RS Hoffman

N. K. Vereshchagin

THE MAMMALS OF THE CAUCASUS

A History of the Evolution of the Fauna

TRANSLATED FROM RUSSIAN

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N.K. VERESHCHAGIN

THE MAMMALS OF THE CAUCASUS

A History of the Evolution of the Fauna

(Mlekopitayushchie Kavkaza)(Istoriya formirovaniya fauny)

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PREFACE

N.K. Vereshchagin's book is somewhat unusual: although it is not a comprehensive treatise of the past and present evolution of the fauna of this interesting and complex area, he has succeeded in producing the first generalized and complete picture of the development of terrestrial fauna in the Caucasus from Neogene to Recent times against a background of the geological history and landscape shifts.

In his work the author draws on the entire body of biological science, from paleontological data on individual stages in the phylogeny of Quaternary mammals to the voluminous data of modern zoogeographical and ecological conditions of contemporary forms.

The author believes that the eastern Mediterranean (including the Caucasus) was characterized in the Neogene by a unique process in the mammalian evolution — faunal complexes replacing one another, as commonly occurred throughout the Recent in the Holarctic region.

The Quaternary mammalian faunas of the Caucasus have their roots deep in the Pliocene. The Caucasian faunas proper of the mountain forest community evolved locally since at least Upper Miocene time. However, in the Quaternary the evolution of mammals in the Caucasus took place primarily through species invasions and extinctions.

The evolution of new species on the Caucasian Isthmus was not as significant as other evolutionary processes in fauna formation.

Vereshchagin's statements on the absence of saltations in the morphological evolution of the Quaternary mammals will require additional study before they are confirmed.

Emphasis is placed on the destructive activity of humans which caused the extinction of many game mammals from the Upper Paleolithic to the Recent. Many examples are given of the ecological changes and readjustments of the surviving mammals in various zones.

This work on the many questions relating to the development of fauna will undoubtedly inspire other intensive paleontological and zoological studies, not only on the Caucasus, but also on other parts of Russia. As an initiator, Vereshchagin has made a notable contribution to the methodology of his subject.

The book also presents important data on the commercial value of autochthonous and introduced species, as well as information of concern to conservationists.

The history of the development of mammalian fauna in the Caucasus will undoubtedly be of interest to a wide audience of botanists, geologists, archaeologists and geographers, as well as to zoologists.

E.N. Pavlovskii, Academician,
Lieutenant General, Medical Corps.

5 INTRODUCTION

A study of the distribution of organisms in time and space in the course of their evolution presents problems at once interesting and difficult. Their study is necessary for the reconstruction of faunal history and the advancement of faunalogical investigations.

The study of the development of fauna on the Caucasian Isthmus is complicated by the fact that throughout the Cenozoic, this area was the scene of marine transgressions and regressions, mountain-building processes and glaciations. As a result of these processes, the climate and landscape changed within short distances.

In the physiographic sense, the Caucasus is large and varied. Its geologic structures, its flora and fauna, and the history of its peoples have been studied by outstanding scientists for almost 250 years.

Studies of the mammalian fauna of the Caucasus have been primarily concerned with the identification and geographic distribution of species. Few workers were concerned with the ecology, and even fewer with the history of the fauna. The main works are those of K. A. Satunin, N. Ya. Dinnik, N. A. Smirnov, M. V. Shidlovskii, Z. S. Rodionov, P. A. Sviridenko, S. I. Ognev, L. B. Beme, S. S. Turov, V. G. Geptner, A. I. Argiropulo, A. A. Nasimovich, S. K. Dal', I. V. Zharkov and P. P. Gambaryan.

The vast collection of data by Russian zoologists on Caucasian animals can only be partly reflected in the bibliography of this book.

Much paleontological work on the fossil mammals of the Caucasus has been done by V. V. Bogachev, A. A. Borisyak, V. I. Gromov, E. I. Belyaeva, V. I. Gromova, R. D. Dzhafarov, L. K. Gabuniya, N. O. Burchak-Abramovich, myself and others. The osteological collections of archaeologists (S. N. Zamyatnin, G. K. Nioradze, A. P. Kruglov, E. I. Krupnov and others) were of particular value.

6 These studies and collections facilitated my investigations of the origin and history of the development of Caucasian mammals.

The history of the mammalian fauna of the Caucasus is intimately related to the evolution of landscapes, vital forms and ranges of species distribution.

The marine transgressions and regressions during the Tertiary in the eastern part of the Mediterranean geosyncline (the Recent Black Sea, Caspian Sea and the Caucasus) and the evolution of the molluscan fauna of this area have been studied in great detail by geologists: Academicians Andrusov (1888) and Arkhangel'skii (1934), Arkhangel'skii and Strakhov (1938), Zhizhchenko, Kolesnikov, Eberzin (1940) and others, mainly in the course of petroleum explorations. The Neogene, in particular, has been thoroughly studied. A detailed zoogeographic summary on the faunas of the Caspian and Black seas was published by Sovinskii (1904).

Geobotanists and paleobotanists have also published a number of histories of the land flora of the Caspian lands, particularly of the Caucasus (N.I. Kuznetsov, 1909; Palibin, 1936; Grossgeim, 1936, 1948; Maleev, 1941; and others).

Studies to date on the history of Caucasian land fauna have been quite generalized and were based mostly on fossil material. These studies include Academician Menzbir's (1934) history of the fauna of the European U.S.S.R., Serebrovskii's (1935) history of the fauna of the U.S.S.R., Bogachev's (1938) review of the Tertiary of the Caucasus, and Borisyak and Belyaeva's (1948) review of the Tertiary mammalian fossil localities in the Caucasus. The history of the Quaternary fauna has been treated by Gromov (1939, 1948), Gromova (1948), Burchak-Abramovich (1951c) and Pidoplichko (1951, 1954).

The history of the land mammals of the Caucasus has also been treated from the point of view of zoogeographical studies of the Recent by Satunin (1896, 1901a, b, 1904, 1909, 1913), Dinnik (1911), and Shidlovskii (1940a, 1941b, 1945, 1947), and more recently by B.A. Kuznetsov (1949, 1950).

There are fewer studies on the evolution of other classes of terrestrial vertebrates: birds (Puzanov, 1938b) and reptiles and amphibians (Nikol'skii, 1913; Sobolevskii, 1929; Lyaister, 1931; Chernov, 1939).

The history of terrestrial invertebrates on the Caucasus has been discussed in the studies of scorpions by Byalynitskii-Birulya (1917)*; of dragonflies by Bartenev (1933, 1934 — in which he also discussed mammals, reptiles and amphibians); of Coleoptera by Semenov-Tyan-Shanskii (1936) and Bogachev (1947); and of Orthoptera by Uvarov (1921).

All of these studies have one feature in common: the history of the fauna is treated either from a purely paleontological or from a purely zoogeographical point of view, without synthesis or consideration of the ecological and morphophysiological data.

Obviously, this approach cannot give a true picture of a process as complex as the development of fauna at any given stage of geologic time. It is more correct to view the process of the development of fauna as a combination of three interrelated processes:

1. Evolution of the environment and of those life conditions of individual species which were controlled by secular changes in climate, in elevation and subsidence of the earth's crust, and of the biocenosis proper. In more recent times the human factor also assumes great importance.

2. Morphological evolution of individual species, which is affected by both external environment and internal developmental patterns.

3. Ecological evolution of individual species and of entire biocenoses which is caused by continuous evolution of the conditions of life, and the further evolution of the biocenoses, in turn, through extinctions, transformations, invasions and migrations of species.

Data on these three processes of faunal evolution are not equally available to paleontologists, zoogeographers and ecologists. A synthesis of the data and conclusions of each discipline is indispensable.

The Caucasus has had a complicated geological, pedological and floral history, and a long pattern of changing human cultures. The influence of

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* [Arthrogastran Arachnids of Caucasia: Scorpions. Translated into English by IPST in 1964, OTS No. 64-1114.]

man on the land and the fauna became progressively more pronounced with time. Therefore, in order to understand the basic features of the evolution of Caucasian fauna, it is necessary to draw on the data of geology, geomorphology, geobotany, archaeology, paleontology, systematics, ecology and zoogeography.

The complexity of the problem required a limitation on our studies and an organization into three interrelated subdivisions:

1. Paleontological and archaeological evidence of the history of the development of the fauna.

2. Analysis of the origins and distribution of the Quaternary mammals with reference to their ecology and morphogenesis.

3. The mammalian geography of the Caucasian Isthmus and the most recent manifestations of local faunal evolution.

In each of the subdivisions, progress of the work depended upon the material and technical facilities available.

Materials, routes and methods

The main source of mammalian material of the Tertiary and Pleistocene is in the paleontological, geological and archaeological collections of: Museum of Natural History of the Academy of Sciences of the Azerbaidzhan S.S.R.; Zoological (ZIN) and Paleontological (PIN) Institutes of the Academy of Sciences of the U.S.S.R.; All-Union Geological Institute, Institute of Geology of the Academy of Sciences of the Georgian S.S.R.; Institute of Geology of the Academy of Sciences of the Armenian S.S.R.; and the city museums of Pyatigorsk, Stavropol, Krasnodar, Temryuk, Novocherkassk, Rostov and Astrakhan. Our own collections and observations on Tertiary mammals were taken from the Miocene site near Belomechetskaya in central Ciscaucasia, from the Pliocene site at the Kosyakin quarry near
8 Stavropol and from the Upper Pliocene and Lower Quaternary sites along the Psekups and on the Taman Peninsula (Figure 1). Collections of Pleistocene mammals and plants were taken from Pleistocene river sands in the Kuban and the Kuma river valleys, near Krapotkin and Georgievsk in Ciscaucasia, and from the bituminous formations of the Apsheron Peninsula in Transcaucasia (Figure 2).

Small collections of bones and flint tools and additional observations were made at old excavation sites in paleolithic caves on the Black Sea coast and in the Rion River basin (Akhshtyrskaya, Sakazhia and Gvardzhilas caves) and in the recently excavated Kudaro cave.

More than 55,000 Pleistocene bone fragments and 1,500 Tertiary bone fragments were examined.

In order to trace the distribution of game animals and small rodents in the Holocene, the following types of fossil material from a variety of sites were studied:

1. Food and industrial wastes of man from strata containing remains of campsites and settlements from the Mesolithic to the last centuries of the Recent (Sarkel, the ancient town of Semibratnoe, Elizavetovskoe, Cepi, Phanagoria, Taman, Gelendzhik, Anaklia, Kalakent, Mingechaur, Baku, and others).

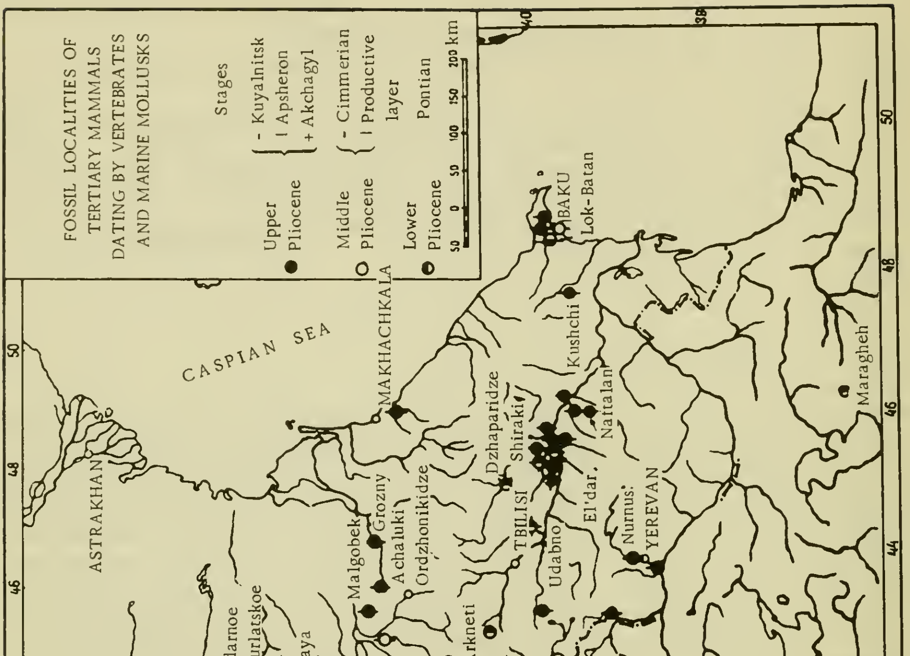
FOSSIL LOCALITIES OF
TERTIARY MAMMALS
DATING BY VERTEBRATES
AND MARINE MOLLUSKS
Stages
● Upper Pliocene
- Kuyalnitsk
I Apsheron
+ Akchagyl
○ Middle Pliocene
- Cimmerian
I Productive layer
◐ Lower Pliocene
Pontian
50 0 50 100 150 200 km
Upper Miocene
× Meotian
+ Sarmatian
Middle Miocene
Chokrak
Oligocene
CASPIAN SEA
BLACK SEA
SEA OF AZOV
ASTRAKHAN
MAKHACHKALA
BAKU
Lok-Batan
Kushchi
Naftalan
Dzhaparidze
Shiraki
El'dar
TBILISI
Udabno
Nurnus
YEREVAN
Maragheh
Grozny
Malgobek
Achaluki
Ordzhonikidze
Arkneti
Benara
BATUMI
SUKHUMI
Blagodarnoe
Burlatskoe
STAVROPOL
Kosyakin quarry
Belomechetskaya
Petrovskoe
Armavir
Bakinskaya
KRASNODAR
Sinyaya gulley
Tsimbal quarry
Leventsovka
Novocherkassk
Khapry
Aksai
ROSTOV
Morskaya
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FIGURE 1

