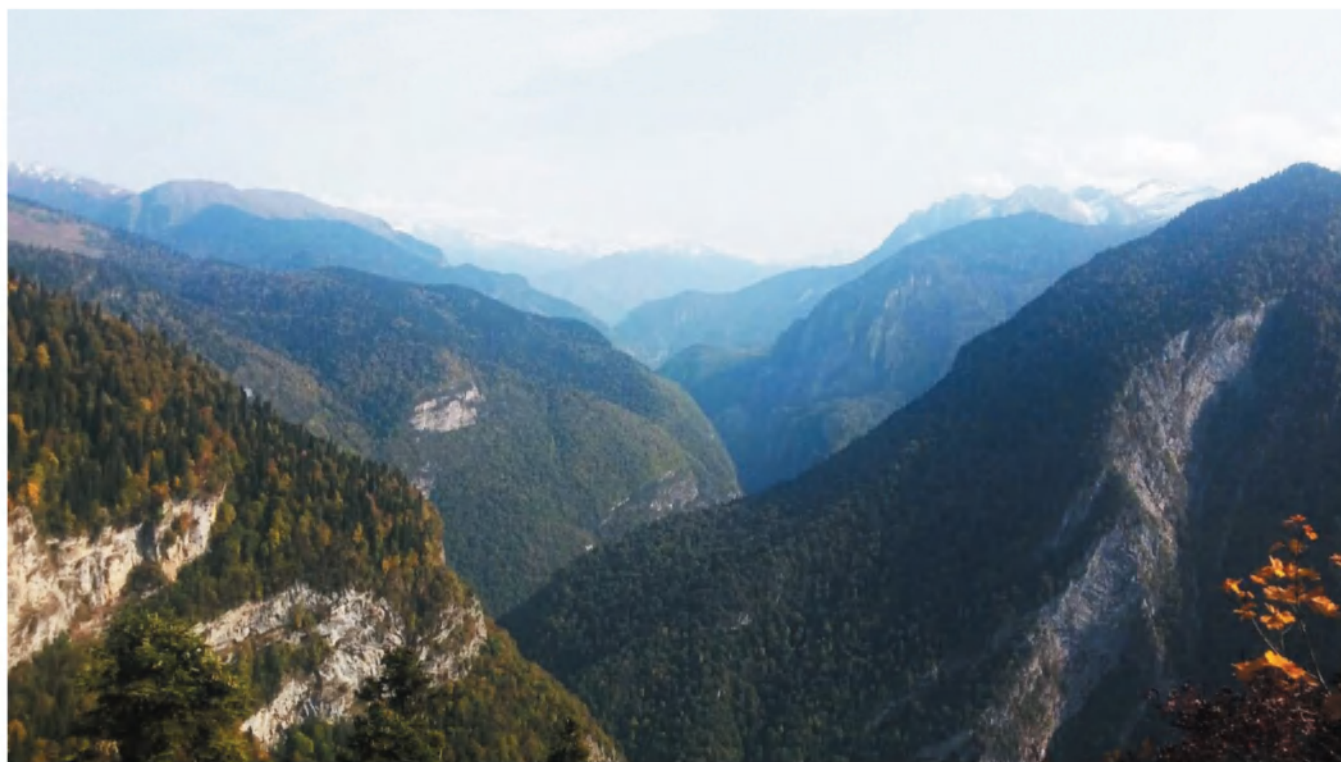


Fig. 188. Bzyb Gorge, Abkhazia. Habitats of *Natrix megalcephala*, *Natrix tessellata*, *Zamenis longissimus*, *Coronella austriaca* in the forest belt, *Pelias dinniki* and *Coronella austriaca* — in the alpine belt.

Holocene when, in its xerothermal period, Mediterranean species of plants and animals won the most isolated and steep maritime slopes back from the Colchis and even moved deeper into the continent by 10–15 km (Tuniyev et al., 2014). In the meantime, the Holocene was marked by the advancement of European steppe species, including mammals, along the Black Sea coast (Figs. 189–190) (Vereschagin, 1959). On this coastline, Mediterranean species possibly never crossed the Inguri River and spread eastwards only to the Kodori River. Even though I.S. Darevsky (1963) was right saying that orogenic processes led to the disjunction of the primary ranges of some xerophilic species in the Caucasus (*Lacerta media*, *Pseudopus apodus*, *Platyceps najadum*, *Testudo graeca*), we do not agree with his opinion about the secondary extinction of these reptiles in western Georgia. Xerophilic conditions and, hence, related species never existed in western Georgia and only low plateaus of the Imereti acted as the north-westernmost (!) boundary for the distribution of drought-tolerant species in the highlands of Asia Minor (Vereschagin, 1959).

This was the reason for the discovery of *Testudo graeca* in the Belaya Peschera near Tskhaltubo (Vekua et al., 1979) together with drought-tolerant mammals (*Hystrix* sp.) under the dominance of forest mesophilic species (*Talpa caucasica*, *Erinaceus europaeus*, *Castor fiber*, *Ursus arctos*, *Martes martes* and others). So, *T. graeca* did not have the continuous range from Novorossiysk to the Caspian Sea as mentioned by A.K. Vekua et al. (1979). Even now, the species *Zamenis hohenackeri* and *Platyceps najadum* have been the “witnesses” of landscape aridity in the Imereti highlands as they are absent in the rest of the Colchic Lowland.

Specific conditions of the Black Sea refugium also corrected some microevolutionary processes, having led to the occurrence of melanistic individuals of *Platyceps najadum* in Abkhazia and the Adler district of Sochi area (south-west of the refugium) and also of neotenic *Lissotriton lantzi* (Rudik, 1989). These processes were likely stimulated by the maximum air temperatures in the arid periods of the Holocene when *L. v. lantzi* could survive only by living exclusively in water bodies, e.g. in the Inkit or Zmeinoe (Snake) lakes in the Mediterranean landscapes of Pitsunda. Recently, neotenic *L. v. lantzi* were found also in the Malaya (Lesser) Ritsa Lake (Tuniyev, 2005).

The nuclei of the recent amphibian and reptile fauna in the highlands of the north-western Caucasus is composed of 6 species (*Lissotriton lantzi*, *Rana mac-*

rocnemis, *Anguis fragilis*, *Darevskia alpina*, *Coronella austriaca*, *Pelias dinniki*), of which two (*D. alpina* and *P. dinniki*) are autochthonous for the axial part of the north-western Caucasus and their ranges do not go beyond the subalpine and alpine zones (Figs. 191–192). The forest species occurring on the southern slopes of some areas present the vestiges of the Colchic refugium and serve an important component for the understanding of possible ways of the prochoresis of different herpetological complexes.

The main ranges of *L. alpina* and *P. dinniki* encompass the mountain meadows to the east of the Mt. Chugush. Along the marginal ridges branching off the Greater Caucasus Ridge, both species reach the Perekovoi (Front) ridges in the north and south where they are known from the peaks of Pshekish, Alous, Yatyrgvarta, Magisho (north), Achishkho, Aibga and Agepsta (south). Beyond the disjunction in the area of the Kolkhidskie Vorota (Colchic gates), they re-appear in the Fisht-Oshten area. Some isolated patches of *P. dinniki* range are scattered to the west, in the subalpine meadow zone of the seaward ridges (peaks Autl, Khakudj, Bekeshei, Grachev Venets). Here, *L. alpina* has been replaced by the Artvin lizard (*D. derjugini*) and the Brauner's lizard (*D. brauneri*) which are usually allopatric with *L. alpina* and normally live in forests. In its turn, an isolated and unusual forest-dwelling population of *L. alpina* exists on the Mt. Sakharnaya (Sugar). The large Pleistocene refugium of high-mountain flora is described from the Ahtsu River valley in vicinity of Adler (Timukhin, Tuniev, 2018).

These examples of contemporary chorology indicate the large scales of the Pleistocene glaciation and resultant downward movements of the mountain meadow zone in the north-western Caucasus. The presence of these indicator species far away from their main ranges has been an indirect evidence of the continuous spreading of subalpine meadows to the closest vicinities of Tuapse and Sochi (peaks Lysaya, Nauzhi, Sakharnaya and others) in the past. The absence of *L. alpina* to the west of the Mt. Khuko indicates a substantial expansion of forest vegetation during the Holocene which led to the substitution of this lizard by systematically and ecologically similar species occurring today in the meadowy seaward mountaintops. The traces of xerothermal period can be found also in the specific composition of the meadows in which the highland species (*Polygonum carneum*, *Campanula tridens* and others) co-exist with thermophilic species of lower forest belts



Fig. 189. Akhtanizovsky mud volcano, Taman Peninsula, Krasnodar Territory, Russian Federation. Habitats of *Elaphe sauromates*, *Natrix natrix scutata*.



Fig. 190. Taman Peninsula, Krasnodar Territory, Russian Federation. Habitats of *Natrix natrix*, *N. tessellata*, *Dolichophis caspius*, *Elaphe sauromates* and *Pelias renardi*.



Fig. 191. Stone scree in the highlands of the Western Caucasus, Krasnodar Territory, Russian Federation. Habitats of *Pelias dinniki* and *Coronella austriaca*.



Fig. 192. Alpine meadows and rhodorets of the North-West Caucasus, Krasnodar Territory, Russian Federation. Habitats of *Pelias dinniki* and *Coronella austriaca*.

(*Cephalanthera longifolia*, *Pteridium aquilinum* and many others).

During the Holocene, the foothills of the southern macroslope of the north-western Caucasus had been largely inhabited by Mediterranean species and Colchic Tertiary relicts which had recovered their ranges up to middle elevations. Like in highland species, their distribution is patchy. The known examples of local populations include *Pelias kaznakovi* from the Guzeripl and Babuk-Aul sites and the peaks of Assara and Aibga; *Lacerta agilis grusinica* from the Laura and Babuk-Aul, Azhek area and the Aibga village; *Lacerta agilis exigua* from vicinity of Ligotkh, Mt. Semiglavaya, the Guzeripl and Kisha sites; *Darevskia pontica* from the Babuk-Aul, Guzeripl, Mt. Tur and the Sosnovoe (Pine) area in the Bolshaya Laba riverside; *Triturus karelinii* from the Bzych Ridge and the Guzeripl site, *Pseudopus apodus* from Mt. Bolshoi Pseushkho and many others.

The East Caucasus, like some longitudinal ridges in the central Caucasus, was dominated by arid and moderately warm areas which were particularly common in Dagestan. The most warmth-loving species also tended to disappear, but the zones of sibliak and oreoxerophytes expanded in the Holocene across the areas where they shrank in the Pleistocene. Galushko (1974) acknowledged the ancientness of Dagestan and Elbrus oreoxerophytes and supposed that their permeation into the depressions of Checheno-Ingushetia occurred only in the Holocene. Even now, semiarid depressions of the East Caucasus protected from cold northern air masses by the Skalistyi Ridge have shallow and short-living snowcover, early spring and longer summer with strong fluctuations in air temperatures (Amirkhanov et al., 1989). The Holocene impacts on the central and especially East Caucasus landscapes are well-known and described in a number of semiarid depressions with oreoxerophytes (Krasnov, 1894; Grossgeim, 1948; Shiffers, 1953; Galushko, 1974). In the highlands of the north-western Caucasus, the xerothermic period did not entail sharp changes in vegetation and fauna, but its influence is evident on the northern slopes (Mt. Tru-Yatyrgvarta; Altukhov, 1967) and the southern slopes (shadow effect in the Mzymta headwaters; edaphic aridity on the Fisht, Oshten, Aibga and Bzych mountain slopes).

Here, apart from the characteristic species such as *Juniperus sabina* and *Spiraea hypericifolia*, some limited areas are covered by cushion and rosette communities, tomillares and sibliaks. Their total coverage is

insignificant, hence different biogeographical considerations often ignore them. However, these habitats and other patches of amphibian and reptile ranges are essential to reconstruct the genesis of the fauna and landscapes in the north-western Caucasus. A notable case is the species *Lacerta agilis mzymtensis* Tuniyev et Tuniyev, 2008 recently described from the Aishkha Ridge and later also found in the upper reaches of the Avadhara River (Tuniyev, 2017). In this site, the shadow effect allowed to retain a number of xerothermic relicts, including the isolated population of the Caucasian oak (*Quercus macranthera*) which is located far away from its main range in Chechnya, Dagestan, eastern Georgia, Azerbaijan and Armenia.

The Transcaucasus did not experience glaciation, except for the highest areas of the Lesser Caucasus and the Armenian Highland (Fig. 193). The downward shift of altitudinal zones and the fringing steppes of the Russian Plain had some impact, but it was much milder than in the West Caucasus where the only Pleistocene record of *Emys orbicularis* is known from the Mt. Mashuk, Pyatigorsk (Alekperov, 1978). During this period, South European steppe landscapes passed the Caucasus from the east and moved into the semi-arid foothills of the southern slopes of the East Caucasus. That is how *Pelias renardi* permeated onto the left bank of the Kura River and survived as a relict of the She-makhi district (Azerbaijan) and, possibly, the adjacent areas of eastern Georgia.

The preservation of Mediterranean species in the Kura-Arax refugium during the Pleistocene is particularly important. Through the floristic analysis of the Binagady fossil site, V.A. Petrov (1939) claimed the existence of savannas or arid sparse forests on the Apsheron Peninsula. The numerous remains of *Testudo graeca binagadensis*, Lacertidae and *Ophisaurus (=Pseudopus) apodus dzhafarovi* were found here (Alekperov, 1978). The Upper Pleistocene *Ophisaurus (=Pseudopus) apodus dzhafarovi* and *Testudo graeca ibera* were documented from the neighbouring Fatmayi area of Azerbaijan (Alekperov, 1978). The latter species was found out in the Pleistocene sites of the eastern Transcaucasus: Georgia – Minge-chaur, Imeris-Gora, Tsopi, Arukhlo, Darkvetis Ekhi, Gienovaya (Hyena) cave; Armenia – Verin Khatunorkh; Azerbaijan – Damjily, Azykh, Talgar (Bakradze, Chkhikvadze, 1984). From the Upper Pliocene to the Middle Pleistocene, the eastern Transcaucasus was dominated by arid foothills covered by steppe-like vegetation (Fig.194) which



Fig. 193. Mt. Sevsar, Saragyukh, Ashotsk, Armenia — type territory of *Pelias darevskii*.

faded away in summer (Vereschagin, 1959). In the same period, mountains of the eastern Transcaucasus continued to retain mesophilic species as shown by the findings of *Lacerta* cf. *agilis*, *Rana* sp. and *Bufo* sp. from the Kudaro-1 Cave in South Ossetia (Darevsky, 1980; Chkhikvadze, 1984; Zerova, Chkhikvadze, 1984; Roček, 1993).

In the lowlands of the eastern Transcaucasus, faunistic changes in the Pleistocene occurred coherently with the sequential substitutions of the Baku, Khazar and Khvalyn Seas. Possibly, the Turanian taxa permeated to the plains of the eastern Transcaucasus three times (Aleksperov, 1978), either passing by the Caspian Sea from the north and south or through the Apsheron-Krasnovodsk Bridge that existed during the maximum regression of the Caspian Sea (Darevsky, 1957a, b; Rustamov, 1981a, b). We surmise that the following species colonized the Caucasus from Central Asia in the Pleistocene: *Ablepharus pannonicus*, *Eremias velox*, *E. arguta*, *Elaphe dione*, *Phrynocephalus mystaceus*, *Ph. guttatus*, *Cyrtopodion russowi*, *Trapelus sanguinolentus* and *Eryx miliaris*. Colonization of *Phrynocephalus horvathi*, *Cyrtopodion caspius*, *Psammophis lineolatum* and *Gloydus caucasicus* took place in the earlier times, possibly already in the Pliocene.

The transgression of the Caspian Sea left the foothills of Dagestan southwards to the Terek River unsubmerged. The Mediterranean landscapes common in the southern part of the East Ciscaucasus Lowland (meadows with *Imperata cylindrica*, thickets of *Paliurus spina-christi*, *Rhamnus pallasii* and others, as well as the vine *Periploca graeca* oakeries) demonstrate that this territory (from the Terek-Sulak Lowland to the south) was not flooded by the Caspian transgressions since the age of the Apsheron Sea (Fig. 195) (Shiffers, 1953). Mediterranean species that spread in the late Pliocene (Grossheim, 1936) were frozen to extinction in the Pleistocene in the Ciscaucasus, but survived in its warmest south-eastern part (Shiffers, 1953) and, to a lesser extent, in Taman.

In the Pleistocene, not only lowland regions of Ciscaucasia, the Kuro-Araks lowland (Figs. 196, 197), but also the southern coastal Dagestan and the Absheron peninsula were repeatedly flooded by Caspian Sea. This makes clear the poor representation of ancient Mediterranean species in these areas and a significant proportion of the presence of late Turanian migrants.

The Pleistocene was marked by repeated inundations of the Ciscaucasus lowlands, Kura-Arax Plain, southern part of maritime Dagestan and the Apsheron



Fig. 194. Loess cliffs, Gobustan, Azerbaijan. Habitats of *Macrovipera lebetina*, *Natrix tessellata*, *Natrix natrix*, *Hemorrhhois ravergieri*, *Eirenis collaris*, *Telescopus fallax*.



Fig. 195. Spring in Nogai Steppe, Dagestan, Russian Federation. Habitats of *Eryx miliaris nogaiorum*, *Dolichophis caspius*.



Fig. 196. Shirvan Steppe, Azerbaijan. Habitats of *Malpolon insignitus* and *Dolichophis schmidtii*.



Fig. 197. Sand dunes of the Caspian coast, Azerbaijan. Habitats of *Elaphe dione*, *Natrix tessellata*.

Peninsula. Therefore, these areas are poor in ancient Mediterranean species, but rich in late Turanian colonizers.

In the Pleistocene, the plateaus and mountains of the Armenian Highland located to the south of the Kura-Arax refugium were struck by the strong glaciation and, then, by the development of steppes and (in foothills) deserts (Fig. 198). As a result, today's Çoruh River basin and the Artvin Depression are bounded by the Colchic Province (Fig. 199) from the north and west (Menitsky, 1984) and adjoin the Armeno-Iranian botano-geographical province (Fig. 200) which has the same boundary as the Anatolian diagonal (Davis, 1971).

In the same time frame, the Upper Kura refugium shrank and, along with the glaciation of the Lesser Caucasus and the Armenian Highland, was affected by active volcanism. Lava flows covered about 50% of the Armenian Highland (Maruashvili, 1946) and, possibly, also ensured the lack of forests (Fig. 201) in recent Armenia according to Yaroshenko (1941).

One of the key processes in the Palearctic history was the survival of the Mediterranean herpetofauna in the Caucasus during the Pleistocene glaciations. The

total coverage and species diversity of the region's refugia are comparable with those of the Balkans, Aegian islands and other parts of the East Mediterranean. The colonization of the Caucasus and the Mediterranean by boreal taxa was one-way; the Mediterranean species themselves are more stenotopic and do not move beyond the Mediterranean biogeographical province (Vereschagin, 1959; Scherbak, 1984).

The effects of the Pleistocene glaciations on the herpetofauna of the western and central Caucasus were multiple: (1) reduction in species numbers and confinement of ranges to a series of local refugia on both macroslopes of the Greater Caucasus Ridge; (2) accumulation of original traits in the refugia with the subsequent development of geographical varieties (subspecies) on the opposite slopes of the western and central Caucasus; (3) formation of the periglacial centre of neoenendemism among the highland reptiles; (4) reproductive changes in autochthonous Colchic amphibians towards the microthermal preferendum.