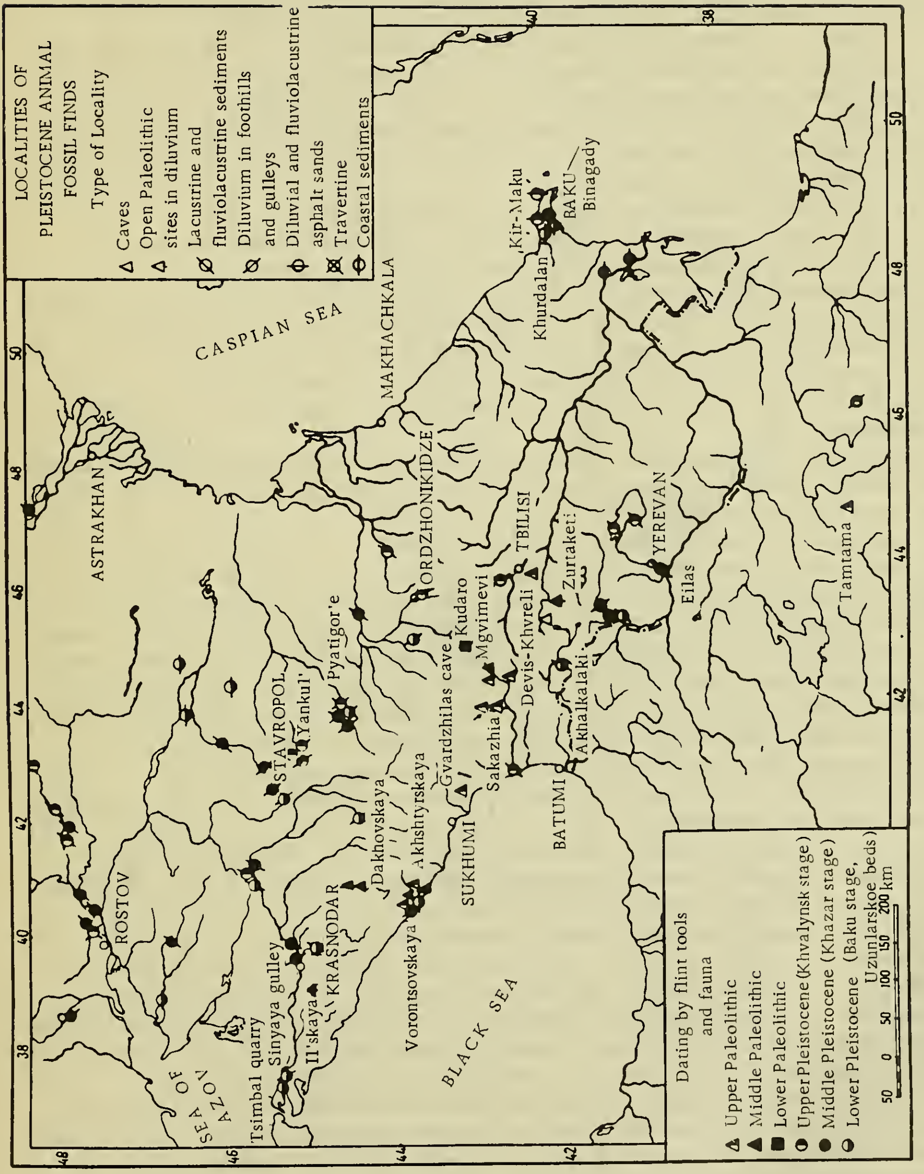
LOCALITIES OF PLEISTOCENE ANIMAL FOSSIL FINDS
Type of Locality
Caves
Open Paleolithic sites in diluvium
Lacustrine and fluviolacustrine sediments
Diluvium in foothills and gulleys
Diluvial and fluviolacustrine asphalt sands
Travertine
Coastal sediments
Dating by flint tools and fauna
Upper Paleolithic
Middle Paleolithic
Lower Paleolithic
Upper Pleistocene (Khvalynsk stage)
Middle Pleistocene (Khazar stage)
Lower Pleistocene (Baku stage, Uzunlarskoe beds)
50 0 50 100 150 200 km
CASPIAN SEA
BLACK SEA
SEA OF AZOV
ASTRAKHAN
MAKHACHKALA
ROSTOV
STAVROPOL
Yankul'
Pyatigor'e
ORDZHONIKIDZE
KRASNODAR
Il'skaya
Tsimbal quarry
Sinyaya gulley
Vorontsovskaya
Akhshtyrskaya
Dakhovskaya
Gvardzhilas cave
Kudaro
Mgvimevi
SUKHUMI
Sakazhia
Devis-Khvreli
TBILISI
Zurtaketi
Akhalkalaki
BATUMI
YEREVAN
Eilas
Tamtama
Kir-Maku
Khurdalan
BAKU
Binagady
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FIGURE 2

2. Bone artifacts, ornamental objects, skulls and skeletons of wild and domestic animals from ritual burial grounds (Nal'chik, Samtavro, Trialeti, Sevan and others).

9 3. Skulls of artiodactyls from mountain caves and shelters where they had accumulated over the centuries as the residue of rites and feasts dedicated to the hunting god (a number of ravines in Ossetia).

4. Bones of rodents and insectivores deposited by owls during the last centuries in caves, under ledges and in the small cavities of rocks (the foothills and mountain regions of Cis- and Transcaucasia).

5. Bones and horns of drowned animals and kitchen middens of tribes which lived in pile dwellings along the shores of Lake Sevan. (The lake is at present receding rapidly.)

6. Isolated occurrences of bones in Holocene loams.

In all, nearly 52,000 identifiable bones and bone fragments from approximately 70 Holocene sites (Figure 3) were studied.

Penetration of species in postglacial times and their role in the evolution of faunal complexes were the primary considerations in our selection of smaller areas of Holocene localities such as the Pleistocene localities of the Apsheron Peninsula, Stavropol Plateau and Pyatigor'e area (Vereshchagin, 1949c, 1953a). We particularly searched out food rests of eagle owls.

Mapping of the fossil localities and searches in the extensive literature
10 produced a general picture of the distribution of bone-bearing deposits of
the Tertiary and Quaternary.

The elevation of the Caucasus in the Cenozoic resulted in an accretion of very thick strata of gravels, sands and silts in the piedmont plains. Part of the terrigenous material was reworked by waves in the surf zone and part was deposited in the quiet water of bays on the margins of sea basins.

Accumulation and burial of skeletons occurred mainly along the deltas and coastal bays, where they were carried by streams. Cenozoic bone-bearing sandy-gravelly lenses are usually found in erosional channels cut through older beds; this type of burial is common in the valleys of Ciscaucasia, Stavropol and in the broad intermontane valleys of Transcaucasia. The bone-bearing formations are exposed in the processes of erosion and quarrying.

Caves containing bones of Tertiary age have not yet been found in the Caucasus. This is probably accounted for by the changes in the relief and river network which destroyed the older karst.

Archaeologists have searched for Paleolithic localities in the regions of
11 developed Quaternary karst. The Paleolithic collections usually contain
"fauna", i.e., bones left in the caves by prehistoric hunters and by
predatory animals and birds. The latest, post-Paleolithic (post-Pleistocene)
bones occur mainly in surface loams, diluvial gulleys, alluvial deposits
in the first terraces of rivers, in caves and under rocky ledges.

The positioning of most Holocene bone-bearing burials accessible to excavation and investigation was determined by early hunters and predatory birds. However, evidence of mass extinction of wild animals and preservation of their remains even in Recent times can be found in the Caucasus (Vereshchagin, 1951b; Figure 4).

It is clear that the paleontological record of the origin of Caucasian mountain fauna (which is the background of this work) is not complete.

(10)

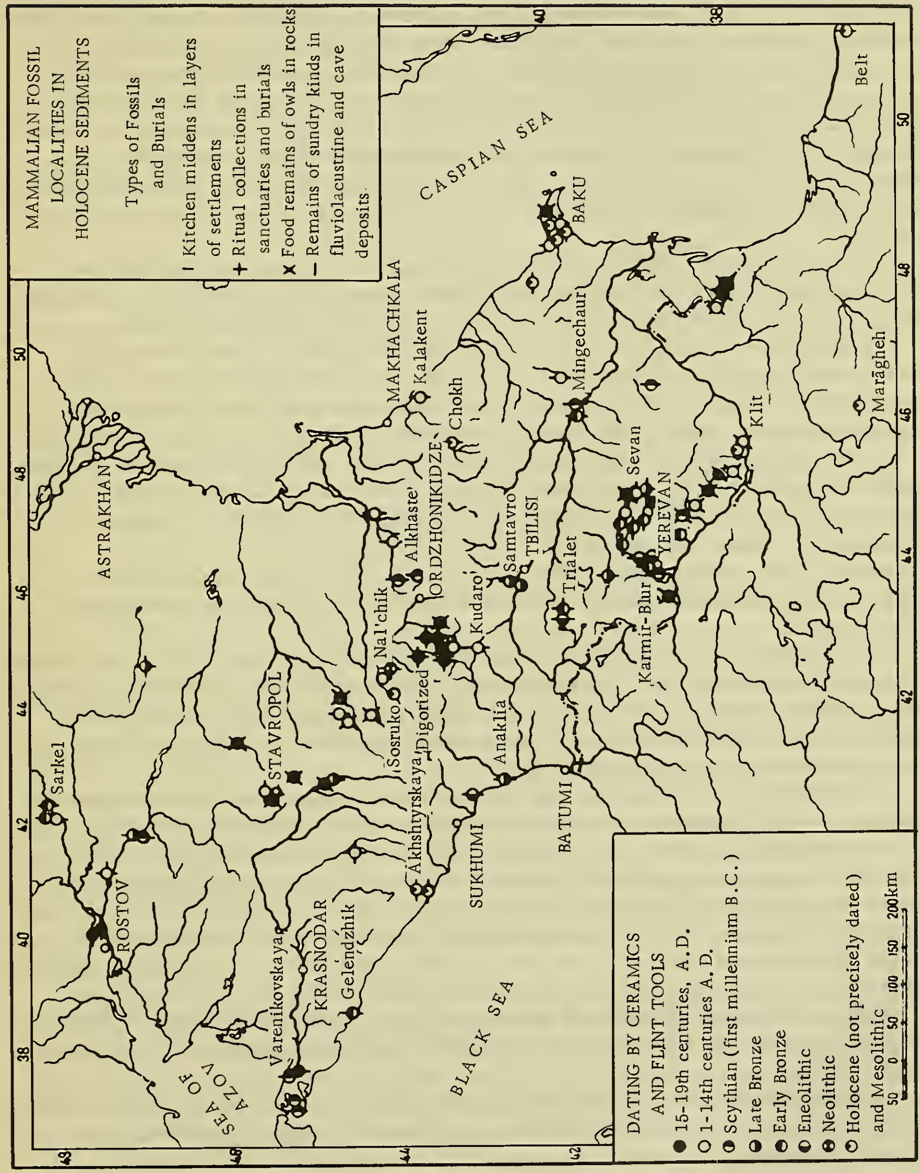
MAMMALIAN FOSSIL LOCALITIES IN HOLOCENE SEDIMENTS
Types of Fossils and Burials
I Kitchen middens in layers of settlements
+ Ritual collections in sanctuaries and burials
X Food remains of owls in rocks
— Remains of sundry kinds in fluviolacustrine and cave deposits.
DATING BY CERAMICS AND FLINT TOOLS
● 15-19th centuries, A.D.
○ 1-14th centuries A.D.
◐ Scythian (first millennium B.C.)
◐ Late Bronze
◐ Early Bronze
◐ Eneolithic
◐ Neolithic
◐ Holocene (not precisely dated) and Mesolithic
50 0 50 100 150 200km
CASPIAN SEA
BLACK SEA
SEA OF AZOV
ASTRAKHAN
Sarkel
ROSTOV
Varenikovskaya
KRASNODAR
Gelendzhik
STAVROPOL
Akhshtyrskaya
Sosruko
Digorized
Nal'chik
Alkhaste
ORDZHONIKIDZE
MAKHACHKALA
Kalakent
Chokh
Kudaro
Samtavro
TBILISI
Anaklia
SUKHUMI
BATUMI
Trialet
Karmir-Blur
YEREVAN
Sevan
Mingechaur
BAKU
Klit
Marāgheh
Belt
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FIGURE 3

The reasons for this are taphonomical, i. e., the lack of accessible areas of sediment accumulations in the highlands and the absence of caves containing Pliocene fossils. (See Efremov: "Taphonomy" (Tafonomiya) 1950. *)

A critical evaluation of the available paleontological material requires a complete account of burials, their peculiarities and the ways by which bone remnants and matter were preserved in them. Therefore, a section dealing with the transport pathways and the burial of fossils has been added to each of the chapters devoted to the regional stratigraphy of the localities.

A correct evaluation of the modes of preservation leads to important conclusions regarding the ancient landscapes and the conditions of life and of death of organisms. However, this factor was often ignored by paleontologists and, as a result, they were led to erroneous interpretations, particularly in cases where fossils of varying ages occur at the same locality.

In most instances, the paleontologist deals with a collection of fossil remains which reflects only the conditions peculiar to a particular locality, rather than the ecological associations of the entire ancient region.

The degree of "universality" of a burial is related to the number of preservable species of animals and plants which inhabit the area and to the proximal degree to which the distribution of species and individual specimens in the dead assemblage resembles that of the living community.

Three sets of conditions determine the degree of universality of a fossil assemblage: 1) the circumstances of the animal's death; 2) the manner in which the remains accumulated in sediment; and 3) their "behavior" and preservation within the sediment.

Clearly, any possibility of reconstructing ancient biocenoses and landscapes from fossil material is determined by the sets of conditions given above.

The Binagady burial on the Apsheron Peninsula (Chapter II) is an example of a highly universal fossiliferous site. There a Pleistocene assemblage of plants, birds, insects, jerboas and rhinoceroses was preserved in thick layers of asphalt; this mode of preservation permits a highly reliable restoration of the ancient landscape.

12 The situation is quite different when fossils are preserved in sediments of diluvial, river, lacustrine or marine origin, or at Paleolithic sites or in caves.

Accumulation of bone material in river sediment results from river erosion of bone-bearing beds (Vereshchagin, 1953c), as well as from the occurrence of animal deaths in the mainstream and on the floodplain. Once in the mainstream, the bones are subject to mechanical reworking like gravel and pebbles and they are sorted and distributed according to specific gravity and size.

Thus, a complex of animals which died in a river valley can be seen accurately only if the bones are collected from different facies, i. e., gravels, sands, silts.

Available collections by earlier investigators were not, as a rule, made in this way and consequently reflect only the last stage of sorting, i. e., excavation.

Distribution of bones in different facies also occurs in lakes and marine bays to which they are carried by rivers. Burial in deltaic sediments is more common, since floating bodies of animals can be carried long

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* [The term "taphonomy," meaning "the study of the formation of burials of fossils, plants and animals," was introduced by Efremov in this work.]

distances by currents to sink later into the silty and shell-covered bottoms of quiet bays.

Accumulation of bones in the Paleolithic and post-Paleolithic strata of camp sites, settlements and burial grounds was primarily dependent upon the particular hunting traditions and customs of local tribes. (Deposition by flowing water is rarely encountered in caves.) Remains of men's food was often found in caves mixed with remains of the food of predatory animals (bears, wolves, hyenas, panthers) and predatory birds (eagle owls and little owls). Clearly, gross errors are possible if, in drawing conclusions, human hunting customs and animal behavior patterns are ignored, as was done in those investigations which are limited to a count of domestic and wild animals in strata of varying ages and cultures. For example, it is known that contemporary Caucasian hunters often carry 30-40 kg of wild goat, gazelle or swine meat over distances of 20-25 km on mountain trails. Caucasian goats can climb 1,500-2,000 m in a day. We have observed eagle owls in the cave region of Imeretia flying frequently from caves in the foothills to seek prey on the subalpine meadows and attaining heights of more than 1,000 m in their ascents.

Thus, reconstructions of the paleolandscape and of changes in the position of the snow line based on occurrences in caves of the remains of highland animals (goat and Prometheomys) can be made only if all the processes involved in the accumulation of bones are considered.

Similarly, conclusions on the accumulation of index gama fauna of one area cannot be based on a comparison of the material from an unlike area, e.g., material from the Greek towns of the Taman Peninsula (Phanagoria, Cepi) compared with the kitchen middens of a small hunting and fishing village of Roman time found at the ancient site of Semibratnoe in the mouth of the Kuban River. In this case the size of the settlement and its topographic location would be much more important considerations than the occurrence and disappearance of game animals in the surrounding area.

14 Quantitative data on the composition and size of burials in the Caucasus are given here for the first time whenever adequate material was available. These data contribute to an understanding of the development of tribal culture and economy and of the nature of the landscape. To take one example: unverified ancient writings have led some geologists to believe that dry valleys existed in Colchis in the first millennium B.C. This theory is disproved by the absence of horse remains and the abundance of boar remains in the Colchis burials, which indicate that the marshlands of the Eneolithic and Bronze Ages were very similar to those of approximately 50 years ago.

The species composition and distribution of wild animals were also inferred from the drawings and sculptures of the Bronze and Iron ages. Particularly interesting are the bronze, silver and gold objects with animal representations collected from the burials of the Armenian Highland, the Kura River valley and the Trans-Kuban sloping plain (Tsalka, Samtavro, Maikop, Kellermes, etc.). If one takes into account the probable origins of these objects, the aesthetic criteria of their consumers (Urartus, Scythians, Kobanians) and the ecology of the depicted, the realistic art of these ancient craftsmen can be of great aid in studying the distribution and gradual extinction of some of some of the larger animals.