The Holocene warming in the West Caucasus opened up the opportunities for the following events: (1) coming out of Colchic species from microrefugia



Fig. 198. View from the Khosrov reserve (Armenia) on the peaks of the Great and Small Ararat (Turkey). Habitats of *Macrovipera lebetina*, *Hemorrhhois nummifer*, *Hemorrhhois ravagieri*, *Telescopus fallax*, *Xerotyphlops vermicularis*, *Eirenis punctatolineatus*, *Eirenis collaris*, *Eirenis modestus*, *Platycephalus najadum*, *Eryx jaculus*, *Rhynchocalamus satunini*.



Fig. 199. Lazistan Range in the area of the Atrvin, Turkey. Habitats of *Coronella austriaca*, *Natrix megalcephala*, *Pelias barani*.



Fig. 200. Mountain forests near the Berd, northeastern Armenia. Habitats of *Zamenis hohenackeri*, *Coronella austriaca*, *Hemorrhois ravergieri*, *Platyceps najadum*.



Fig. 201. Javakheti Highlands, dormant volcano Didi-Abuli, Georgia. Habitats of *Coronella austriaca*, *Natrix natrix*, *Pelias darevskii*.

and the recovery of a significant part of their pre-Pleistocene ranges; (2) reduction, fragmentation and disjunction of highland species ranges in the west and their expansion in the central part; (3) permeation of European steppe species from northern foothills, and of East Mediterranean species to the Black Sea coast, along the riversides. In the East Caucasus and the Armenian Highland, the Pleistocene glaciation had led to (1) reduction and, in some areas, complete disappearance of mesophilic fauna; (2) range disjunction with further stabilization of the main refugia of the xerophilic fauna; (3) wavelike impacts of the European steppe and Turanian desert faunas; (4) enhancement of speciation processes in mid-elevation areas under the pressure of volcanogenic activities. In the eastern Transcaucasus, the Holocene warming reduced the xero-mesophilic part of the Mediterranean group, accelerated its retreat

to the mountaintops and provoked the freeing of living spaces in plains and foothills for the Turanian and Asia Minor colonizers.

During the last decade's extensive research of some groups of herps inhabiting the Caucasian Ecoregion were conducted in light of the development of vicariance biogeography (Tarchnishvili et al., 2012; Freitas et al., 2016 et others). This approach is considered these days as the effective technique valuable for understanding the relationships between the speciation and distribution of animals. We can expect the new important results from integrative studies of the Caucasian herpetofauna using traditional methods of disperse biogeography with GIS modelling and multilocus phylogeographic analysis. VWe icThese biogeography provides the most powerful

Chapter 6.

SNAKE ECOLOGY IN THE CAUCASUS

Information about snake ecology is fragmentary and incomplete, primarily because of problems associated with research of these cryptic animals.

Below, we will divide snakes into the ecological groups according to their habitat use, patterns of seasonal and daily activity, requirements for temperature and humidity, diet and feeding, and reproduction. Of course, these factors alone cannot embrace all actual complexity of ecological relationships and in many cases the spatial-temporal or trophic characteristics cannot be unambiguously determined. Nonetheless, we believe that these ecological groups can be a useful tool for better understanding of the role of ophidiofauna in rich biodiversity of the Caucasus.

Spatial distribution

Snakes living in the Caucasus can be divided into terrestrial, fossorial, semi-arboreal or climbing, and riparian (Table 5). The truly arboreal and aquatic species, like freshwater snakes of the subfamily Homalopsinae or sea snakes Hydrophiidae, are not present in this region, but *Natrix natrix* and *N. tessellata* regularly occur in rivers, lakes and even salt waters of the Black and Caspian seas. A great majority of local snakes (41 out of 44, or 93%) are terrestrial, but some of them can also lead fossorial life (*Eryx miliaris*, three *Eirenis* spp.), semi-arboreal or scansorial (*Elaphe sauromates*, *Zamenis longissimus*, *Z. persicus*, *Telescopus fallax*, *Macrovipera lebetina*, *Montivipera raddei*) or riparian life (*Elaphe dione*, *Dolichophis caspius*, *D. schmidtii*, three *Natrix* spp.). Only three snake species (*Xerotyphlops vermiculatus*, *Eirenis persicus*, *Rhynchocalamus satunini*) can be considered as truly fossorial; other 3 species of *Eirenis* genus are both terrestrial and fossorial. They are also very cryptic, creeping deep into the underground during the summer to avoid overheat and dehydration. So, the Caucasian snakes are ecologically quite uniform. The characteristics of their habitat

use are described in species accounts in this monograph and are mainly dictated by species requirements for temperature and humidity.

Many Caucasian snake species are flexible in habitat selection. Only *Eryx miliaris nogaiaorum* can be regarded as a stenobiont living in moving and semi-fixed dunes of sand deserts, as well as in loose soils of wormwood-saltwort and saltwort semi-deserts and deserts. The species *Psammophis lineolatus* is also specific in habitat use, since in the Caucasus it occurs only in the very hot-temperature Nakhichevan Depression but is quite flexible in selection of different semi-deserts, deserts and altitudinal distribution in the more eastern parts of its range. *Natrix natrix*, *N. tessellata*, *Dolichophis schmidtii*, *D. caspius*, *Coronella austriaca*, *Gloydius caucasicus* are ecologically most flexible in the Caucasus.

For example, *Natrix natrix* and *N. tessellata* live in almost all landscapes and elevation zones of the Caucasus Ecoregion. *Coronella austriaca* has a wide distribution area too, except for semi-deserts and deserts. Grass and dice snakes are limited only by the absence of water bodies and smooth snakes ignore the areas without locally mesophilic sites. *Dolichophis schmidtii* and *D. caspius* can exist in waterless conditions of a sandy steppe or stony semi-desert and in riparian reedbeds, hunting and lurking on the bottom of a water body. The pitviper *Gloydius caucasicus* is distributed from humid and swampy subtropical lowlands to dry semi-deserts and mountain steppes in the Talysh Mts. *Macrovipera lebetina* is present in diverse ecosystems of the Caucasus.

The truly forest-dwelling species of the Caucasus Ecoregion are *Zamenis longissimus*, *Z. persicus*, *Natrix megaloccephala*, *Pelias kaznakovi* and *P. pontica*. The mostly sylvan species are *Vipera transcaucasiana*, *Pelias barani*, *P. orlovi* and *P. magnifica*. The species *Coronella austriaca*, *Dolichophis caspius*, *Platyceps najadum*, *Eirenis modestus*, *Zamenis hohenackeri*, *Macrovipera lebetina*, *Montivipera raddei*, *Pelias dinniki*

Table 5. **Biotopic and altitudinal distribution of the Caucasian snakes**

№	SPECIES	Terrestrial	Fossorial	Semiarboreal	Riparian	Elevation a.s.l. (m)
1	<i>Xerotyphlops vermicularis</i>		+			0-2000
2	<i>Eryx jaculus</i>	+	+			600-1700
3	<i>Eryx miliaris</i>	+	+			0-100
4	<i>Platyceps najadum</i>	+				0-2200
5	<i>Hemorrhois nummifer</i>	+				600-1300
6	<i>Hemorrhois ravergeri</i>	+				200-2300
7	<i>Dolichophis caspius</i>	+			+	0-1000
8	<i>Dolichophis schmidti</i>	+				0-2000
9	<i>Coronella austriaca</i>	+				0-3000
10	<i>Eirenis collaris</i>	+	+			0-1600
11	<i>Eirenis modestus</i>	+	+			200-2000
12	<i>Eirenis persicus</i>		+			400-800
13	<i>Eirenis punctatolineatus</i>	+	+			600-2000
14	<i>Elaphe dione</i>	+			+	0-600
15	<i>Elaphe sauromates</i>	+		+		0-2500
16	<i>Zamenis hohenackeri</i>	+				200-2500
17	<i>Zamenis longissimus</i>	+		+		0-1200
18	<i>Zamenis persicus</i>	+		+		0-1500
19	<i>Malpolon insignitus</i>	+				0-1500
20	<i>Natrix megalcephala</i>	+			+	0-1800
21	<i>Natrix natrix</i>	+			+	0-2500
22	<i>Natrix tessellata</i>	+			+	0-2500
23	<i>Psammophis lineolatus</i>	+				up to 600
24	<i>Rhynchocalamus satunini</i>		+			600-1200
25	<i>Telescopus fallax</i>	+				0-1800
26	<i>Gloydus caucasicus</i>	+				0-2200
27	<i>Macrovipera lebetina</i>	+		+		0-2000
28	<i>Montivipera albicornuta</i>	+				1300-2300
29	<i>Montivipera raddei</i>	+				1000-2450
30	<i>Montivipera wagneri</i>	+				1200-1500
31	<i>Pelias barani</i>	+				600-1800
32	<i>Pelias darevskii</i>	+				1900-2800
33	<i>Pelias dinniki</i>	+				1200-3100
34	<i>Pelias ebneri</i>	+				2000-2700
35	<i>Pelias eriwanensis</i>	+				1000-2400
36	<i>Pelias kaznakovi</i>	+				50-1000
37	<i>Pelias lotievi</i>	+				900-2200
38	<i>Pelias magnifica</i>	+				700 -1000
39	<i>Pelias olguni</i>	+				1600 - 2100
40	<i>Pelias orlovi</i>	+				150- 1100
41	<i>Pelias pontica</i>	+				400-1000
42	<i>Pelias renardi</i>	+				0 - 1200
43	<i>Pelias shemakhenisis</i>	+				600-900
44	<i>Vipera transcaucasiana</i>	+				400-1700
	TOTAL	41	8	4	5	

occur in forests only occasionally. The snakes *Dolichophis caspius* and *Platyceps najadum* live predominantly in open landscapes, but along the Black Sea coast of the Caucasus, they live in foothill woodlands. *Montivipera raddei* in Armenia and *Pelias dinniki* in the West Caucasus are often confined to ecotones – *Quercus macrantha* forests and beech-birch crooked, maple and pine forests, respectively. *Zamenis hohenackeri* and *Macrovipera lebetina* inhabit mostly treeless areas, but are truly sylvan in Dagestan (*Z. hohenackeri*) and the Tsav riverside in Armenia (*M. lebetina*).

Some snakes, e.g. the Viperidae, *Natrix natrix*, *N. tessellata* and *Malpolon insignitus* can live in human-dominated landscapes. *Telescopus fallax*, *Zamenis longissimus* and *Macrovipera lebetina* often live in homesteads and outhouses. The mesophilic species are more tolerant to human influences than more specialized species living in arid conditions of steppes, deserts and semi-deserts (*Eryx miliaris*, *Pelias renardi*, *Pelias shemakhensis* and others).

Many Caucasian snakes live in arid and semi-arid foothills and mountains with xerophytic vegetation, and a great majority of them is petrophilic: *Eirenis persicus* and other species of *Eirenis* genus, *Rhynchocalamus satunini*, *Telescopus fallax* all Viperidae spp. (except for *Pelias renardi*), *Hemorrhois ravergieri*, *Dolichophis schmidtii* and *Zamenis hohenackeri*. As montane landscapes prevail in the Caucasus Ecoregion, many snakes live on steep slopes, but for some species living at higher elevations and on precipitous hillsides can be a secondary adaptation caused by full destruction of habitats on plains (for example *Pelias shemakhensis* in Azerbaijan).

Eurytopic species are also more flexible in altitudinal distribution. The ophidiofauna of the Caucasus comprises inhabitants of foothill steppes, plains and mountains of different zonation patterns and, as an opposite, the eurybiont species occurring along a wide gradient of elevations. Most snakes living in the Caucasus are adapted to a great variety of elevations (from 0 to 1600–2450 m asl): *Xerotyphlops vermicularis*, *Platyceps najadum*, *Eirenis collaris*, *Eirenis modestus*, *Coronella austriaca*, *Zamenis hohenackeri*, *Dolichophis schmidtii*, *Hemorrhois ravergieri*, *Elaphe sauromates*, *Natrix natrix*, *N. tessellata*, *Telescopus fallax*, *Macrovipera lebetina* and *Gloydus caucasicus* (Table 5). Within this group, an arbitrary sub-group of snakes inhabiting sites from 600 to 1500–2000 m asl can be selected. The members of this sub-group are *Eryx jacu-*

lus, *E. punctatolineatus*, *Hemorrhois nummifer*, *Natrix megalcephala* and *Vipera transcaucasiana*.

The species living in plains and foothills at 0–1500 m asl are *Eryx miliaris*, *Dolichophis caspius*, *Malpolon insignitus*, *Elaphe dione*, *Z. longissimus*, *Psammophis lineolatus*, *Eirenis persicus*, *Pelias kaznakovi*, *P. orlovi*, *P. magnifica*, *P. pontica*, *P. renardi* and *P. shemakhensis*.

Ten species occur in a range of 1000–2450 m asl: *Montivipera albicornuta*, *M. raddei*, *M. wagneri*, *Pelias barani*, *P. darevskii*, *P. dinniki*, *P. ebneri*, *P. eriwanensis*, *P. lotievi* and *P. olguni*. The species *P. ebneri* and *P. darevskii* live at the highest elevations on mountain tops.

The highlands are characterized by the mean annual air temperature 3.9°C, mean annual air humidity 75% and the least daily and seasonal temperature variations. For example, in the North-West Caucasus winters have stable frosts without the warm-up periods in daytime (Tuniyev, 2007). The absolute maximum was +29°C in July 1957 and the absolute minimum was –29°C in January 1932 (Rybak, 2006). The prevailing precipitation is snow which makes stable snow cover last over half a year (190 days per annum at the Achishkho station) and even the whole year in some places. The mean snow thickness is 482 cm. Even in years with little snow, its cover reaches 2 m. Such severe conditions have stimulated the formation of a fauna of obligate oreophilic snakes: *Pelias dinniki*, *P. darevskii*, *P. ebneri*, *P. eriwanensis*, *P. lotievi* and *P. olguni*. Possibly, the origin of current ranges of the last three species was caused by aridization of the Caucasian highlands.

Some snakes from the Greater Caucasus are optionally oreophilic. These are *Coronella austriaca*, a ubiquitous species widespread from seashores to highlands inclusive. Records of *Natrix megalcephala*, *Elaphe hohenackeri* and *Platyceps najadum* are known from the border of midlands and highlands; in Transcaucasus also *Natrix tessellata*.

Seasonal and daily activity

Snakes of the Caucasus have very different periods of seasonal activity and even sympatric species vary in activity peaks. The shortest period of activity (no more than 3 months) is recorded in *Pelias darevskii* and in some highland populations of *P. dinniki*. No longer than 4–4.5 months is the activity period of *Pelias eriwanensis*, *P. ebneri*, most populations of *P. dinniki*, *P. lotievi*, *P. olguni* and of *Coronella austriaca* from highlands.

The longest activity period is found in autochthonous Colchic species *Pelias kaznakovi*, *Natrix megalcephala* and *Zamenis longissimus*. It lasts from early February to early December, i.e. 10–11 months, and the hibernation is most likely represented by a diapause or a series of diapauses. Interestingly, the Mediterranean snakes co-existing with the Colchic species (*Dolichophis caspius*, *Platycephalus najadum*, *Natrix tessellata*) demonstrate a shortened period of seasonal activity confined to the warmest period from early April to early October, i.e. 6 months, which is a half of that in Colchic snakes.

The species of wide altitudinal distribution experience a reduction of seasonal activity over elevations. The Colchic water snake is continuously active in foothills, but on upper limits of its distribution (1600–1800 m asl) it is active only from May to mid-September. Smooth snakes are active from late March-early April to October on seashores and from late April-May to late August-early September in mountains (Tuniyev, Tuniyev, 2006). Also, the same species have a longer (by 1–1.5 months) activity period on the southern than on the northern macroslope of the Greater Caucasus Ridge because of their exposure to the sun (Tuniyev, 1987).

Seasonal activity of the fossorial and semi-fossorial species (*Xerotyphlops vermicularis*, *Eirenis collaris*, *E. punctatolineatus*, *E. persicus*, *Rhynchocalamus satunini*) is quite short and lasts from April to early June when these snakes crawl in the topsoil, under stones or, at nighttime, on the ground. With the summer heat, they move deep into the soil and rock crevices. Summer hibernation is also recorded in some populations of both species of *Eryx*. In early June, we observed the mass basking of *Eirenis modestus* on the surface after a heavy and long downpour in the Tbilisi suburbs. At 13:00–17:00 snakes were basking under the sun, lying on flat stones in xerophytic vegetation.

An overwhelming majority of snakes in the Caucasus (41 out of 44, 93%) are diurnal. One-fourth of them (11 species, 25%) have mixed (diurnal and crepuscular) activity and only 3 species (7%) are crepuscular and nocturnal. Climatic conditions can cause some shifts in activity patterns. For example, nocturnal activity of normally diurnal snakes *Natrix natrix* and *N. tessellata* was recorded in different areas of the West Caucasus (Tuniyev, 2001) as well as for *Pelias shemakhensis* in Eastern Georgia (Tuniyev et al., 2018b).

Research in Khosrov Forest Reserve of Armenia (Tuniyev, Unanyan, 1986) has enabled to identify three groups of reptiles according to their daily activ-

ity patterns in late spring: (1) Species active throughout a hot period of the day; (2) Species with clear double-peak activity in warm morning and evening hours; and (3) Species active in evening time. A.M. Sergeev (1939) noted that in reptile's body temperature has been regulated in daytime by behavior of an animal which chooses the place with optimal temperatures in compliance with the primary adaptation mechanisms related to the areas of the species origin. In case of the three groups of reptiles in Khosrov Forest, the first group comprised the species active from 9:00–9:15 to 17:00–18:00 when the temperature of the near-surface air was no less than 7°C. They were active at the highest temperatures (+38°C), but lurked in shadows during the hottest hours. These species belong to the Asia Minor (Iranian) zoogeographical group and have been its endemics. The second group was represented by the Mediterranean species – dice snake and blunt-nosed viper. These species are active in 10:00–13:00 and 15:30–18:00 when the air temperature is 8–27°C. The third group comprised the autochthonous species – spotted whip snake and Transcaucasian ratsnake. These reptiles are active only in 15:30–17:30 at temperatures 19–27°C. During 4–5 hours (8:00–13:00), the temperature of the near-surface air remains very low, then it heats up in a very short period to reach over 20°C. The species originated from the warmer regions (Iranian and Mediterranean groups) use all or almost all daytime to heat and hunt. In contrast, speciation of autochthonous snakes proceeded in rather harsh conditions of the Lesser Caucasus and the Armenian Highland, so they use only the most optimal space of time, i.e. the evening, when the scorching stones and ground begin to gradually cool.

In late September-early October daily activity of most snakes changes. The species of the Iranian group are active in the hottest hours around the noon when they bask near the entrance to the shelter. In opposite, autochthonous species become active during the entire daytime.

The crepuscular and nocturnal species are the Mediterranean Cat Snake, Javelin sand boa and desert sand boa, all living in arid conditions. Obligatory existence of these nocturnal species in different temperature conditions often confirms the postulates about considerable homogeneity of thermal biology in large taxonomic groups, thus emphasizing the role of historical factors in formation of herpetological complexes (Ananjeva et al., 1997).

Diet and feeding

In the Caucasus, snakes feed predominantly on small vertebrates and, to a lesser extent, on arthropods (e.g., small fossorial snakes – *Eirenis* species). The stenophages having a limited diet are only few. The European blind snake is among a few North Palearctic species specializing on certain food items. Its main food comprises imagines, larvae and eggs of ants.