(13)

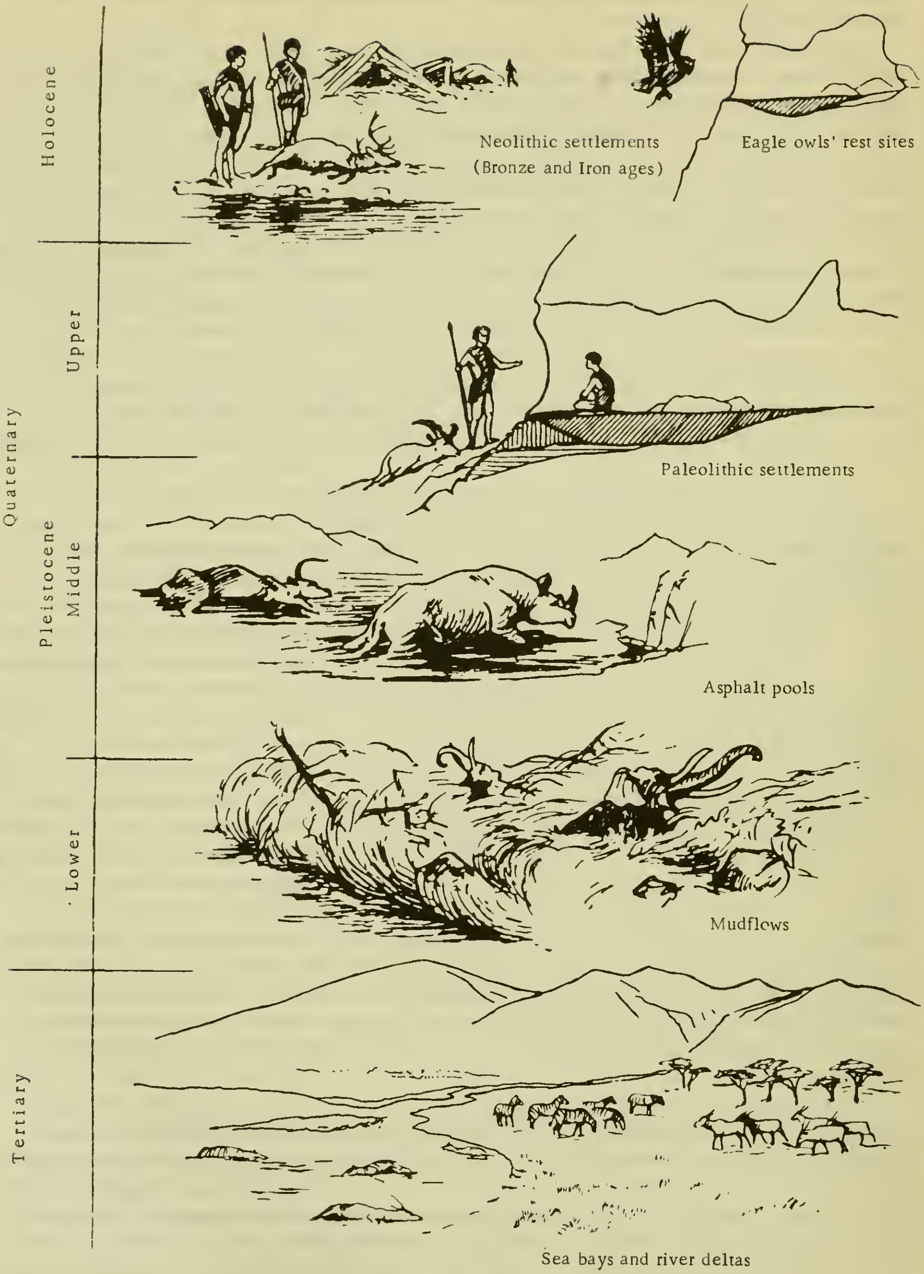

FIGURE 4. Predominant circumstances of animal death and types of fossil burials in the Cenozoic of the Caucasian Isthmus

Although it is possible to find fossils of large animals of the present period, their number has decreased to an extent that makes this a negligible probability. Consequently, the zoologist who is called upon by archaeology to furnish morphological and zoogeographic data for the identification of depicted animals will attach great importance to the so-called "animal style" in the art of the first millennium B.C.

We have reviewed the published data of Tolstoi and Kondakov (1889), Uvarova (1900), Kuftin (1940) and others on precious stones in the "animal style" from the Caucasian burials of the Kobanian, Khodzhalian, Scytho-Sarmatian and other cultures, as well as the collections of the Hermitage (Leningrad), the Georgian Museum (Tiflis) and the Historical Museum (Moscow). Our conclusions, as they relate to species and ranges, are discussed in Chapter III. The "animal style" of these Caucasian antiquities deserves a special zoological-ethnographical study in itself.

In the study of the Cenozoic faunas of the Caucasus we used the geochronological subdivision of the Neogene of the eastern Mediterranean (Black and Caspian seas, Caucasus) as given by Academicians Andrusov (1918) and Pavlov (1925), with later additions by Kovalevskii (1933, 1936), Zhizhchenko, Kolesnikov and Eberzin (1940).

We placed the Pliocene-Pleistocene boundary (in agreement with Pavlov, 1936, and Vardanyants, 1948) at the end of the Apsheron stage. The boundary probably corresponds to the last stage of existence of the Taman-Psekups fauna in Ciscaucasia, which was originally discovered by Gromov (1948, 1950) and is described in Chapter II of this book.

15 The Quaternary of the Caucasus is subdivided into the Pleistocene and Holocene. Everywhere on the Caucasus the development of faunal complexes during the Pleistocene extended over a fairly long period, from the Upper Apsheron to the end of the last glaciation on the Caucasus and the onset of the xerothermic period which marks the beginning of the Holocene. The Pleistocene is subdivided into the Lower, Middle and Upper Pleistocene, which correspond to the stratigraphic stages of the Caspian region: the Baku, Khazar and Khvalynsk, containing mammalian fauna known from the entire Russian plain. The subdivision of the Quaternary in the foothills of the Caucasian Isthmus and the correlation of the river terraces with cave deposits and marine terraces were established following the studies of Mirchink (1937b), Gromov (1948), Vardanyants (1948) and Nikolaev (1953).

The archaeological chronology of the Caucasus is similar to the European (West Mediterranean) schematic chronology developed by Obermaier (1913), Osborn (1924) and Penk (1939). For date determinations of the Caucasian Paleolithic as guide lines to grouping mammalian ecological complexes, we used the papers of Zamyatnin (1950b, 1957) and other archaeologists. Geological dating was a primary concern in our studies of bone material.

The problem of determining the relative and absolute age of fossil bones is becoming increasingly significant for geology, paleontology and archaeology. Fossil age is determined by: 1) physicochemical composition (the methods of calcination and radiocarbon dating); 2) taxonomic characters (generic, specific, subspecific); 3) inclusion in one faunal complex or another (faunal assemblages); 4) artifacts occurring with the fossils (stone tools, pottery, etc.); 5) evidence of associated invertebrate fauna and indirect geomorphological data (for example, the age of marine and river terraces); 6) type of preservation of the bone material.

Each of the methods mentioned has disadvantages. The physicochemical methods give comparable results only when all the bones studied are less than 500,000 years old and have been preserved under the same conditions. The factors which affect the data obtained by this method are the composition of the sediments and their radioactivity, the water-salt relationship in the soil at the time of burial, etc.

However, the method of calcination and comparison of the coefficients of the organic residue used by Pidoplichko (1952) can be used in absolute and relative dating provided that separate chronological scales are constructed for each physicogeographic region and for each type of locality.

Radium-, uranium- and thorium-isotope dating methods (Cherdyntsev, 1955) yield inconsistent results.

Determination of geologic age by specific and faunal characters is 16 possible only if the evolution of morphological characteristics is known in detail for the given genus or species. The taxonomic method can only be used with extremely well-preserved material, particularly in the case of skull specimens.

Stone tools, pottery and other artifacts are reliable indicators of the relative age of fossiliferous strata only in those geographically defined areas where the chronology of the human cultures is known. By the latest consensus, the development of the Paleolithic cultures in Western Europe did not coincide in time with the Paleolithic in Eastern Europe. The occurrence of the bones in situ is another prerequisite for successful application of this method.

Determination of the age of the geologic formations is of little use in determining the age of bones in Quaternary sediments which were often redeposited. The problem of dating is usually reversed since the Quaternary beds are dated by the vertebrates found in them.

This method uses the simplest organoleptic analysis to determine the mode of preservation of bone material. But it requires considerable experience for an unbiased judgment and only yields indexes of relative age.

It was necessary to review the entire body of Quaternary paleontological material taken from the Caucasus, since the indiscriminate application of morphological and morphometric criteria by earlier investigators had only resulted in confusion and redundancy in lists of species.

With careful consideration of the mode and conditions of preservation, the age of the bone material can be placed within the major subdivisions of the Quaternary. The loss of organic matter (fossilization) and the secondary permineralization of the bones must also be taken into account by observing the new saturation of the bone material by salts, the color of fresh fracture, the degree and depth of colorization and the smell of fresh bone when scraped with a knife. A table is given for the determination of the relative age of Quaternary bones (Vereshchagin and Gromov, 1953a).

The geographic distribution of Recent species was studied, with interruptions, from 1935 to 1941 in Azerbaidzhan and Armenia, and from 1945 to 1952 in Azerbaidzhan, Georgia, North Ossetia, Kabarda, Svanetia and Dagestan. Our collecting routes are shown on the map (Figure 5).

Studies were made of the collections of ZIN, the Zoological Museum of Moscow University, The Georgian Museum and Institute of Zoology of the Georgian Academy of Sciences (collections to 1944), the Institute of Zoology of the Armenian Academy of Sciences (collections to 1943), the Institute of Zoology of the Azerbaidzhan Academy

MAP OF
AUTHOR'S ROUTES
(1931-1949)
and
LOCATIONS OF
PELT-RECEIVING
CENTERS
(1930-1950)

FIGURE 5

(collections to 1948) and the Stavropol and Baku anti-plague stations (collections to 1945). A total of 13,500 excellent specimens of skins, stuffed animals, skulls and specimens preserved in alcohol (taken from over 3,300 locations) comprised the material used.

Conclusions on the most recent changes in the density of 23 species of fur-bearing animals were based on the data collected over 25 years (1925-1950) by the governmental fur stations in Ciscaucasia and Transcaucasia.
17 The data of 257 pelt-receiving centers for the period 1945-1948 were used in the final refinement of the areas of distribution of species, as shown in Figure 5. The statistics on the preparation of furs are shown separately on the graphs for Ciscaucasia and Transcaucasia, and for the republics and regions (except the Astrakhan Region, for which no data were available).

The occurrences of fossils and the recent yield of small fur-bearing animals are entered on a specially prepared map drawn to a scale of 1:5,000,000. The population density of each species, as estimated from the mean annual number of furs received by the pelt-receiving centers, are indicated by small dots on the map. The total number of pelts exceeds 3,665,000. Range boundaries have been drawn only for stenotopic species (i.e., those with a narrow geographic range). The occurrences of widely distributed animals, such as boar, gazelle, deer, antelope, saiga, goat and otter, are given according to our own observations.

Data from the literature, not confirmed by observation, are entered with a query.

The history of the development and the present state of distribution are given only for the stenotopic species and for those which are well represented in the paleontological record.

The history of animal distribution in the Caucasus is closely connected with the climatic zones of the Quaternary. A relationship between vegetation and species distribution is also valid for this period during which there was a successive displacement of xerophytic desert vegetation, first by a steppe landscape, then by a mesophytic, and lastly by a forest landscape followed by a reversal of the entire process of vegetation displacement. The relationship, however, is not as clear in the older periods. It is certain that conclusions on distribution areas are easier to reach and are more reliable, as the species association with a given type of vegetation and landscape is longer and its ecologic niche is more limited.

Gaps in distribution and the influence of ecological barriers are only considered as they relate to types of vegetation and to barriers which were geophysical and climatic in nature. Ecological barriers which are determined by physiological reaction norms and morphological adaptations of the species require additional study. The validity of our theoretical assumptions was confirmed by the finding of the indicator species associated with a given type of vegetation and landscape in every case.

The morphology was studied mainly from the Quaternary fossil material in relationship to its stratigraphic distribution and the rate of evolution of the species. The morphological studies were primarily of carnivores (Vereshchagin, 1951b) and of some rodents and hoofed species (Chapter IV). The geographic variability of some Recent carnivores, ungulates and rodents was also
18 investigated in order to understand their origins and geologic age.

The taxonomic classification of fragmentary bones of Quaternary mammals proved to be a problem. Some mammals, known from the Middle Pleistocene to the Recent, show gradually evolving successive forms with very few morphological differences. Other lineages of mammals are represented by a succession of more or less distinguishable forms which can be discussed as subspecies of the Recent or fossil species, or as species.

As a rule, paleontologists either classify the Upper Quaternary forms as subspecies of existing species, or they identify the fossil with the Recent species. This identification of a fossil form as a subspecies of a Recent species is unsound, as the criteria for subspecies distinction are quite often only conventional and subjective.

Although we are out of agreement with this practice of classification, we retained in Tables 62 and 103 the names of the subspecies found in the literature. Those subspecies whose stratigraphic records are inadequate are entered with the qualifications conformis (similar) and affinis (related). Unfortunately, the Rules of Zoological Nomenclature (1932) do not cover this problem.

Wherever possible, we applied ecological data of the Recent to the past, and the study of the "universal" death assemblage at Binagady proved the effectiveness of this approach.

Although a certain constancy of predominant features is recognizable in Quaternary organisms, it is probable that there was a fairly rapid and extensive evolution of the physiology. This brought about modifications in the mode of life without changing the former morphological features.

The zoogeographical analysis of the entire fauna of the Holocene mammals of the Caucasus is the culmination of studies of the history of faunal complexes. The analysis is based on genetic and stratigraphic principles. Rather than adhering to geomorphological and phytogeographical units, we have emphasized the evolutionary aspects of areas of species distribution and of faunal complexes.

The problem of the geographic origins of species is discussed in Chapter III along the lines of criteria proposed by Arldt (1919).

In any discussion of the future evolution of ranges, the chief consideration for any geological stage is undoubtedly the human factor. With this in mind, we studied the numbers and behavior of animals in their original
19 biotopes and in those influenced by man, selecting various geographic zones mainly in the eastern Caucasus.

These investigations add to our understanding of recent evolutionary development or degradation and direction of the fauna.

Quantitative studies of animal populations in nature preserves were carried out during the expeditions (1938-1948) of the Azerbaidzhan antiplague station and the Institute of Zoology of the Academy of Sciences of the Azerbaidzhan S.S.R. Most of the studies employed commonly known methods, although in some cases special new methods had to be devised.

Studies of recent changes in virgin steppelands were done mainly in Azerbaidzhan and should be carried out in the future in Ciscaucasia where shelterbelts have been planted.

Introduction by man of new species into the existing fauna is not discussed in detail in this book. Acclimatization of new species and the biotechnical procedures of game farming, which have been studied by many scientists, are separate problems. Nevertheless, some examples are given in this book of the rates and patterns of distribution of some introduced carnivores and rodents.*

The effects of man's alterations of the landscape were clearly observable in the most recent changes in ecological assemblages; in fact, they may completely overtake the natural processes of change. For example, the development of stunted thorny shrubs in the place of forest in the foothills of eastern Ciscaucasia is a result not only of the Recent climatic trend, but also of deforestation and cattle grazing. Another example is the artificial drainage and forestation of the central parts of the Colchis Plain, which completely suppresses the development of water-logged soils and hydrophilic vegetation. In both cases the original assemblages of large and small mammals were completely destroyed.