Cryptic snakes, mostly burrowers, can eat secretive invertebrates without emerging on the surface. A comparative analysis of diets of three dwarf snake species has shown their separation in food niches and led to a hypothesis that the dominance of spiders in the diet of *E. collaris* is caused by cryptic life of this snake and its feeding beneath the stones (Dotsenko, 1987). The other two species (*E. modestus*, *E. punctatolineatus*) were indeed recorded by us more often on the surface what contributed to active feeding on orthopterous insects.

Most of the Caucasian snakes are euryphages feeding on almost all amniotic vertebrates (Table 6). These are *Hemorrois nummifer*, *H. ravergeri*, *Dolichophis caspius*, *D. schmidtii*, *Elaphe dione*, *Telescopus fallax*, *Gloydus caucasicus*, *Macrovipera lebetina obtusa*, *Pelias lotievi*, *Montivipera raddei*, *Vipera transcaucasiana* and others. Some of them prey mainly on rodents and birds: *Elaphe hohenackeri*, *E. longissima*, *E. persicus*, *Malpolon insignitus*, *Pelias dinniki*, *P. eriwanensis* and *P. kaznakovi*. Many snakes hunt on other reptiles (Table 6). The ratsnakes *Elaphe dione* and *E. sauromates*, like other scansorial species, also feed on bird eggs and have special morphological adaptations for crushing eggshell (Chernov, 1959). The lower processes of the vertebrae (hypopophis) jut out into the dorsal wall of the esophagus and break the shell of a swallowed egg by squeezing it from the opposite sides.

The *Natrix* species, especially water snakes, are ichthyophages and batrachophages feeding on fishes and amphibians, respectively. Grass snakes feed equally on amphibians and fishes, but for fish-eating dice snakes amphibians are supplementary food. Large-headed or Colchic water snakes prey exclusively on amphibians. and, as an exception, on mammals. All *Natrix* spp. swallow their prey alive.

The Caucasian snakes also comprise saurophages, i.e. lizard eaters. These are the Dahl's whip snake, smooth snake and Montpellier snake, but they also feed on snakes and rodents. The steppe ribbon racer show typical saurophagy throughout a range (Ananjeva et al., 1997).

Age-dependent changes in snake predation patterns are poorly studied. It is known that size limitations play a major role in feeding of juvenile snakes. Juvenile individuals of vipers (*P. dinniki*, *P. renardi*, *P. kaznakovi*, *P. shemakhensis*, *Montivipera raddei* and even *V. transcaucasiana*) feed on small lizards, chelicerates and orthopterous insects. Feeding on orthopterans also was reflected in the name of the genus *Acridophaga* Reuss, 1927 which once comprised *Pelias eriwanensis* and *P. renardi* (Golay et al., 1993). A comparative study of the toxicity of venoms of the *Pelias* vipers for crickets *Gryllus assimilis* found different effects among the species (Starkov et al., 2007). The vipers *Vipera berus* and *V. nikolskii* (= *Pelias berus* and *P. nikolskii*) do not eat insects, but *Vipera renardi*, *V. lotievi*, *V. kaznakovi* and *V. orlovi* (*Pelias renardi*, *P. lotievi*, *P. kaznakovi* and *P. orlovi*) do. The venom of the second group's snakes is more toxic, so the authors suppose that entomophagy is a genetically imprinted trait and not a dietary adaptation.

The diet of snakes is also affected by their spatial distribution and hunting behavior (Greene, 1997). Active foraging, passive foraging (sit and wait) and prey killing ways play an important role in prey selection (Ananjeva, Orlov, 1983). Sand boas and their relatives kill their prey through constriction by body coils. Smooth snakes and Montpellier snakes also use similar tactics while hunting. The snakes of genera *Dolichophis*, *Hemorrois* and *Platyceps* kill by keeping their prey down to the ground. Feeding strategy between compressing rings and crushing to the substrate is observed in species of the genera *Elaphe* and *Zamenis*.

Dotsenko (1987) noted different feeding strategies among the *Eirenis* spp. and explained them by dietary variation. The Caucasian species of *Dolichophis*, *Hemorrois*, *Platyceps*, *Psammophis* and *Natrix* use active chase. A Dahl's whip snake is wide foraging species: it will chase its prey and capture it on the run, swallowing small lizards alive and killing larger organisms pinning them down to the ground. The Viperidae, including the Caucasian species from the subfamily Viperinae and the Siberian pit viper, are sit-and wait foragers, they lurk and kill from ambush.

Using venom apparatus is an essential tool of feeding behavior in snakes. Among the Caucasian species, the rear-fanged colubrids with large fangs (Montpellier snake, Steppe Ribbon Racer, Mediterranean Cat Snake) kill their prey by venom injection. The most sophisticated venom apparatus is developed in viperids. Their

Table 6. Feeding and reproduction patterns of the Caucasian snakes

№	Patterns Species	Mode of feeding						Mode of reproduction	
		Ichthyophagy	Arthropodophagy	Batrachophagy	Herpetophagy	Ornithophagy	Therophagy	Egg-laying	Ovoviviparity
1	<i>Xerotyphlops vermicularis</i>		+					+	
2	<i>Eryx jaculus</i>				+		+		+
3	<i>Eryx miliaris</i>				+		+		+
4	<i>Platyiceps najadum</i>				+++	+	+	+	
5	<i>Hemorrhois nummifer</i>				+	+	++	+	
6	<i>Hemorrhois ravergieri</i>				+	+	++	+	
7	<i>Dolichophis caspius</i>			+		+	++	+	
8	<i>Dolichophis schmidtii</i>				+	+	++	+	
9	<i>Coronella austriaca</i>				+++	+	+		+
10	<i>Eirenis collaris</i>		+					+	
11	<i>Eirenis modestus</i>		+					+	
12	<i>Eirenis persicus</i>		+					+	
13	<i>Eirenis punctatolineatus</i>		+					+	
14	<i>Elaphe dione</i>				+	++	+++	+	
15	<i>Elaphe sauromates</i>				+	+	+++	+	
16	<i>Zamenis hohenackeri</i>				+	++	+++	+	
17	<i>Zamenis longissimus</i>				+	+	+++	+	
18	<i>Zamenis persicus</i>				+	+	++	+	
19	<i>Malpolon insignitus</i>				++	+	+	+	
20	<i>Natrix megalcephala</i>			+			+	+	
21	<i>Natrix natrix</i>	+		++				+	
22	<i>Natrix tessellata</i>	+++		+				+	
23	<i>Psammophis lineolatus</i>				+++		+	+	
24	<i>Rhynchocalamus satunini</i>		+					+	
25	<i>Telescopus fallax</i>				+++		+	+	
26	<i>Gloydus caucasicus</i>		+		+	+	+++		+
27	<i>Macrovipera lebetina</i>		+		+	++	+++	+	
28	<i>Montivipera albicornuta</i>		+		+	+	++		+
29	<i>Montivipera raddei</i>		+		+	+	++		+
30	<i>Montivipera wagneri</i>		+		+	+	++		+
31	<i>Pelias barani</i>		+		+		++		+
32	<i>Pelias darevskii</i>		+		++		+		+
33	<i>Pelias dimmiki</i>		+		++	+	++		+
34	<i>Pelias ebneri</i>		+		+		+		+
35	<i>Pelias eriwanensis</i>		++		++		+		+
36	<i>Pelias kaznakovi</i>		+		+	+	++		+
37	<i>Pelias lotievi</i>		++		++		+		+
38	<i>Pelias magnifica</i>		+		+		++		+
39	<i>Pelias olguni</i>		+		++		++		+
40	<i>Pelias orlovi</i>		+		+		++		+
41	<i>Pelias shemakhensis</i>		++		++	+	++		+
42	<i>Pelias pontica</i>		+		++		++		+
43	<i>Pelias renardi</i>		++		++	+	++		+
44	<i>Vipera transcaucasiana</i>				+	+	++		+
	Total	2	24	4	34	22	36	23	21

venom glands represent the transformed salivary glands connected by special venom-conducting ducts with the long and tubular fangs located on the mobile maxilla. This effective mechanism of invenomation allows vipers to kill rather large-bodied prey from ambush (Pough, Groves, 1983; Greene, 1992). Prey differentiation is also an important factor of hunting success. It is studied mostly in terrariums and only singular research efforts are carried out in the wild to supplement the extant knowledge.

It was found out that regardless of prey body size (unfledged chicks, rodent offspring, newborn kittens) blunt-nosed vipers did not use venom to kill defenseless prey, but ate it right after the chemotactile observations. Animals moving away for a short distance after the bite (lizards, rodents) were struck by a classical short bite with venom injection. Finally, the victims that could become unavailable to vipers after the bite (adult passerines) were firmly held in jaws until death. This phenomenal ability of vipers to recognize physiological and age characteristics of prey is a subject of evolutionary and behavioral studies of venomous snakes.

Reproduction

A significant part of the Caucasian snakes (21 of 44, i.e. 48%) are ovoviviparous (Table 6) and the remaining reproduce by laying eggs, so are oviparous. Ovoviviparity is a mode to produce offspring in which an embryo develops fully in the egg inside the mother's body, but is released from shell membranes immediately after oviposition and its connection with mother even resembles the mammalian placenta. This mode of reproduction is common in the subfamilies Erycinae, Crotalinae and Viperinae, i.e. the groups the Caucasian species of the genera *Eryx*, *Gloydius*, *Montivipera* and *Pelias* belong to. This reproduction mode can contribute to living in mountains with extreme climate and short periods of activity.

Ovoviviparity has often been considered as an adaptation to population self-maintenance in conditions of shortened period of activity caused by harsh climatic conditions of high latitudes or altitudes (Sergeev, 1940; Tinkle, 1977). The obligate oreophilic snake species in the Greater Caucasus are *Pelias dinniki* and *Pelias lotievi*, i.e. just ovoviviparous species. The ovoviviparous smooth snake *Coronella austriaca* widespread from the seashore to highlands is an optional oreophile. In the meantime, oviparous species such as *Natrix megaloc-*

cephala, *Zamenis hohenackeri* and *Platyceps najadum* can also be present in the transition zone of mid-elevations and highlands. So, co-existence of ovoviviparous and oviparous snakes in the mountains makes the hypothesis of climatic effects on reproduction modes quite ambiguous (Sergeev, 1940; Tinkle, 1977).

The survival of obligate oreophiles in highlands can result from specific reproduction strategies maintaining the species' reproductive capacity. Over 30 years of research have shown that *P. dinniki* come out of their hibernacula in a period from the last week of May to the first half of June when the mean daily air temperature near the surface reaches +11°C (Tuniyev, 2008). The duration of seasonal activity of these vipers depends entirely on weather conditions. Hibernation in subalpine and alpine zones begins in the second half of September. In overcast summer days snakes are active throughout a day under the air temperature above +10°C. When the air temperature decreases to +8°C, vipers do not emerge on the ground. Reproduction of wild and captive *P. dinniki* is confined to late August-early September.

However, in some populations scattered across the West Caucasus pregnant females captured in the wild and placed then in terrariums produced their offspring later, from the last week of September to the first week of November. The sites where these lingering females came from comprised the Mt. Khakuj (western part of the Trasnodar Territory), Mt. Oshten in the highland limestone Fisht-Oshten massif (Republic of Adygeya); Aishkha Ridge (a part of the Greater Caucasus Ridge), Lake Kardyvach (Krasnodar Territory) and the Kamennyi Klad (Stony Treasury) Ridge (Arabika Massif, Abkhazia) (Table 6). The mean daily air temperatures in this period in the wild varied from 3 to 8°C. In highlands, the first snow fell in mid-September and the steady snow cover was formed in mid-October. Under these unfavorable weather conditions, females had to leave for hibernation pregnant.

Now it becomes clear why the recently born young-of-the-year of *P. dinniki* were recorded in the wild in late June-early July (Table 6). Ability of female Dinnik's vipers to hibernate during pregnancy is not mass, but regular in certain localities. Possibly, Bozhansky's (1982) findings of non-breeding females in marked *P. dinniki* populations in the next summer are relevant to this issue too. Naturally, females having parturition in the beginning of the next summer do not mate and stay barren.

Another interesting feature in reproduction of highland snakes is their ability to produce offspring a year after the last copulation. It was found out in captive individuals of *P. dinniki* and *Natrix natrix persa*. Two pregnant females of *P. dinniki* were captured in July 1988 near the Lake Kardyvach at 1870 m asl. In late August of the same year, they produced 5 and 7 offspring. Then these females were kept in isolation in terrariums and in the next August they produced 2 offspring each. A similar situation was observed in a female of *N. n. persa* captured in Armenia on the Javakheti Highland, near Ashotsk above the Lake Arpi at ca. 2000 m asl. In July, this female laid 13 eggs from which the offspring hatched after incubation. In the next year, the same female kept in isolation laid 7 eggs. Incubation of this fully fertile clutch has led to the emergence of healthy neonates. Asexual reproduction of female snakes in highlands can be related to optional parthenogenesis, long-term retention of viable sperm or to delayed development of fertilized eggs. Parthenogenesis is not excluded, but hardly possible for these species as *P. dinniki* and *N. natrix* are bisexual species of quite high population densities. In the past decade, parthenogenesis is recorded in snakes of the families Acrochordidae (Dubach et al., 1997), Crotalinae and Colubridae (Schuett et al., 1997; our data) and Boidae (Kuhn, Schmidt, 2004). As relevant investigations are problematic in the wild, these results were obtained in captivity. Biological meaning of parthenogenesis is usually attributed to populations with low chances of encounters between the opposite sex individuals (Lenk et al., 2005), so we believe that asexual reproduction of the Caucasian snakes can be caused by sperm retention or delayed egg development. Only special histological and molecular genetic studies can give answers to this question.

Retention of viable sperm in a female's oviduct is recorded in all squamate reptiles, except for the amphisbaenians (Sever, Hamlett, 2002; Siegel, Sever, 2006). The mechanisms of related adaptations in highland snakes of the Caucasus could appear in the Pleistocene when the main and marginal glaciers disintegrated the continuous ranges of the ancestor species. Thaw patterns are very variable even now across the sites and years. In the Pleistocene, timing of hibernation end and duration of activity periods were different even within an area occupied by a single micropopulation. Such variation could decrease population densities, shift mating periods and, eventually, hinder the contacts between

potential parents. So, unique reproductive properties of snakes living in highlands of the Caucasus were likely formed in the glacial period during the autochthonous development on mountaintops.

Sympatric species

The numbers of sympatric species vary across the regions of the Caucasus depending on species and habitat diversity per unit of area. The same species can be sympatric to each other in one area, but allopatric or parapatric elsewhere. There are almost no sympatric species to *Pelias darevskii*, but *Coronella austriaca* can act as such in some sites (Table 7). Twenty species (46.5%) are sympatric to 2–9 species, 18 species (41.9%) to 10–20 and 4 species (9.3%) to 25–31. The four species capable of co-existing with maximum numbers of other snakes are *Natrix natrix*, *N. tessellata*, *Coronella austriaca* and *Platyceps najadum*. The *Natrix* species separate by preferring habitats near water, whereas smooth snakes and Dahl's whip snakes are champions in their ability to live near people.

The lowest numbers of sympatric species are recorded along the shorelines of the Azov, Black and especially Caspian seas (*Natrix natrix*, *N. tessellata*) and in psammophilic habitats of the East Ciscaucasus (*Eryx miliaris*, *Dolichophis caspius*). On the border with the Caucasian Isthmus, in Kalmykia, *Eryx miliaris* is sympatric with *Malpolon insignitus*. The snakes living on mountaintops are also few – *Pelias dinniki*, *P. lotievi* and *Coronella austriaca* in the Greater Caucasus; *Pelias eriwanensis*, *Coronella austriaca*, *Natrix natrix* and *N. tessellata* in the Lesser Caucasus and the Armenian Highland; *Pelias ebneri* and *Coronella austriaca* in the Talysh and Alborz Mts.; *Pelias barani* and *Coronella austriaca* in subalpine and alpine zones of the Lazistan Ridge. The most diverse set of sympatric snakes is recorded on the Meghri Ridge in southern Armenia which includes *Montivipera raddei*, *Macrovipera lebetina*, *Dolichophis schmidtii*, *Elaphe sauromates*, *Zamenis hohenackeri*, *Platyceps najadum* and *Coronella austriaca*.

In the Caucasus Ecoregion, the sympatry gradients grow from north to south and from mountaintops to foothills. The most representative complexes of snake species are located in foothills encircling the Kura-Arax Lowland and the Arax Canyon. The Talysh foothills, Artvin Depression and the Black Sea coast of the Caucasus also comprise diverse snake complexes.

Chapter 7.

CONSERVATION OF SNAKE DIVERSITY IN THE CAUCASUS ECOREGION

Snakes are one of the most sensitive components of natural ecosystems, so they respond negatively to environmental changes and demand for urgent preservation. Only few species are capable of living near humans and, considering the man's hatred and fear of these reptiles the survival rates of snakes killed in every available opportunity are low. Sadly, the long-term existence of viable snake populations is possible only in protected areas.

Wildlife research and conservation are historically active in the North Caucasus. N.Ya. Dinnik, N.V. Nasonov, N.A. Bush, Kh.G. Shaposhnikov, F.K. Lorenz, N.F. Reimers, Kh.G. Nasimovich and many others worked hard in environmental studies, establishment and maintenance of protected areas in the North-West Caucasus. The beginning of nature conservation was laid in 1888 when Imperial family of Russian Empire leased lands in the Belaya River and Bolshaya Laba River interfluvium for hunting. Later on, this area was transformed into Kavkazsky (Caucasian) Reserve (now - Caucasian State Nature Biosphere Reserve, named after Kh. Shaposhnikov).

Currently, the Caucasus Ecoregion is covered by the dense network of protected areas comprising 51 reserve, 24 national parks, 162 sanctuaries and numerous natural monuments, protected landscapes etc. Among the region's countries, they are distributed as follows:

ABKHAZIA

R e s e r v e s (3): Pskhu-Gumista, Pitsunda-Mussera, Skurtcha.

N a t i o n a l p a r k s (1): Ritsa Relict.

The establishment of Kodori National Park is planned.

AZERBAIJAN

R e s e r v e s (14): Ismaili, Pirgulu, Ilisu, Zakatala, Eldar Shami (Pine), Garayazi, Korchay, Shahbuz, Besitchay, Kyzyl Agach, Shirvan, Turianchay, Mud Volcanoes of Baku-Absheron Peninsula, Gara Gol.

N a t i o n a l p a r k s (11): Samur-Yalama, Altyaghaj (Altiagac), Goygol, Aggol (Agh Gol), Hyrkan, Shirvan, Absheron, Zangazur, Shahdag, Ordubad named after Hassan Aliyev, Gobustan.

S a n c t u a r i e s (20): Ismaili, Korchay, Sheki, Ordubad, Zuvand, Kichik Kizil Agac, Gusar, Barda, Garayazi-Aghstafa, Gubadly, Gabala, Gizilja, Dashatly, Arazboyu, Gil adasi, Bendovan, Gakh, Hirkan, Shamkir, Lachin

ARMENIA

R e s e r v e s (3): Khosrov Forest, Shikahogh, Erebuni.

N a t i o n a l p a r k s (4): Sevan, Dilijan, Arevik, Lake Arpi.