The following ecological and zoogeographical terms are used throughout the book:

Ecological assemblage of mammals — a group of species which inhabit one biotope. The morphological and physiological features of the species are the result of evolution within the framework of the existing ecological conditions.

Faunal complex — a number of ecological assemblages occurring within one homogeneous geographic zone.

20 For example, the faunal complex of the arid eastern Transcaucasian plains from the Pleistocene to the Recent includes ecological assemblages of semidesert, tugai** vegetation, reed-grown lakes and swamps and other types. This complex has evolved since the Pliocene under dry and moderately warm climatic conditions.

The term 'fauna' is used in the book to designate a number of faunal complexes occurring in a multizonal territory. The word 'fauna' is commonly used by geologists, paleontologists and archaeologists to designate any collection of fossils. We do not use the word in this sense: where it was necessary to employ it, it appears in quotation marks ("fauna"). It is a mistake to identify a selected collection of fossil remains of animals, possibly of different ages, with the fauna, or the faunal complex, of a given region or country.

Our terms are quite applicable to paleogeography, i.e., to the older stratigraphic stages. A faunal complex can exist throughout an entire geological epoch, during which its composition will gradually evolve. The extent to which it is possible to reconstruct fossil ecological assemblages and faunal complexes depends upon the degree of completeness of the geological record. It is for this reason that index species which occur in large populations at certain stratigraphic horizons are indispensable to a reconstruction.

From the occurrences of such index species of the Pleistocene steppes of Eurasia as mammoth, horse, bison, saiga and other species, it is possible to infer the occurrence also of suslik, marmot, corsac fox, Siberian polecat, steppe skunk and related species. Similar inferences can be made from the occurrences of mountainous index species.

In the process of preparation of this book, it was necessary to use extensive paleontological, zoological, botanical, geological and archaeological literature. Of the more than 3,200 sources consulted, only the most frequently quoted are given in the bibliography.

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* The author participated in the introduction of nutria, common raccoon and mink into the Caucasian fauna and served as a consultant in a number of other experiments.

** [Tugai — a bottomland complex with forests, bushes and meadows in river valleys of Central Asia.]

The writings of ancient Greek, Roman, Arab and Armenian naturalists, historians and geographers in translation, as well as the reviews of Gan (1884-1890), Latyshev (1893-1904, 1947, 1948), and Karaulov (1901) were used as source material.

Of the voluminous literature on species systematics only the titles most essential to the Caucasian fauna are given.

The Caucasus (Caucasian Isthmus) is considered to lie within the following boundaries: the Kuma and Manych rivers to the north, and the international boundary of the Trancaucasian republics to the south.

Of the many questions and problems which arose during the course of the field work and preparation of the book, some of the most important
21 involved the stratigraphic correlations of paleolithic localities in mountainous country wherein several climatic, floral and faunal provinces are joined.

The present work could have been accomplished only with the support of the Directors of the Zoological Institute of the Academy of Sciences of the U.S.S.R., and the Presidium of the Azerbaidzhan Academy of Sciences. The author is indebted to B.S. Vinogradov and A.A. Strelkov for valuable editorial comments and advice.

The line drawings were done by V.N. Lyakhov, the drawings of animals by E.Ya. Zakharov and Prof. K.K. Flerov. All the photographs were taken by the author.

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I thank all those who, in one way or another, contributed to the completion of my work.

The first and more detailed manuscript was completed in 1954; in the process of preparation for this publication, many sections were shortened and new material was included.

Part One

PALEONTOLOGICAL AND ARCHAEOLOGICAL BACKGROUND OF FAUNA FORMATION

Chapter I

DEVELOPMENT OF CAUCASIAN LANDSCAPES AND MAMMALIAN FAUNA IN THE TERTIARY

TERTIARY BONE-BEARING LOCALITIES

Abundant remains of Carboniferous plants in the slates and sandstones along the northern slopes of the Main Range indicate that land existed in the Caucasus as far back as the Paleozoic.

Individual islands appeared after the broad transgressions of the Mesozoic, and later merged gradually into one landmass.

FIGURE 6. Land formations (cross-hatched) in Eastern Europe and Southwest Asia (from Arkhangel'skii and Strakhov, 1938) Dot indicates Upper Oligocene locality at Benara

The Caucasian islands were covered by ferns, ginkgos and cycads in the Jurassic, but the paleobotanical record only commences with the Cretaceous when plane, poplar, dryandra, myrica and giant conifers (araucarias, sequoias and others) appeared.

Iguanodons which occur in travertine encrustations in the Satapliya cave near Kutaisi are the only fossils representative of the terrestrial vertebrates of the islands (Kandelaki and Dzontsenidze, 1937; Gabuniya, 1956b).

According to Pavlov (1936), the area between southwest Asia and the Baltic was dry land in the Paleocene. The Caucasus was built of gently folded Jurassic and Cretaceous strata.

At a later stage, the transgression of Tethys covered southern Europe, the Ukraine, the Crimea and part of the Caucasus, and Tethys became connected with the Asian sea extending to the southeast.

Thus, the formation of land in the Caucasus, which determined the evolution of the Quaternary faunas, took place entirely during the Cenozoic.

26 In the Eocene the northern coast of Asia Minor, Surami, Kazbek and Elburz were sites of intensive vulcanism, which probably produced the high relief of the island lands of the Caucasus (Figure 6). There are no data on the Eocene flora.

Small whales of the genus Zeuglodon (Archaeoceti) lived in the sea surrounding the island of Caucasus. Their fossilized remains occur in the Koun beds of the Apsheron Peninsula and in the area of the Sumgait rivulet.

The first occurrences of terrestrial vertebrates in the Caucasus are in the Oligocene.

OLIGOCENE

The tropical character of the Caucasian landscape persisted through the Oligocene. The tuffaceous sandstones of Lower Oligocene age in Mount Darry-Dag and the Araks valley contain ferns (Blechnum brauni, Pteris oeningensis), palms (Sabal hearingiana), conifers (Podocarpus), Lauraceae (Cinnamomum), myrica, zelkova, and small grasses (Panicum miocenica and other forms). Palibin (1936) correlated the Darry-Dag Oligocene flora with the Lower Oligocene floras of the Balkans and central Europe. He thought that the Darry-Dag is indicative of humid tropical forests covering volcanic islands.

No bones have as yet been found in the Lower Oligocene beds of the Caucasus. However, it is possible that the island of Caucasus and the adjacent land masses to the south were inhabited by the same fauna of primitive carnivores and hoofed mammals which are well-known from the Eocene and Oligocene deposits of Western Europe.

Bogächev (1938d) mentions a footprint of a creodont about the size of a large dog from a layer of silicified volcanic ash in the Darry-Dag near the town of Dzhulfa.

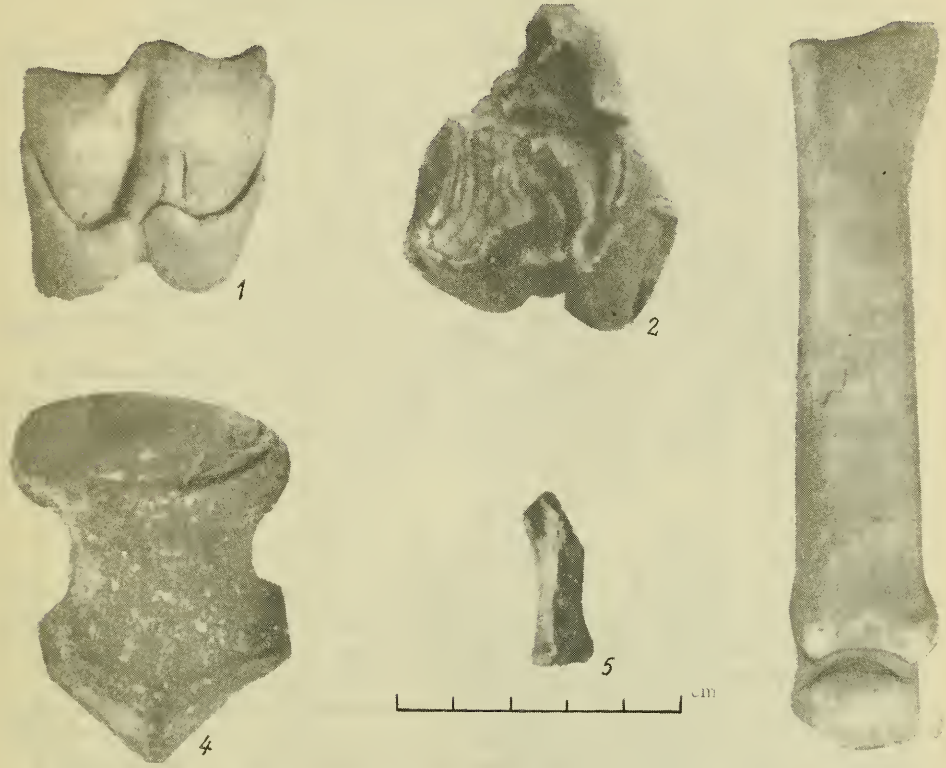
The marine (Middle Oligocene) Maikop beds of Cis- and Transcaucasia contain abundant remains of cod and herring. Occurrences of Halitherium cf. schinzi Kaup. and other, unidentified, sirenian species (possibly the ancestors of dugongs) are known from the Chiaturi manganese basin of Georgia, on the southern coast of the Black Sea, and from the Maikop beds in the Akhzy-Khazry area of the Apsheron Peninsula (Bogachev, 1938c). The whales Zeuglodon (Microzeuglodon) caucasicum Lyd. and Iniops caucasicum Lyd. have been described from beds that are probably the same age (Lydekker, 1892).

Remains of Microzeuglodon aff. caucasicum Lyd. have also been described from the beds eroded by the Sumgait rivulet 20 km north of Baku (Ryabinin, 1938).

Occurrences of the whale genera Microzeuglodon, Iniops, Delphinus (sensu lato) and Zeuglodon have been recorded (Bogachev, 1938c, 1939a) from the Maikop beds of the Apsheron Peninsula.

The same Maikop beds along the Sumgait rivulet contain fossil leaves of the evergreens Combretaceae, Sapotaceae, Ternstemiaceae, with an admixture of tropical conifers.

(27)



FIGURES 7. Bones of hoofed mammals from the Oligocene of Benara

1-4 — Pm_3 and os lunatum of Benaratherium callistrati Gab.; 2 — M^3 of Aceratherium cf. filholi Osb.; 3 — metatarsus of Schizotherium chučua; 5 — fragment of scapula of small artiodactyl

The abundance of marine mammals and the dense land vegetation attest to the earlier existence of tropical conditions on the island of Caucasus and of Sargasso-type lagoons on its southern coast. Observations on the
27 southern slopes of the Taurus Mountains indicate that Asia Minor was also covered with such forms as podocarpus, myrica, oak, cinnamon, andromeda and eucalyptus in the Oligocene.

A burial containing Oligocene land mammals was discovered by the geologist M. F. Khuchua in 1948 at Benara in the Akhaltsikhe region of southern Georgia. A few poorly preserved bone fragments and teeth were found in upper multi-colored sandstone, conformably overlying the lignite beds (Figure 7). The mode of preservation in situ was inadequately studied.

Small bone fragments occur mainly in the concretions made of hard sandstone. The material was identified and described by Gabuniya (1951a, b, 1953, 1955a, b) as rodent and ungulate:

Rodentia

Fam. gen.

Perissodactyla

Schizotherium chučua Gab.
Benaratherium callistrati Gab.

Artiodactyla

Anthracotherium sp.
Lophiomeryx benarensis Gab.

28 Gabuniya has correlated the Benara locality with the Oligocene phosphorite beds of Quercy in France and with the Middle Oligocene localities of Mongolia and Kazakhstan, where bones of Schizotherium and Lophiomeryx are known from the Upper Oligocene.

The fauna from the vicinity of Akhaltsykh confirms the paleobotanical evidence of the land connections which existed, with interruptions, between the Caucasus and central Asia and between the Caucasus and Western Europe in the Oligocene.

MIOCENE

In the Lower Miocene the island of Caucasus extended from the vicinity of Anapa in the west to the upper reaches of the Samur River in the east. The area of the Dzirul crystalline massif was also an island of smaller dimensions. The region of Trialeti-Akhaltsikhe and Borzhomi was covered by sea. Sands were deposited in the sea, although toward the close of the Lower Miocene the area became dry land (Zhizhchenko, Kolesnikov and Eberzin, 1940). Only marine mammals are known from the Lower Miocene beds.

Bones of the seal Phoca sp., resembling P. vindobonensis Toula (Bogachev, 1927b), occur in the Miocene beds at Lok-Batan, south of Baku. Remains of Phoca sp. have also been reported from the limestones of the Kilyazinskaya spit north of Baku, and of the whale Cetotherium meyeri Brandt from Lok-Batan and the village of Dzhorat on the Apsheron Peninsula (Bogachev, 1938c).

29 The geography of the island of Caucasus at the beginning of the Middle Miocene, in the so-called Helvetian stage, was essentially the same as in the Lower Miocene. The sea, in which Tarkhan and Chokrak sediments accumulated, covered the entire area from the northern coast of the island of Caucasus to Rostov in the northwest, and Stepnoi (formerly Elista) in the northeast. At that time the landmass of Caucasia Minor probably appeared south of Surami island, and the Caucasian island increased in size.

The vegetation of the islands in the Middle Miocene, as shown by the incidence of fossils in Cis- and Transcaucasia, retained its subtropical character (Palibin, 1936) though with a small admixture of deciduous trees (Castanea sativa) and conifers (Pinus neptuni) of northern origin. In the Middle

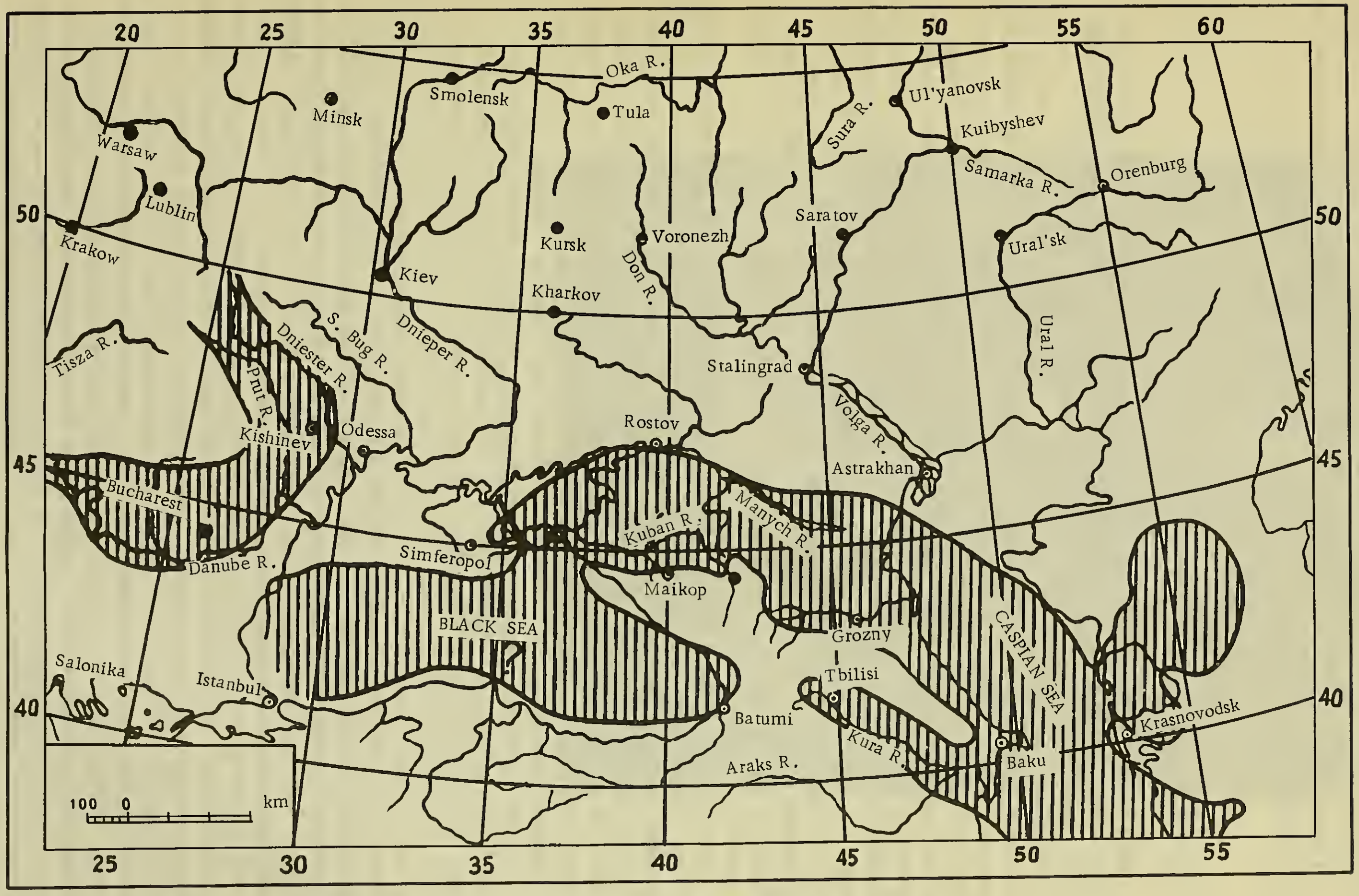


FIGURE 8. Land formations in the Middle Miocene (from Zhizhchenko; see Zhizhchenko and others, 1940)

Dot indicates locality at Belomechetskaya

Miocene, in Chokrak time, the Caucasian land gradually became higher and, in the process of growth, became a peninsula of the southwest Asia massif (Figure 8).

The sediments of Chokrak age in Ciscaucasia contain abundant remains of terrestrial mammals.

Central Ciscaucasia

Belomechetskaya. This locality, discovered by A. V. Danov in 1926, is near the Cossack village of Belomechetskaya, on the right bank of the Kuban River, north of Cherkessk (Figure 1).

In this region of the plateau, the Chokrak beds, 60 m thick, are mostly coarse-grained sandstones plus a combination of sand, clay and calcareous sediments. In a number of places, sandy bone-bearing lenses have been exposed in the Miocene hills by the eroding action of the Recent Kuban River approximately 50 m above the present water level. These were probably formed in a river which cut through the Chokrak beds eroding an ancient accumulation of skeletons in a lake or a marsh. The bone-bearing lense at the southern outskirts of Belomechetskaya is made up of gravelly quartz sand, with grains measuring 0.5-1.0 mm in diameter, slightly cemented by silt. Parts of the outcrop are iron-stained in vertical and diagonal bands. There is no pronounced bedding, which, however, may be a result of metamorphism.

Areas of silty sandstone, more strongly cemented and of grayish color, occur within the mass of the gravelly quartz sand. The silty sand indicates changes in the river current regime. The exposed thickness of the bone-bearing layer at this locality is 3.5-4.0 m. It is overlain by a limestone layer 30-40 cm thick. This layer probably corresponds to a brief marine transgression. Higher in the section the sands alternate with limestones. In places the sands are covered by Quaternary loams (Figure 9).

The remains of land and marine animals (bones and bone fragments, fragments of skulls, isolated teeth) are scattered throughout the layer. They occur in the gravelly sand and more often in the bluish, cemented, silty and iron-stained sand. The surface of the bones is pale yellow, light brown or dark brown in color. In fresh fracture the diaphyses are light brown, the cracks and the pores of the epiphyses are stained with ferric or, more rarely, ferrous oxide. The tooth dentine is also stained; the
30 enamel is glossy and dark blue, or sometimes black at the base of the crown. The old factures on the long bones were rounded by water and the cavities in the bones were filled with sand.

No tooth marks of predators were found on the bones. It is difficult to determine why and in what season of the year the animals died. It seems doubtful that death was caused by catastrophe. The variety and the fragmentation of the bones, and the abundance of teeth of small herbivores which occur sometimes in horizontal, sometimes in vertical positions within the sediment, indicate several cycles of redeposition. The death assemblage contains both young and old herbivores and carnivores. Remains of the swamp mastodon (Platybelodon) consist of a fragment of the facial part of the skull and mandibles which belonged to one adult and one young individual.

FIGURE 9. Bone-bearing bed at Belomechetskaya

Photograph by author, 1950

The bone material at this locality includes both terrestrial and marine mammals, and the aquatic turtle Trionyx. The mode of preservation of
31 all the bones is very much the same. This indicates the redeposition of the bones in alluvium. The bones were probably washed from the skeleton-bearing lenses of Oligocene-Miocene age by rivers or, less likely, by sea waves. In this process the bones became sorted and redistributed in the sediments of the river bed. The first burial of the bodies of land animals, as indicated by the iron stain on the bones, took place in a basin of standing fresh water, probably on the floodplain. Thus, it is evident that the existence of the Belomechetskaya "fauna" antedates the deposition of most of the animals in the fossiliferous layer, although some few of the "fauna" undoubtedly died during the time of deposition. In this process the bodies of land animals carried by the river and the floating bodies of marine mammals entering the river mouth were macerated and their remains incorporated into the sediment.

The collections of PIN, ZIN and the Institute of Paleontology of the Georgian Academy of Sciences include the species and groups of mammals given in Table 1.

TABLE 1. Species and number of mammal bones from the Middle Miocene beds at Belomechetskaya*

	Number of bones
Carnivora	
Amphicyon sp.	9
Hyaena sp.	6
Ursavus sp.	4
Tubulidentata	
Orycteropus sp.	1
Rodentia	
Palaeocricetus caucasicus Arg.	6
Proboscidea	
Platybelodon danovi Boris.	4
Mastodon sp.	131
Perissodactyla	
Paranchitherium karpinskii Boris	20
Anchitherium aurelianense Cuv.	4
Dicerorhinus caucasicus Boris.	172
Chalicotheriidae gen.	3
Fam. gen.	1
Artiodactyla	
Kubanochoerus robustus Gab.	1
Hippopotamidae (?) gen.	1
Micromeryx flourensianus Lartet	7
Dicrocerus elegans Lartet	3
Paratragocerus caucasicus Soc.	8
Eotragus cf. martinianus Lartet	12
Hypsodontus miocenicus Soc.	1
Fam. gen.	52
Cetacea	
Fam. gen.	34

* Material identified with the aid of Borisyak (1928a, 1943), Argiropulo (1938, 1940c), Sokolov (1949), Gabuniya (1955d, 1956a) and unpublished data of K.K. Flerov and of the author.

The collections also include fish and aquatic turtle (Trionyx). The total number of known Miocene mammals from the Belomechetskaya is approximately 20, although the taxonomic identity of some specimens remains unknown (Figures 10-15).

Paranchitherium, Anchitherium, Rhinoceros and Platybelodon were considered stratigraphic index fossils by Borisyak (1937, 1938b). The degree of specialization of Paranchitherium from
32 Belomechetskaya is the same as that of Parahippus from the Miocene of North America. Anchitherium, which is probably an earlier form, is characteristic of the Miocene of Eurasia.

The Belomechetskaya rhinoceros was considered by Borisyak as one of the most primitive Dicerorhininae. The dentition shows both primitive and specialized features. Possibly it should be regarded as the oldest representative of Rhinoceros schleiermacheri.

A peculiar mastodon, Platybelodon, is closest to the genera Phiomia and Palaeomastodon of the Oligocene of Africa, which may possibly be the ancestors of the long-snouted mastodon. The lower tusks of Platybelodon, flattened dorsoventrally and firmly joined, form an elongated scoop similar in shape to the tusks of Amebelodon fricki Barb. from the Pliocene of Nebraska. According to Borisyak (1928b)

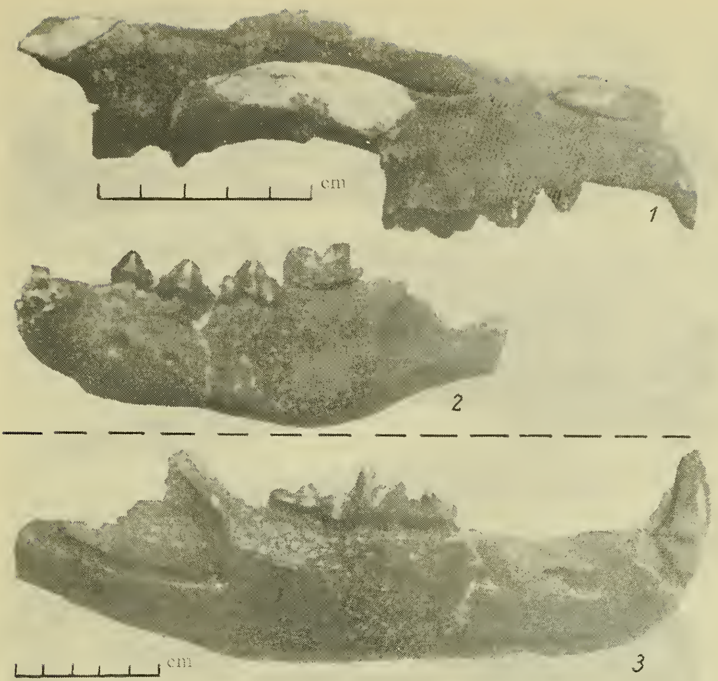


FIGURE 10. Bones of carnivores from Belomechetskaya

1, 2 — Hyaena sp.; 3 — Amphicyon sp.

and Osborn (1936) these mastodons had no trunk. They lived on the shores of lakes and river backwaters, digging with their flattened tusks for the succulent water plants and roots which were their food.

Small Dicrocerus, Micromeryx and Eotragus are the main index fossils of the Middle and Upper Miocene of Eurasia. In general the fossiliferous layer at Belomechetskaya contains mammals of stratigraphically different ages. In view of this, it is difficult to identify the index species of the Middle Miocene faunal complex.

33 The peculiar features of the Belomechetskaya "fauna" do not permit an easy comparison with other Miocene faunas of Eurasia and therefore its zoogeographical relationships are not clear. However, since the autochthonous development of such a fauna on the small landmass of the Caucasus is unlikely, an earlier land connection between the Caucasus and the continental landmass in the south can be regarded as certain.

A reconstruction of the Caucasian landforms of the time when the animals
preserved at Belomechetskaya lived would include mountain ridges and
34 broad valleys with forests, bushland, lakes and quiet rivers as part of the
landscape. The backwaters of those rivers and lakes were probably the
feeding grounds of Platybelodon.

Fossil insects and plants occur in the Middle Miocene beds which contain marine mollusks. These beds belong to the Karagan and Konka stages.

(33)

FIGURE 11. Skull and tooth of *Platybelodon danovi* (from Borisyak, 1928b)

Poplars (*Populus mutabilis*), *Sapindus fulcifolius* and evergreen cinnamons (*Cinnamomum scheuchzeri*) occur in the Karagan beds of Dagestan. The sandy-clayey littoral sediments of the Spanidontella sea, southwest of Derbent, contain leaves of evergreen species characteristic of the Upper Oligocene and Lower Miocene of Europe: *Myrica hakeaefolia*, *Laurus primigenia*, *Ardisia* cf. *oceanica*, *Diospyros paradisiaca* and other forms. The fauna of marine mollusks indicates that the Miocene sea became progressively less

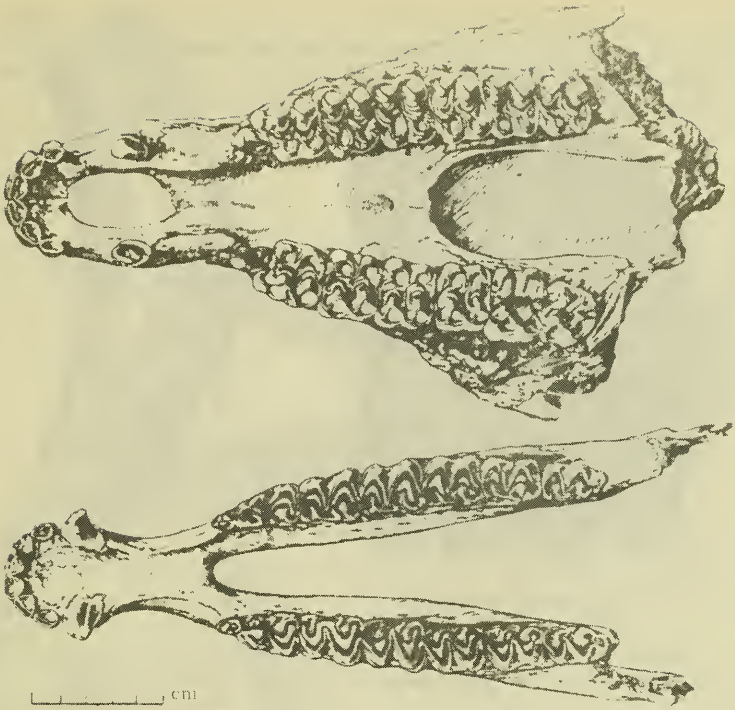


FIGURE 12. Skull and tooth of Paranchitherium karpinskii (from Borisyak, 1937)

saline due to its isolation from the Tortonian basin of the Balkan region, that the climate became more humid and that the rivers carried more water (Zhizhchenko, Kolesnikov and Eberzin, 1940).

The richest "fauna" of insects (some 90 identified species) was discovered in bedded marls of the Karagan stage west of Stavropol. The insects were probably carried by streams into the shallow lagoons of the northern coast and buried in the silty sediment. The following aquatic insects are common: mayflies (Ephemeroptera), dragonflies (Odonata), true bugs (Gerridae), water beetles (Dytiscidae, Hydrophilidae), caddis flies (Trichoptera) and mosquitos (Diptera). Among the terrestrial phytophagous, saprophagous, predaceous and parasitic forms are Orthoptera, Hemiptera, aphids, cockroaches, termites, cicadas, butterflies (Lepidoptera), Diptera, Hymenoptera and beetles (Rodendorf, 1939).

This assemblage suggests a subtropical climate and profuse grassy vegetation in the Caucasus at the end of the Middle Miocene.

The numerous plant fossils from the Krynka River valley in the Donets Basin (Krishtofovich, 1930) indicate that the vegetation on the northern shores of the Konka basin was of the temperate type and strikingly different from the subtropical flora of the Caucasus in the Neogene.

In the Upper Miocene the seas still covered the southern Ukraine, the Crimea, Ciscaucasia, most of the Transcaspian land and possibly Iran.

FIGURE 13. Upper incisors of giant perissodactyl from Belomechetskaya

FIGURE 14. Canine of an unknown artiodactyl (Hippopotamidae?) from Belomechetskaya

The fauna of the Sarmatian sea reflects a further decrease in salinity and shows considerable variability in facies and in stratigraphic age.

In the Lower Sarmatian the Caucasian landmass grew southward. The thickness of the Sarmatian sediments indicates that the relief of Japhethida and of the coastal areas was essentially the same as in the Middle Miocene. The areas of maximum uplift in the Lower Sarmatian were in the Guri ridge and in Khevsuretia, and in the Middle Sarmatian, in inner Dagestan. The
36 northwestern coast remained a plain. The sea in this area became shallower due to the uplift of the Stavropol massif.