N a t u r e p a r k s (1): Tatev

S a n c t u a r i e s (26): Zangezour, Goravan Sands, Akhnaabad yew grove, Aragats alpine, Arzakan-Meghradzor, Hazel, Banks' pine, Boghakar, Gandzak, Getik, Juniper sparse forests, Gyulagarak, Goris, Eghegnadzor, Ijevan, Khor Virap, Hankavan hydrological, Herher sparse forests, Margahovit, Caucasian rosebay, Vordan Karmir, Jermuk, Jermuk hydrological, Plane tree grove, Lake Sev, Zikatar.

Also, there are 230 natural monuments in Armenia. The establishment of Gnishik and Khustup sanctuaries is ongoing.

GEORGIA

R e s e r v e s (14): Borjomi, Kintrishi, Kobuleti, Adjameti, Sataplia, Kazbegi, Tusheti, Batsar, Babaneuri, Lagodekhi, Mariamjvari, Vashlovani, Saguramo, Algeti.

N a t i o n a l p a r k s (5): Borjomi-Kharagauli, Colchic, Tusheti, Vashlovani, Mtirala.

S a n c t u a r i e s (11): Ito, Lagodekhi, Kobuleti, Katsoburi, Gardabani, Iori, Korugi, Chachuna, Nedzvia, Ktsia-Tabatskuri, Tetrobi.

N a t u r a l m o n u m e n t s (3): Alazani, Artsivi Canyon, Takhti-Tefa.

Protected landscapes (1): Tusheti.

The establishment of five protected areas (Java-kheti, Tbilisi, Svaneti, Racha-Lechkumi, David-Goredji) is planned.

IRAN

There are 204 protected areas in Iran, including 25 national parks, 39 wildlife refuges, 140 protected areas and 13 natural monuments. The Caucasus Ecoregion encompasses 1 national park, 6 wildlife refuges, 10 protected areas and 6 natural monuments.

National parks (1): Bujagh.

Wildlife refuges (6): Kiamaki, Amir Kolayeh, Londvil, Selkeh, Sarkhangol, Chokam.

Protected areas (10): Agh Dagh, Marakan, Arasbaran, Siah Kashim, Gasht Rudkhan and Siah Mazgi, Bujagh, Siah Rud, Sarvelat and Javaher Dasht, Lisar, Chahar Bagh.

Natural monuments (6): Khoshke Daran, Sosan Sefid, Serv Kharzevil, Alamkuh, Gharyahkan, Sebelan.

RUSSIA (Map 47)

Reserves (8): Kavkazsky, Teberdinsky, Kabardino-Balkarsky Vysokogorny (High-mountain Kabardino-Balkarian), Severo-Osetinsky (North-Ossetian), Erzi, Dagestansky, Rostovsky, Chernye Zemli, Utrish. Total coverage 5025 km².

National parks (4): Sochi, Prielbrusie, Alania, Kislovodsky. Total coverage 3475 km².

Nature Parks (1): Bolshoy Tkhach (3705 ha).

It is planned to establish Irbis Nature Park in Ingushetia

It is planned to expand Sochi National Park by incorporating the Loo Forest Farm, the establishment of Samur National Park in Ashotsk.

There are 92 sanctuaries (State and Regional) and several hundreds of natural monuments in the Russian part of the Caucasus Ecoregion, including 324 natural monuments in the Krasnodar Territory alone (Tilba et al., 2002).

Krasnodar Territory - 5 State Sanctuaries: Krasnaya Gorka, Priazovsky, Sochinsky, Tamano-Zaporozhsky, Tuapsinsky; 10 Regional Sanctuaries: Abrausky, Agriysky, Belorechensky, Gorjache-Klyuchevskoy, Kamyshanova Polyana, Krymsky, Novo-Berezansky, Psebaysky, Srednelabinsky, Chernogorye.

Adygheya - 2 State Sanctuaries: Dakhovsky, Shovgenovsky.

Stavropol Territory – 44 State Sanctuaries: Alexandrovsky, Azgirsky, Bazhigan, Batalinsky, Besh-taugorsky, Bolshoy Essentuchok, Buguntinsky, Burukhunsky, Vishnevaya Polyana, Vostochny, Vshivoe Ozero, Galyugaevsky, Gora Budarka, Debri, Dyuna, Irgaklinsky, Kravtzoovo Ozero, Krasnogvardeysky, Kumagorsky, Lesnaya Dacha, Liman, Maly Essentuchok, Manych-Gudilo, Novoselitzky, Novotroitsky, Ozero Tambukan, Priozerny, Russky Les, Safonova Dacha, Solenoe Ozero (Krasnogvardeisky District), Solenoe Ozero (Petrovsky District), Sotnikovsky, Stavropoletz, Stavropolsky Chernozem, Stepan Bugor, Strizhament, Udachny, Budarka, Urochoszhe Peski, Formika, Chograysky.

Karachay-Cherkessia – 1 State Sanctuary – Dautsky; 8 Regional Sanctuaries: Cheremukhovsky, Arkhyzsky, Chiliksky, Damkhurz, Khasautsky, Elburgansky, Labinsky, Belaya Skala.

Kabardino-Balkaria – 8 State Sanctuaries: Verkhne-Kurpsky, Tersko-Alexandrovsky, Ozreksky, Kara-Su, Chegemsky, Verkhne-Malkinsky, Nizhne-Malkinsky, Tambukansky; and 1 – regional Ekaterinogradsky Sanctuary.

Ingushetia – 1 State Sanctuaries: Ingushsky.

North Ossetia-Alania – 2 State Sanctuaries: Turmonsky, Tzeysky; 2 Regional Sanctuaries: Zamanikulsky, Zmeysko-Nikolaevsky.

Chechnya – 1 State Sanctuary – Sovetsky and 8 regional: Shalinsky, Vedensky, Urus-Martanovsky, Argunsky, Bragunsky, Stepnoy, Parabachevsky, Zelenaya Zona Groznogo.

Dagestan – 3 State Sanctuaries: Agrakhansky, Samursky, Tljaratinsky; 10 Regional Sanctuaries: Andreyaulsky, Meleshtinsky, Kajakentsky, Deikagarsky, Kasumkentsky, Charodinsky, Bezhtinsky, Tarumovsky, Kosobo-Kelebsky, Yangijurtovsky.

SOUTH OSSETIA

There is one South-Ossetian State Reserve (former Liakhvi Reserve).

TURKEY

The Turkish part of the Caucasus Ecoregion is covered by 9 protected areas, of which there are 1 biosphere reserve, 4 national parks and 4 sanctuaries.

Reserves (1): Camili Biosphere Reserve.

National parks (4): Altyndere, Karagöl-Sahara, Hatila Vadisi National Park, Kaçkar Dağlary.

Sanctuaries (4): Dilberduzu, Yailalar Koyu, Gorgit, Efeler.



Map. 47. Administrative map of the Caucasian Ecoregion, 1 — Rostov Province, 2 — Kalmykia, 3 — Stavropol Territory, 4 — Dagestan, 5 — Krasnodar Territory, 6 — Adygheya, 7 — Karachay-Cherkessia, 8 — Kabardino-Balkaria, 9 — North Ossetiya-Alania, 10 — Ingushetia, 11 — Chechnya.

In the Caucasus Ecoregion, like in many other regions worldwide, snake conservation is effective only in reserves and national parks, but is perfunctory in lower-level protected areas. So, the analysis of compliance of the extant Econet (network of protected areas) to the needs of ophidiofauna preservation becomes a profoundly important task.

The Priority Conservation Areas (PCA) and the corridors between them designated by CEPF in the Caucasus (Map 2) almost fully represent the key areas of the most important ecosystems in Armenia, Geor-

gia, Azerbaijan and the neighbouring areas of Turkey and Iran. In these countries, the regional Econets are delineated as based mainly on the existing or planned protected areas. The Caucasian parts of Turkey and Iran are nearly fully set aside as priority areas. The situation in Russia (Map 47) and Abkhazia is different. The central axial part of highlands of the Greater Caucasus Ridge is defined quite artificially and almost deprived of snakes, but the vast tracts of the Black Sea coast, remnants of pristine steppes and meadow-steppes in the West and Central Ciscaucasus, unique dry steppes

and sandy lands in the East Ciscaucasus, foothills and mid-elevations in the northern Jurassic depression between the Skalistyi and Bokovoy ridges, foothills and maritime Dagestan and other snake-rich regions remain greatly underrepresented in protected areas.

Biodiversity should be preserved in its intrinsic diversity and complexity, but the foremost regional goal and responsibility is set on saving endemic species from extinction. The status of such endemic species as *Natrix megalcephala*, *Zamenis persicus*, *Pelias dinniki*, *P. lotievi* and *Montivipera raddei* is quite safe because a substantial part of their ranges is covered by protected areas. Contrary to this, a number of other species are represented in protected areas insignificantly (*Pelias kaznakovi*, *P. magnifica*, *P. eriwanensis*, *P. ebneri*) or not at all (*Pelias orlovi*, *P. pontica*, *P. darevskii*, *Eryx miliaris nogajorum*). Moreover, the habitats of *Pelias orlovi* and *P. magnifica* are not even embraced by CEPF's PCAs.

To preserve the Orlov's viper, it is essential to establish a reserve or a national park between Gelenjik and Jubga, incorporating the peaks Oblego and Papai, and to expand the territory of Sochi National Park so that to include the Mt. Bolshoi Pseushkho (Tuniyev, 2008). Conservation of this relict viper also implies adding the Malyi Bambak Ridge to Kavkazsky Biosphere Reserve. The Black Sea viper can be saved solely by creating a national park near Borçka. The Lake Arpi National Park was established in Armenia in 2009 to a great extent for the sake of the Darevsky's viper. The desert sand boa and associated psammophilic communities can be protected only through the establishment of Nogaysky Steppe Reserve.