In the Upper Sarmatian the sea receded from the northern part of the Caspian and from most of the Transcaspian lands, leaving the Stavropol Plateau as a peninsula projecting into the Ciscaucasian strait. To the south, a wide isthmus extended from Kutaisi to Telavi connecting Japhethida with the Caucasia Minor landmass, and in eastern Transcaucasia a narrow Kura bay formed (Zhizhchenko, Kolesnikov and Eberzin, 1940).

The landscapes of the Caucasus in Sarmatian time can be restored with a high degree of certainty from the available plant and animal fossil material.

37 The littoral marine flora consisted of species of Fucus and Cystoseira, which occur as fossils in the valleys of the Sunzha and the Sulak on the Malokabardinskii ridge.

Seals (Phocidae) and small toothless whales of the genus Cetotherium were abundant in the Sarmatian sea. Bones of Cetotherium have been found in the Sarmatian coquinas and silts near Derbent, in Makhachkala, and in the blue Sarmatian clays near Maikop (Spasskii, 1939). Bones of seal have been found in the white marine sands near Stavropol, in the blue clays near Maikop and Goryachi Klyuch and in a number of other places. The Stavropol seal bones were found with bones of terrestrial Tertiary mammals — undoubtedly species which lived in a warm climate.

(36)

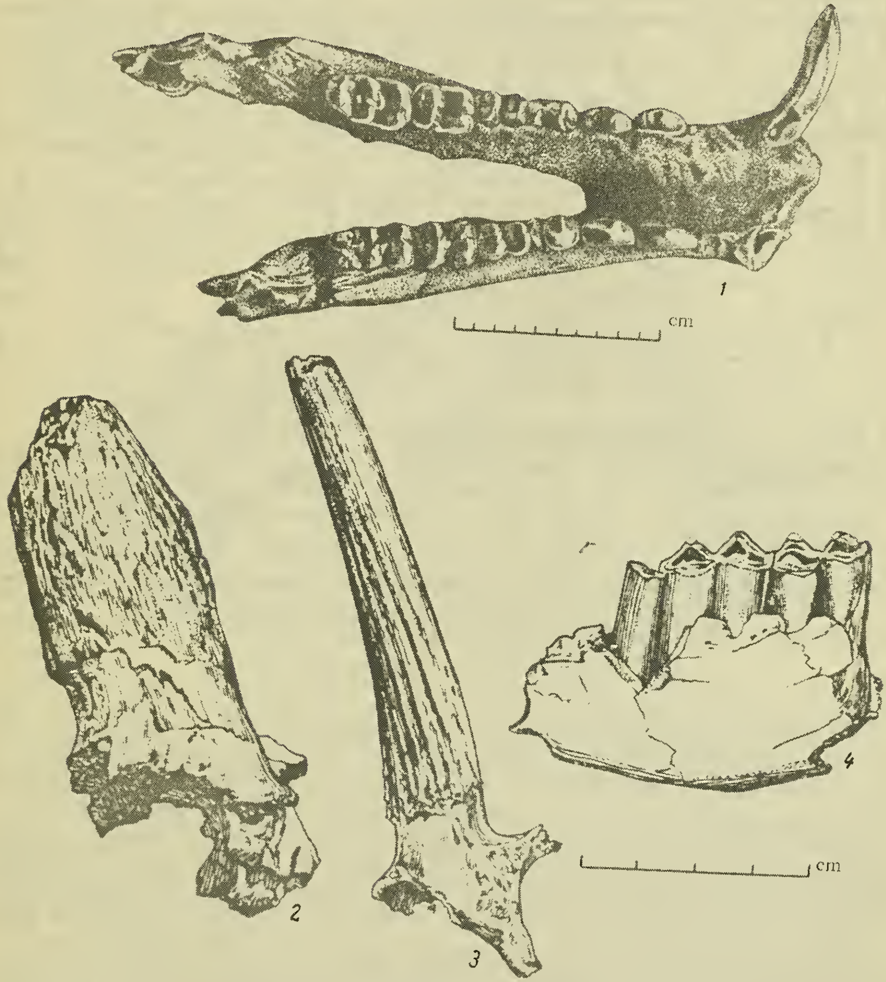


FIGURE 15.

1 — jaw of Kubanochoerus robustus (from Gabuniya, 1955a); horn axes of: 2 — Paratragocerus caucasicus; 3 — Eotragus cf. martinianus; 4 — teeth of Hypsodontus miocenicus (from Sokolov, 1949)

The terrestrial flora of the Caucasus in the Sarmatian is represented by coniferous, evergreen and deciduous species. Remains of spruce

(Abies sp.)*, pines (Pinus sp.) and sequoia (Sequoia sp.) occur in the exposures along the Supsa River. Magnolia, laurel (Laurus primigenius), cinnamon (Cinnamomum polymorphum), elm, willow and pear trees have been identified from the Kakhetian Range and the Trans-Kuban Plain.

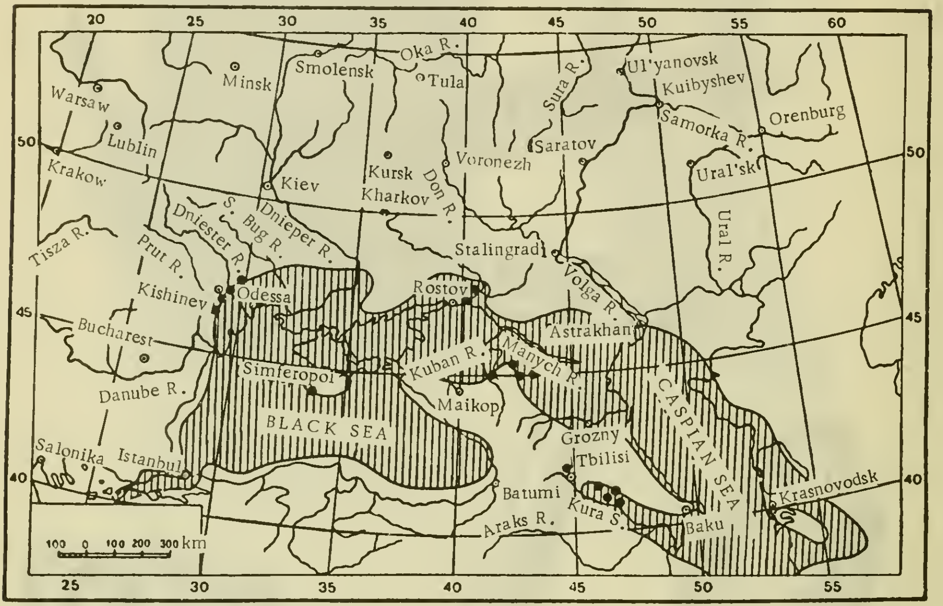


FIGURE 16. Land formations in the Upper Miocene (Upper Sarmatian) (From Kolesnikov; see Zhizhchenko and others, 1940.) Dots indicate main occurrences of land vertebrates

At some of the Middle Sarmatian localities in eastern Georgia as many as 30 arboreal species have been collected. Of these, up to 70% are deciduous and include the Tertiary species of hornbeam (Carpinus), oak (Quercus), willow (Salix), maple (Acer), chestnut (Castanea), zelkova (Zelkova ungeri), and shrubs of Indian hemp (Apocynum), bladder senna (Colutea salteri) and other deciduous species in addition to the evergreen laurel, cinnamon, myrica and magnolia. According to
38 Palibin (1936) the evergreen species of the flora "which covered the entire surface of Japhethida" were the last Sarmatian representatives of the subtropical and tropical flora which flourished on the Caucasus from the beginning of the Tertiary. This first step in the borealization of the flora contributes to an understanding of the later evolution of the fauna. In a comparison of the Caucasian flora with the Upper Miocene flora of Asia Minor, Grossgeim (1936) found that they are very similar, both being characterized by a mixture of boreal and subtropical elements.

The taphonomy of these dead plant assemblages is significant for the ecologist or faunist in the study of altitudinal zonation of flora which

* [There is a discrepancy in the Russian text between the common and the Latin name here. The latter corresponds to the true firs, whereas the Russian gives the name "spruce."]

might have developed in the presence of the mountainous relief that existed in the Middle Miocene. Such a zonation might explain some of the instances of typically "mixed" Miocene flora.

Hipparion fauna appeared in the Caucasus in Sarmatian time, having migrated from the south along the wide Transcaucasian Isthmus (Figure 16); it was probably first discovered in Transcaucasia by Ryabinin (1913).

Ryabinin found bones and teeth of Hipparion gracile Kaup and tooth fragments of Rhinocerotidae in the Kyasaman site and on the left bank of the Iora River. At this locality the vertebrates occur in red clays with sandstone intercalations (which also contain algae (Chara cf. escheri) and mollusks (Planorbis sp.)) and the same mammalian genera were recorded by Ryabinin from gypsiferous clays underlying the Akchagyl beds in outcrops in the Katsakhuris-Kedy ridge.

In 1913, the geologist Dombrovskii, working further south on the right bank of the Iora River, found in the cliffs of the Eilyar-Ouga and Palan-Tikyan ridges a rich locality of Tertiary mammals, known as the El'dar locality (1914).

Kartalinia Plateaus

El'dar. According to the descriptions of Dombrovskii (1914), and Andrianov and Larin (1935), the bone-bearing bed can be traced over 6 km from the gorge which connects the El'dar Steppe with the Iora River floodplain. From west to east the bed grades from a shell conglomerate to sandstone, then to limestone, and again to sandstone which grades into thick upper Sarmatian clays where the bed eventually peters out. The bones (parts of skeletons) occur in pockets, at intervals of 10, 20 and a few hundred meters. Ripple marks occur on the top surface of the bone-bearing sandstone.

The lithology of the bed attests to the existence of a low coast and muddy bay. The bodies of animals were transported into the bay by weak currents and shore waves and were buried in the sandy-clayey bottom sediment. The investigators believe that mass mortality in the animals was caused by steppe fires, earthquakes and mudflows.

According to our observations, all the complete bones, including lower jaws and ribs, were flattened by the pressure of the overlying beds. Some bones were broken in the process of burial; as a consequence, the cavities became filled with sand and silt which preserved the original shape of the bone.

39 The surface of the bones is chestnut or chocolate in color; in fresh fracture, the colors are grayish. Permineralization and diagenesis of the bone material were not significant. Preserved coprolites were also found.

Bones abraded by the surf are rare, and in many cases limbs were preserved with bones intact. In general, a number of features support the conclusions of earlier authors regarding the nature of the burial and the mode of preservation.

Table 2 (Figures 17, 18) lists the species from the Moscow and Baku collections identified by Bogachev (1927a), Alekseev (1930), Borisyak and Belyaeva (1948).

TABLE 2. Species and number of mammal bones from the upper Miocene beds at El'dar

	Number of bones		Number of bones
Primates		Artiodactyla	
Fam. gen.	1	Sus erymanthius Roth. et Wagn.	5
Carnivora		Achtiaria borissiakii Alex.	69
Crocuta eldarica Bog.	4	Camelopardalis (Helladotherium) sp.	
Hyaena cf. eximia Gaudry	6	Tragocerus aff. leskevitschi Boris.	159
Proboscidea		Tragocerus sp. No. 1.	
Mastodon longirostris Kaup	24	Tragocerus sp. No. 2.	
M. pentelici Gaudry		Gazella sp.	6
Mastodon sp.		Pinnipedia	
Dinotherium giganteum Kaup.	3	Phoca sp.	5
Perissodactyla		Cetacea	
Hipparion gracile Kaup.	164	Delphinus sp.	208
Chalicotherium sp.	2	Cetotherium sp.	
Aceratherium transcaucasicum Bog.	6		
Dicerorhinus aff. orientalis Schloss.	65		

The El'dar collection may be regarded as a part of the Upper Miocene faunal complex of Transcaucasia, since there are no signs of redeposition of the bones and most of the species lived at the same time. The most abundant species, as far as the collections show, were Hipparion, ibex, rhinoceros and giraffe.

Udabno. This sizable locality containing Hipparion fauna was discovered in 1931 by N. A. Gedroits near the village of Udabno, on the Kura-Iora water divide of the Garedzhiiskaya Steppe. The locality was later excavated by the Museum of Georgia.

The fossils occur in Sarmatian clays overlain by sandstones of the Shiraki formation. This locality and the El'dar locality are similar to each other, as are the lists of species from each. The material is in the collections of PIN and the Museum of Georgia, and was identified by Burchak-Abramovich and Gabashvili (1945, 1950), Tsereteli (1942), and Borisyak
41 and Belyaeva (1948):

Primates

Udabnopithecus garedziensis Burtsch. et Gab.

Carnivora

Hyaena sp.

Rodentia

Hystricidae gen.

Proboscidea

Mastodon sp.
Dinotherium sp.

Perissodactyla

Hipparion gracile Kaup
Aceratherium sp.

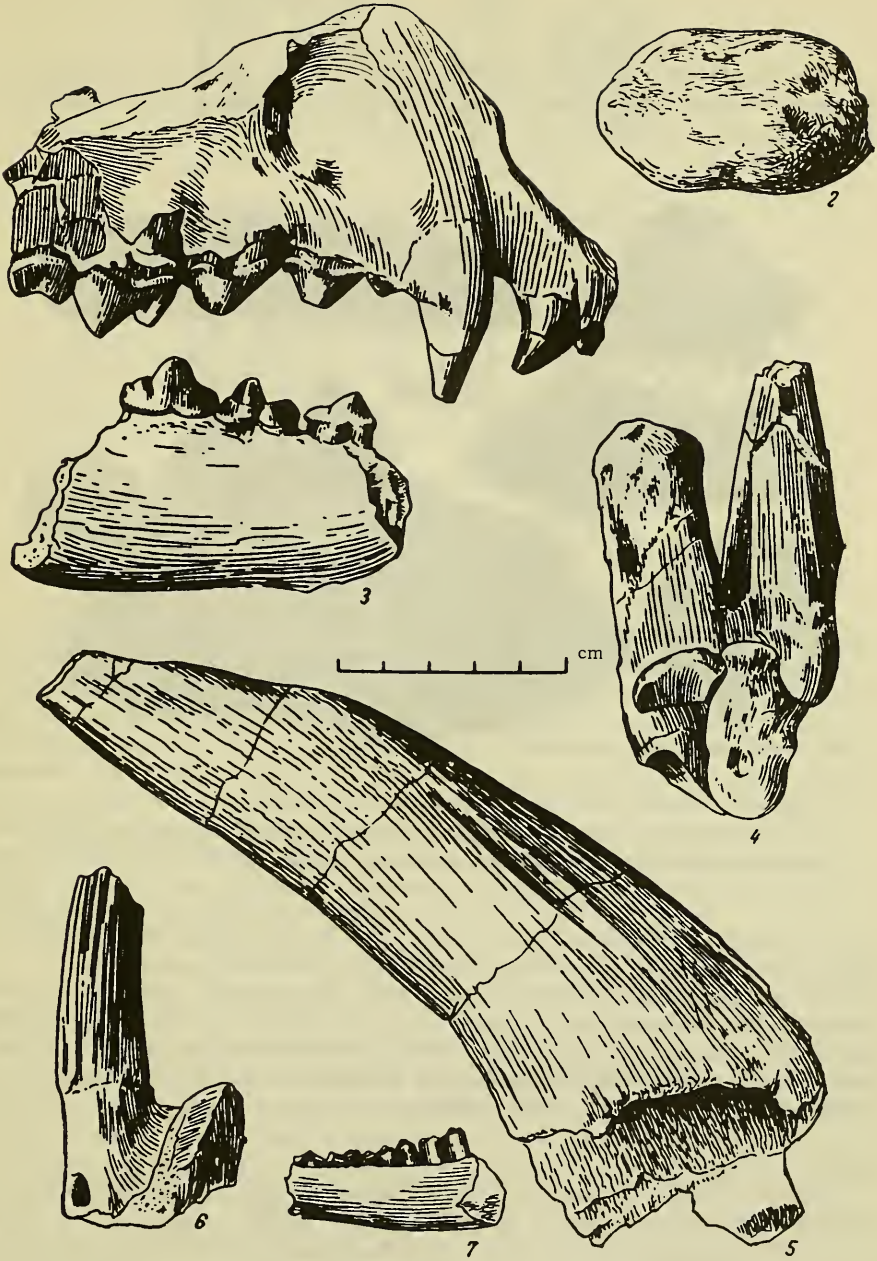


FIGURE 17. Remains of carnivores and hoofed mammals from El'dar

1, 3 — skull of Hyaena sp.; 2 — coprolite of hyena; 4, 5 — tarsal joint and horn axis of Tragocerus sp.; 6, 7 — horn axis and jaw of Gazella sp.