The next regional goal is focused on conservation of globally threatened or endangered species of wide distribution. In the Caucasus, such snakes are *Pelias renardi*, *Elaphe sauromates* and *Hierophis caspius*. The first species is left beyond the PCAs and the last two are almost neglected. No large protected areas can be set aside for *Pelias renardi* for the strong patchiness of its remnant habitats. However, it is feasible to establish zoological natural monuments or cluster sites of existing protected areas, e.g. in the East Priazovye (Yasenskaya Spit and others), foothills of the West and Central Caucasus (vicinities of the Raevskaya village, Maikop and Kislovodsk towns, Gerpegem Ridge), along the Kuma-Manych Depression (Lake Manych-Gudilo shoreline) and near Shamakhi, Azerbaijan. These areas are also important for preservation of the Caspian whip snake and the Eastern

four-lined ratsnake, but it also demands for the establishment of new protected areas between the Cape Bolshoi Utrish and the Kabardinka River on the Black Sea coast, in Primanychie (area around the Lake Manych-Gudilo) and the Kudriavaya (Curly) Ravine in the Stavropol Territory. Caspian whip snakes will also benefit from the above-mentioned Nogaysky Steppe Reserve.

Particular attention should be paid to the hotspots of snake species diversity in the Caucasus. Here, such areas containing at least 7 snake species are the Black Sea coast (excluding the Rioni Lowland), lower Çoruh basin, semi-arid depressions in the East Ciscaucasus, maritime Dagestan, Kura-Arax Lowland (aside from its deserts), Arax riverside in Armenia and Azerbaijan, and the Talysh-Alborz massif.

The analysis of biological diversity, spatial and altitudinal distribution of existing protected areas, including water bodies and wetlands, demonstrates the inability of protected areas to fulfill their goals and to ensure sustainable management of natural ecosystems in their complexity (Krokhmal, Tuniyev, 2003). First of all, the Econet in Russian Caucasus and Abkhazia needs much improvement. In these two countries, protected areas are concentrated in mid-elevation and highland areas of the West and Central Caucasus to protect their natural heritage. In Chechnya and Dagestan (East Caucasus), highlands and mid-elevations are not protected, including the unique limestone region of Inner Dagestan saturated with xerophilic endemics and relicts. In nearly all the North Caucasus, protected areas with stringent protection regime (reserves) are lacking at low elevations 800–1200 m asl. The two areas still retaining the unique for Russia Mediterranean semi-arid juniper and pistachio-juniper forests (Anapa-Gelenjik and foothills of Dagestan) are out of protection as well. The northernmost enclave of the Hyrcano-Alborz biota in the Samur mouth in Dagestan is unprotected.

Much effort in international cooperation is required to establish such transboundary protected areas as East Caucasus Transboundary Area (Russia, Azerbaijan, Georgia), North-West Caucasus (Kavkazsky, Teberdinsky, Pskhu-Gumista reserves and Ritsa Relict National Park in Russia and Abkhazia) and Kolkhida International Biosphere Polygon (Sochi National Park, Psou-Bzyb interfluvium and Pitsunda-Mussera Reserve in Russia and Abkhazia). Implementation of this Econet development programme, along with other conservation measures described above for preservation of endemic and threatened species, will allow to approach the long-

term goal of sustainable conservation of snakes and other biodiversity in the Caucasus Ecoregion.

Some words should be said about the IUCN status of snakes.

Full description of the criteria and their application to species status assessment during the IUCN red listing is provided in 2001 IUCN Red List Categories and Criteria version 3.1 and on the website. <https://www.iucnredlist.org>. The Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) regulates the procedures of wild animal and plant trade. Many species of reptiles and amphibians are included in the categories I, II and III of the CITES Appendix.

I – threatened species. Their trade is prohibited.

II – species not directly threatened, but potentially faced by threats unless their trade is strictly regulated.

III – species not currently threatened, but in demand of control and international cooperation in trade operations.

In relation to the herpetofauna of Europe, an important international treaty is the Convention on the Conservation of European Wildlife and Natural Habitats which was adopted in Bern, Switzerland in 1979. Many species of reptiles and amphibians are included in its appendices.

Distribution of snakes of the Caucasus Ecoregion across the IUCN threat categories is provided in table 8. Their representation in regional red books is shown in table 9.

Table 8. IUCN Red List Category of the Caucasian snakes

№	Species	Red List Category					
		CR	EN	VU	NT	LC	DD
1	<i>Xerotyphlops vermicularis</i>					+	
2	<i>Eryx jaculus</i>					+	
3	<i>Eryx miliaris</i>					+	
4	<i>Platyceps najadum najadum</i> <i>Platyceps najadum albitemporalis</i>					+	
5	<i>Hemorrhois nummifer</i>					+	
6	<i>Hemorrhois ravergieri</i>					+	
7	<i>Dolichophis caspius</i>					+	
8	<i>Dolichophis schmidtii</i>					+	
9	<i>Coronella austriaca</i>					+	
10	<i>Eirenis collaris</i>					+	
11	<i>Eirenis modestus</i>					+	
12	<i>Eirenis persicus</i>					+	
13	<i>Eirenis punctatolineatus</i>					+	
14	<i>Elaphe dione</i>					+	
15	<i>Elaphe sauromates</i>					+	
16	<i>Zamenis hohenackeri</i>					+	
17	<i>Zamenis longissimus</i>					+	
18	<i>Zamenis persicus</i>						+
19	<i>Malpolon insignitus</i>					+	
20	<i>Natrix megalcephala</i>			+			
21	<i>Natrix natrix persa</i> <i>Natrix natrix scutata</i>					+	
22	<i>Natrix tessellata</i>					+	
23	<i>Psammophis lineolatus</i>					+	
24	<i>Rhynchocalamus satunini</i>					+	
25	<i>Telescopus fallax iberus</i>					+	
26	<i>Gloydus caucasicus</i>					+	
27	<i>Macrovipera lebetina</i>					+	
28	<i>Montivipera albicornuta</i>			+			
29	<i>Montivipera raddei</i>				+		
30	<i>Montivipera wagneri</i>	+					
31	<i>Pelias barani</i>				+		
32	<i>Pelias darevskii darevskii</i> <i>Pelias darevskii uzumorum</i> <i>Pelias darevskii kumlutasi</i>	+					
33	<i>Pelias dinniki</i>			+			
34	<i>Pelias ebneri</i>			+			
35	<i>Pelias eriwanensis</i>			+			
36	<i>Pelias kaznakovi</i>		+				
37	<i>Pelias lotievi</i>				+		
38	<i>Pelias magnifica</i>		+				
39	<i>Pelias olguni</i>	Still not assessed					
40	<i>Pelias orlovi</i>	+					
41	<i>Pelias pontica</i>		+				
42	<i>Pelias renardi</i>			+			
43	<i>Pelias shemakhensis shemakhensis</i> <i>Pelias shemakhensis kakhetiensis</i>	Still not assessed					
44	<i>Vipera transeucasiana</i>				+		
	Total	3	3	6	4	25	1

Abbreviations: CR — critically endangered; EN — endangered; VU — vulnerable; NT — near threatened; LC — least concerned; DD — data deficient.

Table 9. Species of the Caucasian snakes included into regional Red books

Species / Territory	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
<i>Xerotyphlops vermiularis</i>																
<i>Eryx jaculus</i>	+			+		+	+		+				+		+	
<i>Eryx miliaris</i>	+					+			+					+	+	
<i>Coronella austriaca</i>		+							+			+		+		
<i>Dolichophis caspius</i>					+		+	+	+	+	+	+	+	+		
<i>Dolichophis schmidtii</i>						+										+
<i>Eirenis collaris</i>				+												
<i>Eirenis modestus</i>																
<i>Eirenis persicus</i>			+													
<i>Eirenis punctatolineatus</i>																
<i>Elaphe dione</i>								+		+		+		+	+	
<i>Eirenis sauromates</i>		+						+	+	+	+	+	+	+	+	
<i>Hemorrhois nummifer</i>																
<i>Hemorrhois ravergieri</i>						+										
<i>Natrix megalcephala</i>					+						+					+
<i>Natrix natrix</i>																
<i>Natrix tessellata</i>																
<i>Platycephalus najadum</i>							+				+		+	+	+	
<i>Rhynchocalamus satunini</i>		+	+													
<i>Telescopus fallax</i>	+		+			+										
<i>Zamenis hohenackeri</i>	+	+	+			+	+						+		+	
<i>Zamenis longissimus</i>	+				+						+					
<i>Zamenis persicus</i>		+														
<i>Malpolon insignitus</i>				+					+					+		
<i>Psammophis lineolatus</i>		+														
<i>Gloydus caucasicus</i>																
<i>Macrovipera lebetina</i>	+					+										
<i>Montivipera albicornuta</i>																
<i>Montivipera raddei</i>		+	+													
<i>Montivipera wagneri</i>																
<i>Pelias barani</i>																
<i>Pelias darevskii</i>			+													
<i>Pelias dinniki</i>	+			+	+	+		+		+	+				+	+
<i>Pelias ebneri</i>																
<i>Pelias eriwanensis</i>			+													
<i>Pelias kaznakovi</i>	+			+	+						+					+
<i>Pelias lotievi</i>								+			+				+	
<i>Pelias magnifica</i>					+						+					
<i>Pelias olguni</i>																
<i>Pelias orlovi</i>											+					
<i>Pelias pontica</i>																
<i>Pelias shemakhensis</i>		+														
<i>Pelias renardi</i>		+			+	+		+	+		+	+		+	+	
<i>Vipera transcaucasiana</i>																

1 — Russian Federation (RF); 2 — Azerbaijan; 3 — Armenia; 4 — Georgia; 5 — Adygheya; 6 — Dagestan (RF); 7 — Ingushetia (RF); 8 — Kabardino-Balkariya (RF); 9 — Kalmykia (RF); 10 — Karachaevo-Cherkessiya (RF); 11 — Krasnodar Territory (RF); 12 — Rostov Province (RF); 13 — North Ossetia-Alania (RF); 14 — Stavropol Territory (RF); 15 — Chechnya (RF); 16 — South Ossetia.

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