Artiodactyla

Sus sp.
Cervidae gen.

Achtiaria sp.
Tragocerus sp.
Gazella sp.

The occurrence of teeth of a large homonid ape (Udabnopithecus garedziensis) is of particular interest in connection with studies of the origin of man (Figure 19).

FIGURE 18. Remains of carnivores and hoofed mammals from El'dar

1 — jaw of Crocuta eldarica; 2 — incisor of Aceratherium transcaucasicum; 3-5 — teeth of Tragocerus leskevitschi (from Bogachev, 1927b)

Arkneti. This locality is 1.5 km east of the village of Arkneti in South Ossetia. It is situated on what was the western part of the Transcaucasian bay of the Sarmatian sea. Fragmented bones of mammals occur in the yellowish gray loams, 1.5-2.0 m thick. Well-preserved bones, some of them joined, and skulls occur in a bone-bearing lense 3 m long and 50-70 cm thick. The artiodactyls and perissodactyls have been identified by Gabuniya (1952b, 1955c):

Perissodactyla

Hipparion sp. (cf. garedzicum n. sp.)

Artiodactyla

Sus sp.
Eostylocerus sp.
Dicrocerus salomeae Gab.
Tragocerus ex gr. leskevitschi Boris.
Tragocerus sp.
Gazella cf. gaudryi Schlos.
Gazella sp.
Giraffidae gen.
Phronetragus arknethensis Gab.

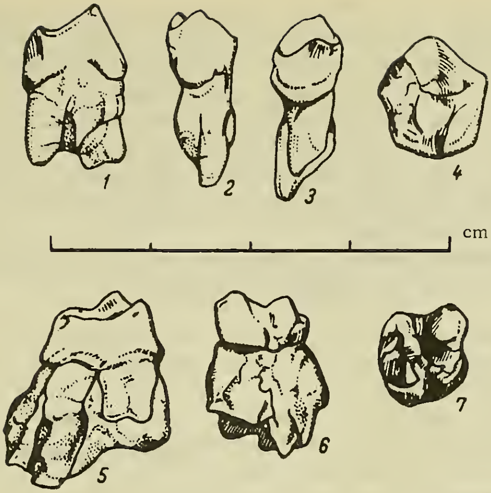


FIGURE 19. Teeth of Udabnopithecus garedziensis

1-4 — Pm^2: anterior, outer, inner surfaces (× 1½), upper surface (× 2¼); 5-7 — M^1 (× 1½) anterior, outer and upper surfaces (from Burchak-Abramovich and Gabashvili, 1950)

42 The age of the "fauna," according to Gabuniya, is very close to the age of the Udabno "fauna"; it may be dated as Upper Sarmatian (Meotian).

The existence of large valleys covered with savannah and tropical forest vegetation on the piedmont can be inferred from the composition of the Sarmatian fauna. Streams originating in the Caucasus Range were evidently sufficiently powerful to transport the bodies of mastodons and rhinoceroses into the coastal bays of the Sarmatian sea.

As a whole, the Sarmatian faunal complex supports a picture of the landscape drawn from the known paleontological data. The plant fossils indicate not only the "mixed" character of the Sarmatian flora, but also the high degree of its differentiation.

Stravropol area

The Hipparion faunal complex occurs in the Sarmatian of the Ciscaucasus. The fauna migrated along the coasts and over the plateaus and ridges of the central part of the peninsula. Hipparion sp. and Dinotherium giganteum Kaup are known from the Middle Sarmatian limestones near the village of Burlatskoe (Khomenko, 1913a). A small giraffe, Camelopardalis parva Weith., is known from the Upper Sarmatian beds near the village of Blagodarnoe in the Stavropol area (Pavlova, 1933a).

Mount Kutsai. A fairly rich locality was discovered by A. A. Ivanchin-Pisarev in 1915 near the village of Petrovskoe, northeast of Stavropol. Like other Transcaucasian burials of Sarmatian age, it contains both marine and terrestrial vertebrates.

The bone-bearing beds of Mount Kutsai are made of sands and clays (Ivanov, 1916). These are underlain by sandy, plastic clays of Middle Sarmatian age; soft limey sandstones overlie the fossiliferous sequence. The fossils occur in medium-grained marine quartz sands. The material is poorly preserved and consists mostly of individual teeth, fragments of vertebrae, metapodia and phalanges. Bones of seal and whale occur in the lower 2-3 m of the Upper Sarmatian clays and sands. The bones of terrestrial forms occur somewhat higher, although still within the lower 3-5 m of the clayey-sandy beds.

Ivanov's (1916) identification of the terrestrial mammals reveals the presence of the Hipparion faunal complex:

43 Perissodactyla

Hipparion gracile Kaup.
Hipparion sp.
Aceratherium sp.
Rhinoceros sp.

Artiodactyla

Listriodon sp.
Sus sp.
Gazella sp.
Fam. gen.

Pinnipedia

Phoca cf. pontica Eichw.

Cetacea

Cetotherium priscum Brandt.
Cetotherium (?) sp.

Remains of birds, turtles and fishes also occur at this locality.

Individual occurrences of the bones of rhinoceros (Dicerorhinus and Aceratherium) are known from the greenish silts and sands near Maikop and from the marine sands near Beshpagir and Stavropol. As a whole, the composition of the fauna of Ciscaucasia in the Sarmatian was very similar to that of the Transcaucasian fauna.

In order to identify the origin of the Hipparion faunal complex which appeared in the Caucasus, we should compare the Sarmatian "fauna" of the Caucasus with other Miocene "faunas" of Eurasia. The following groups are of interest: the Miocene "faunas" of Punjab — in the southern foothills of the Himalayas in the Salt Range in the Indus River valley, and in the Siwalik Range in the Indus and Ganges basins; the Middle Sarmatian "fauna" of the Crimea; the Upper Miocene "fauna" of Iran from the eastern shore of Lake Urmia; and other occurrences in Asia Minor and the Balkans.

The "faunas" of the Siwalik and the Salt ranges occur in continental deposits up to 7,000 m thick (Colbert, 1935). Over 288 species of mammals are known from these Upper Miocene to Lower Pleistocene formations, which evolved from the erosion of the newly uplifted mountain range. At this time detrital material was deposited on a land surface, sometimes partially covered by freshwater bodies.

The Russian paleontologists and geologists are of the opinion, taken probably from Osborn (1921), that the Hipparion "fauna" of southern Asia (Siwalik Range) migrated via the Caucasus into Eastern Europe.

According to Andrusov (1918) the [Hipparion] fauna of the Pikermi type appeared in Europe from the east, following two routes: one along the northern coast of the gradually shrinking Sarmatian sea and one through Asia Minor.

Andrusov shows that the development of the *Hipparion* fauna was not complete in the Middle Sarmatian but continued through the Upper Sarmatian, reaching its maximum level in the Meotian. In southeastern Europe the fauna probably became extinct in the Lower Pontian.

Borisyak (1928a, p. 376) assumed that the *Hipparion* fauna migrated to Europe from Asia via the Caucasus and the Black Sea landmass.

According to Bogachev (1938d, pp. 36-37), "the African-Siwalik fauna spread through Iran and Transcaucasia onto the growing Main Transcaucasian (sic!) Range, and from there, the migration continued across the Stavropol Plateau onto the Ukrainian Steppes. The stages of migration are marked by fossils which occur along the migration route."

44 However, Colbert's lists of the Upper Miocene fauna of Kamlial and Lower Siwalik show that there is practically no resemblance to the Sarmatian fauna of the Caucasus.

Nearly 85 species of primates, rodents, carnivores, proboscideans, perissodactyls (*Hipparion*, rhinoceros) and artiodactyls (swine, tragulids, deer, giraffe), were noted to 1935 in the upper beds of the Lower Siwalik in the Salt area (Chinji). It is significant that no Cavicornia occur in these beds. The equids, rhinoceroses without horns, giraffids and primates are found in both the Caucasian and the Lower Siwalik faunas.

The Sevastopol "fauna" in the Crimea, assigned to the Middle Miocene age, consists of the following forms (Borisyak and Belyaeva, 1948):

Carnivora

Ictitherium tauricum Boris.

Perissodactyla

Hipparion gracile var. *sebastopolianum* Boris

Aceratherium zernovi Boris.

A. zernovi var. *asiaticum* Boris.

Artiodactyla

Achtiaria expectans Boris.

Tragocerus leskevitschi Boris.

Tragocerus sp.

Gazella sp.

Reptilia

Testudo sp.

Trionyx sp.

The Stavropol faunal complex was undoubtedly very similar to the El'dar complex, although the zoogeographical relationships between the two are not clear.

Recent geological data indicate that the *Hipparion* complex could only have reached the Crimea from the southwest at the end of the Middle Miocene or in the Lower Sarmatian. Later migrations can be ruled out, since the Caucasus landmass was probably cut off from the Russian platform and from the Crimea by the sea which existed until Pliocene time (Andrusov, 1918, 1926; Muratov, 1951).

The "fauna" occurring in the clays and sands at the southern slope of Mount Sahand near Marāgheh is of particular interest in the reconstruction of the Miocene landscapes and the faunal ties between Asia and the Caucasus.

According to the identification of Rodler and Weithofer (1890), Mecquenem (1924), Bogachev (1928), and Burchak-Abramovich (1952b), the following species are represented in the Marāgheh "fauna":

Primates

Mesopithecus orientalis Kittl
M. pentelici Gaudry

Carnivora

Hyaenarctos maraghanus Mecq.
Ictitherium hipparionum Gaudry
I. robustum Gaudry
Hyaena eximia Wagner
Meles polaki Kittl
M. maraghanus Kittl
Felis brevirostris Croiz. et Job.
F. attica Wagner
Machairodus aphanistus Kaup
M. orientalis Kittl

Tubulidentata

Oryteropus gaudryi Major

Proboscidea

Mastodon pentelici Gaudry

Perissodactyla

Aceratherium persia Pohlig
Rhinoceros morgani Mecq.
Chalicotherium pentelici Gaudry
Hipparion mediterraneum Hensel

Artiodactyla

Sus (Microstonyx) erymanthius Roth. et Wagner
45 Helladotherium gaudry Mecq.
Alcicephalus neumayri Rodl. et Weith.
Camelopardalis attica Gaudry
Urmiabos azerbaidzanicus Burtsch.
Gazella gaudryi Schlosser
G. brevicornis Gaudry
G. capricornis Rodl. et Weith.
Palaeonyx pallasi Gaudry
Protoryx carolinae Major
Antilopinae gen.?.
Tragocerus rugosifron Schlos.
Protragelaphus scozesi Dames.
Tragelaphus hontom-schindleri Rodl. et Weith.
Helicophora rotundocornis Weith.
Oiceros rothi Wagner
O. atropatanes Rodl. et Weith.
O. boulei Mecq.

Bones of ostrich (Struthio sp.) and Urmiornis maraghanus Meq. have also been recorded at the locality.

The large number of species in the Marāgheh "fauna" attests to a high degree of universality of the death assemblage. Although the taphonomy is not known in detail, it seems likely that the death of the Upper Miocene animals can be attributed to a common cause. This might have been toxic gases (fumaroles), volcanic ash deposits or mudflows. According to Pohlig (1886), the Marāgheh "fauna" was buried near the shores of Lake Urmia, the water level of which was much higher in the Miocene. The sedimentary facies at the locality are similar to the Pikermi locality near Athens and the Val d'Arno locality near Florence. The great variability of the assemblage is reflected in the occurrence of representatives of different ecological habitats: arboreal (e.g., Mesopithecus) and savannah and steppe (e.g., giraffes, gazelles, ostriches), and of different feeding types: carnivores, omnivores, herbivores. A predominance of savannah forms over subtropical forest forms indicates that the landscape was of a mixed savannah-tropical forest type, like that in the northern parts of the Iranian Plateau in the Miocene.

The Marāgheh "fauna" has some "African" elements in it. It is fairly close to, though not identical with, the older Sarmatian fauna of Transcaucasia.

According to Stahl (1907) and Oswald (1915-1916), the interior of Iran and Anatolia became dry land in the Upper Miocene. Salt and gypsum precipitated in the relicts of the Miocene seas. Bogachev and Shishkina (1915) discussed the importance of these geological processes in the formation of bone-bearing deposits. According to these authors, the climate of the country became arid in the Middle Miocene following the uplift and folding which subdivided the marine basin into a number of saline lagoons.

This notion of an arid desert climate is not confirmed by ecological analysis of the Maragheh mammals. It is more likely that tropical forests existed on the shores of the relict basins, although the climate as a whole was dry and hot.

The Marāgheh faunal complex was probably characteristic of all of southwest Asia. This is confirmed by geological data on the paleolandforms of Asia Minor (Furon, 1955).

46 Occurrences of Upper Miocene mammals in Asia Minor are known from Stambul, upper Gediz, Mugla, Galatia and Cappadocia. The collections comprise carnivores (Ichtitherium, Martes, Machairodus), proboscideans (mastodon), perissodactyls (Hipparion and rhinoceros) and artiodactyls (giraffe, gazelle, antelope). A similar "fauna" is found on Samos Island and in the Balkans, near Athens (Pikermi). The volcanic eruptions in Cappadocia, accompanied by ashfalls and mudflows, caused death among animals and subsequent burial in layers of tuff.

As a whole, the Upper Miocene faunas of southwest Asia, the Caucasus, the Crimea and the Balkans are similar to one another. However, the order of appearance of the Hipparion faunal complex in each area cannot be established until all the material has been studied, a task beyond the abilities of one investigator.

At the end of the Miocene, in Meotian and Pontian times, the seas surrounding the Caucasus became shallower and less saline. The Stavropol Plateau continued to grow towards the north, the area of the present Dagestan Mountains extended to the northeast, the eastern Caucasian gulf almost disappeared; and a narrow strait probably existed intermittently in the Manych area.

The major Tertiary uplifts of the Caucasian Range had probably ended by that time, and the highland faunal complexes proceeded to form under conditions of high-zonal climates and probable local glaciations.

There is no evidence of any extensive glaciation in the Caucasus in the Upper Miocene, as hypothesized by Kovalevskii (1936) in his study of the continental formations at Adzhinour. Nor does the paleontological evidence support the hypothesis of Kovalevskii and Grossgeim (1936) of extinction of the tropical flora and fauna in the Caucasus caused by an Upper Miocene glaciation. Neither is there any evidence that the Günz and Mindel glaciers were so large that they could "plough" and fill the Alazan-Agrichai valley in eastern Transcaucasia, which, in any case, is probably not that old.

Grossgeim (1936, 1948) believed that in Meotian time the southern xerophilous flora invaded the Caucasus. However, the fossil record shows that the only flora known is the mesophilous forest flora in Gurie [Western Georgia] in which deciduous species (Fagus orientalis, Acer trilobatum) predominated, but which also included evergreen subtropical forms (Rhododendron ponticum) and some admixture of conifers (Taxus grandis). Mesophilous plants were also recorded at Nakhichevan in the Lower Pliocene rock salt deposit (with paper shales): alder, mazzard, hop, hornbeam, willow, sedge and reed (Palikin 1936, Bogachev and Shishkina 1915).

Fossil plants and animals of the highlands are not known from that period. However, it is possible to assume that, in addition to some endemic evolution, cold-climate flora and fauna migrated to the Caucasus over the ranges of the Alpine region.

47 The extant forms which evolved in the Upper Miocene are the Asia Minor hamsters (Mesocricetus), Prometheomys schaposchnikovi and the wild Caucasian goat.

The Uppermost Miocene terrestrial fauna which inhabited the piedmont plains is as yet little known and poorly dated. The Hipparion faunal complex continued its existence on the plains around the Caucasus mountain system, particularly on those to the southeast.

Rare occurrences of mammals are known in eastern Transcaucasia and in western Ciscaucasia. One was discovered by N. A. Kudryavtsev in 1935 on a northern spur of the Kakhetian ridge in Transcaucasia.

The stratigraphic position of that locality is not clear, although it has been tentatively dated as Upper Miocene or Lower Pliocene. According to Orlov (1936b) the bone-bearing bed is exposed on the left slope of a deep gorge which cuts through the village of Dzhaparidze (near Tsiteli-Tskharo) toward the Alazan River. Scattered and broken limb bones, jaws and teeth of mammals occur in marine (?) clays overlain by continental clays alternating with layers of fossil soils. The following species are known from the locality:

Proboscidea

Fam. gen.

Perissodactyla

Hipparion gracile Kaup
Rhinocerotidae gen.

Artiodactyla

Sus sp.
Cervidae gen.
Giraffidae gen.
Gazella sp.

In Ciscaucasia the Upper Miocene mammals were collected by Ya. M. Eglon in 1940 from the Meotian (?) clays on the right bank of the Kuban River near Armavir. Individual fragments of permineralized bones were identified as Hipparion sp., antelope about the size of saiga (Antilopinae gen.), small beaver (Castoridae gen.), small seal (Phoca sp.) and saber-tooth (Machairodus sp.).

Fragments of molars of a rodent (Muridae), about the size of a house mouse, were found by V. Sizov in the Miocene beds of the River Aksai ravine in the Grozny Region at the boundary of the Upper Sarmatian and Meotian yellow-green clays. Remains of grasses, freshwater ostracods and otoliths of gobies (Gobius) were also collected.

The vertebrates from the continental deposits near Novocherkassk, in the south of the Russian Plain, were tentatively dated Meotian age.

The bodies of animals were probably carried by the paleo-Don into the Tanais Gulf of the Meotian sea where they were buried in the crossbedded white sands. The stratigraphic position of the sands is "between the Pontian and the eroded Sarmatian" (Zhizhchenko, Kolesnikov, and Eberzin, 1940). The sands are up to 12 m thick. Very thin intercalations of bluish gray clay with diatoms, silicified wood and teeth of proboscideans occur in the sands.

Near the village of Yanov, mollusks (Congeria and Neritina) and perch bones (Perca sp.) were collected from the sands. The mammals collected by Lisitsyn and Bykodorov near the villages of Yanov and Popovka and in the quarries along Tuzlovka River were identified by Khomenko, Bogachev and Sokolov (1954) as belonging to four species:

48 Proboscidea

Mastodon borsoni Hays.
M. cf. tapiroides Cuv.
Dinotherium giganteum Kaup

Artiodactyla

Palaeoryx longicephalus Soc.

Thus the end of the Miocene in the Caucasus was characterized by the growth of landmasses, the appearance of northern species in the flora and the development of altitudinal zones of vegetation resulting from cooling of the climate and mountain-building movements. These processes, taken together, promoted the rapid evolution of horses, Cavicornia, ruminants and deer, and a concomitant decline of giraffids.

PLIOCENE

In the Caspian region, four stratigraphic subdivisions of the Pliocene can be recognized through the fauna: Pontian, Balakhany, Akchagyl and Apsheron. In the Black Sea region, there are five subdivisions in the same period: the Pontian and four subdivisions above it corresponding to the three upper subdivisions of the Caspian: Cimmerian, Kuyal'nitsk, Gurie and Chauda.

The outline of the Caucasian Peninsula did not change essentially from the Upper Miocene to the Lower Pliocene (Lower Pontian). The peninsula extended into a slightly saline lake-sea, not connected with the ocean (Andrusov, 1918). Two large open bays cut into the northern coast of the lake: the Kuban bay in the northwest and the Terek bay in the northeast. In the western part of present-day Colchis, the Rion bay extended to the longitude of Kutaisi and to the east lay the Samur and Kura bays. The thick Pontian sediments and the littoral conglomerates (Kolesnikov, Zhizhchenko, and Eberzin, 1940, p. 402, map) indicate that all of these but the Kuban were very deep. Their depth suggests a considerable uplift in the coastal areas of the region which today comprises Abkhazia and northern Azerbaidzhan.

The broad land connections with southwest Asia allowed the migration of southern plants and animals to the Caucasus.

A number of geologists (for example, Sokolov, 1904) have noted that in Lower Pontian time the climate became cooler and the rivers of the Russian Plain periodically froze.

Nevertheless, the climate of the Caucasus remained fairly warm in Lower Pliocene time. The abundant plant remains in the Yergeni beds (50 km north of Stalingrad, in the Ilovlya River Basin) represent deciduous, warm-climate flora of the Upper Miocene-Lower Pliocene. The flora consisted of Corilus fossilis, Alnus incana, Quercus sp., Castanea sp., Parrotia persica, and Araliacea (identified by Baranov, 1952).

The occurrence of the Russian pea shrub (Parrotia persica) in the Yergeni beds is a good indicator of a warm climate in the Lower Pliocene, since this species only survived through the Pleistocene south of the Caspian sea, i.e., 10° in latitude farther south.

With the Middle Pontian, the climate in the Caucasus became warmer, as evidenced by plants collected in stratigraphic sections in the Pontian sediments at Cape Pitsunda (Mchedlishvili, 1954b).

At the end of Pontian time, the seas receded from Ciscaucasia and the water remained in the Caspian region only in the southern part of the basin (Figure 20). Extensive semideserts probably formed in eastern Ciscaucasia and eastern Transcaucasia.

49 Later, in Cimmerian time, the climate became almost tropical, as indicated by the occurrence of banded iron-ores in the Taman and Kerch peninsulas and in the foothills of the northern Caucasus. Tropical conditions can also be inferred from the occurrence of tropical plants in marine littoral sediments (Mchedlishvili, (1954a) and in volcanic tuffs at Goderdzi on the Adzhar-Imeretia ridge in Transcaucasia (Palibin, 1936). The plant remains include Ficus, Araucaria and palms.

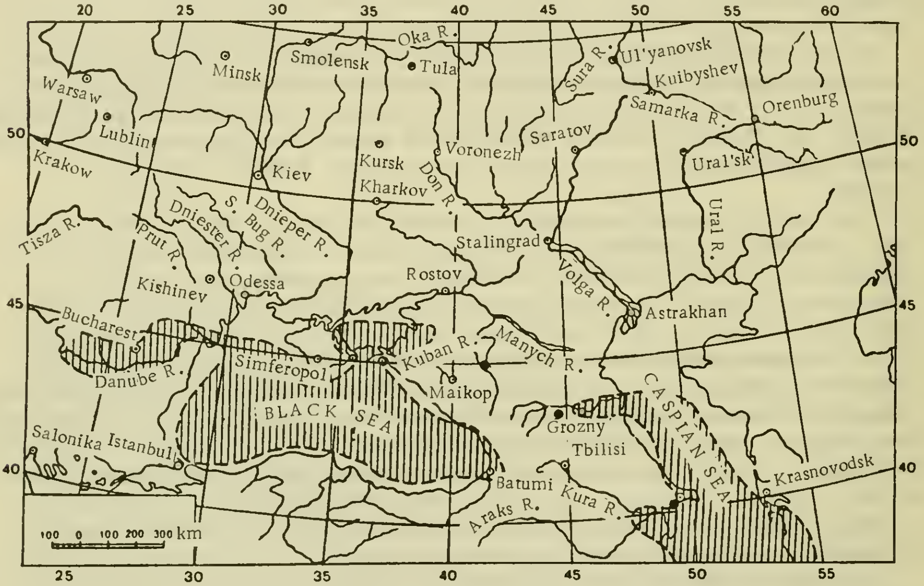


FIGURE 20. Cimmerian and Balakhany basins (from Kolesnikov; see Zhizhchenko and others, 1940)
Dots indicate main localities of land vertebrates

The land connection between the Caucasian Peninsula and the Russian platform was established for the first time in the Cimmerian; this allowed migration of plant and animal species in both directions.

At that time the fauna of the deserts of central Asia could have migrated far west to the eastern plains of the Caucasian Isthmus. During the Cimmerian, the configurations of the Black and Azov seas were similar to their Recent configurations.

Lower and Middle Pliocene terrestrial vertebrates of the Caucasus occur primarily in continental deposits.

Stavropol Plateau

The largest and most complete body of Pliocene material was found
10 km west of Stavropol in a locality of sandy sediments which were exposed
50 in the Kosyakin quarry. A bone-bearing lens, 7-9 m thick and 90 m
wide, was formed in a channel of a Pliocene river which cut through the
Sarmatian limestones at the edge of the Stavropol Plateau (Kaspiev, 1939;
Gnilovskoi and Egorov, 1955).

Seven beds can be distinguished in the old alluvium. The lithology of the beds varies from fine-grained, grayish white sand to gravels with clayey intercalations and clayey pebbles up to 1.5 cm in diameter (Figures 21, 22).

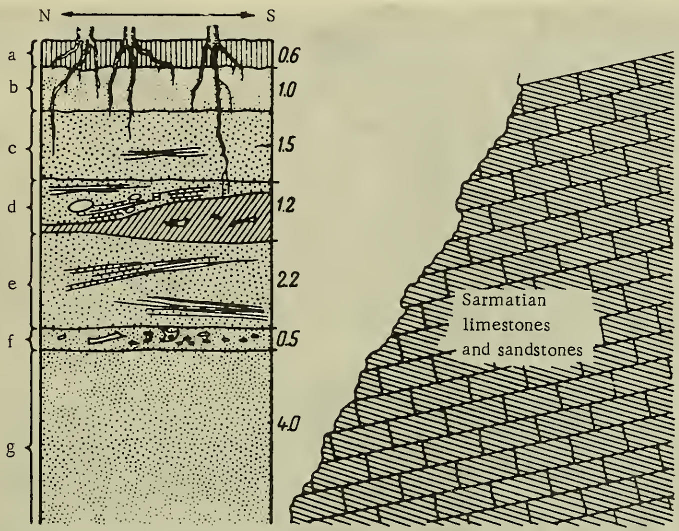


FIGURE 21. Stratigraphic section in the Kosyakin quarry

a, b — loams with humus; c-g — bone-bearing river sands, some of them crossbedded. Numbers on the right indicate thickness in meters

Our observations show that the pebbles in the lower part of the section are made of Sarmatian local rocks, rounded bones of Sarmatian marine mammals and, more often, Pliocene land mammals.

Bones of animals, fractured and redeposited many times, were retained in the gravelly sands which were deposited at [current] velocities of 1.3 m/sec (lower bed) and 0.1 m/sec (upper bed).

The bones were preserved in various stages of abrasion, from complete specimens to rounded pebbles.

Up to 92% of the bones collected in the quarry are free of organic matter and nearly free of permineralization. The bones resemble friable marl or chalk. The surface color of the bones is cream or grayish. All the cracks in the bones of this type are iron-stained. Manganese and iron dendrites occur rarely in the bones. Thin wavy grooves, the marks of

Recent plant roots, are common on the bones. Notches of irregular shape, formed by water erosion and aquatic invertebrates at the time of deposition, were observed on some bones.

The bones in this group are, for the most part, intact; fractures are mainly the result of careless collecting during quarrying. The remaining 8% of the bones are gray, and numerous dendrites give the surfaces a stained appearance. As a rule, these bones are more strongly permineralized and 51 considerably heavier than the "chalky" bones. The tooth enamel is always well preserved; its color is either natural or light pea green or light pink.

Tooth impressions of carnivores are rare: only nine bones show signs of gnawing on the epiphyses.

FIGURE 22. Kosyakin quarry

Photograph by author, 1952

The occasional vertebrae of Sarmatian whales and seals, derived from the Sarmatian limestones, are easily distinguishable from Pliocene bones by the heavy permineralization and grayish brown color.

Variations in the conditions of deposition and in the exposure times on river banks and spits during redeposition account for the differences in the state of preservation of the Pliocene bones.

It seems likely that the physical environment of the valley and stream of the Stavropol paleoriver was similar to the middle parts of the Don, the Volga and the Ural in Quaternary time. Bodies of dead animals accumulated in the oxbow lakes, as well as in the mainstream and backwater.

In the process of erosion of older marine sediments, the river carried the bone material over short distances and redeposited it.

The direction of the stream flow has not yet been established. Perhaps when the sea level was low and the Stavropol area slightly elevated, the river source was somewhere on the Russian Plain (e.g., near Yergeni) rather than on the Caucasus.

In spite of the different ages of the bones at the locality, most of the Pliocene species can undoubtedly be regarded as one faunal complex.

The fragmented material makes identification difficult, and most of the species have not yet been described in detail.

A preliminary list of the species is given in Table 3 (collections of PIN and ZIN: identification by Belyaeva (1940b, 1944), Borisyak and Belyaeva (1948), Argiropulo (1939b, 1940c), and Vereshchagin (1954)).

TABLE 3. Composition of the Pliocene fauna and number of bones from the Kosyakin quarry

	Number of bones		Number of bones
Insectivora		Proboscidea	
* Crocidura sp.	1	Anancus arvernensis Croiz. et Job.	21
* Talpa sp.	5	Dinotherium sp.	12
* Desmana sp.	1	Perissodactyla	
Carnivora		Hipparion sp.	3
* Ursus cf. arvernensis Croiz.	12	Hipparion gracile Kaup	18
Dinocyon cf. thenardi Jourdan	4	Tapirus cf. arvernensis Dev. et Bouill.	3
* Canidae gen.	3	Dicerorhinus orientalis Schlos.	72
Felis cf. issiodorensis Croiz. et Job.	1	Aceratherium cf. incisivum Kaup	8
Lagomorpha		Rhinocerotidae gen. (cf. Chilotherium)	1
* Lepus sp.	25	Rhinocerotidae gen.	33
* Ochotona cf. antiqua	2	Artiodactyla	
Rodentia		Propotamochoerus provincialis Gerv.	10
52 Amblycastor caucasicus Arg.	1	Procapreolus sp.	7
* Steneofiber sp.	3	Pliocervus sp.	9
* Cricetus sp.	37	Pseudalces sp.	2
* Mus sp.	1	Giraffidae gen. (cf. Sivatherium)	2
		Gazella sp.	5

Note. Asterisk indicates author's collection of 1952.

In addition to the land mammals given in Table 3, the material includes birds (Charadrius cf. morinellus L.), aquatic turtles (Trionychiidae — 14 carapace fragments), the lower jaw of a small lizard (Lacertilia), and bones of small anurans (frogs and toads) (Figures 23-25).

The faunal complex of the ancient Stavropol area was well developed. The Stavropol mastodons, tapirs, rhinoceroses and warthogs lived among
53 subtropical mesophilous plants. Groves of tugai vegetation near the rivers probably alternated with open meadows inhabited by moles, hamsters and pikas.

In the preceding sections we reached certain taphonomic conclusions and outlined a landscape scheme. These judgments are, to an extent, confirmed by the following phenomena: the predominance of fossils of animals associated with river valley thickets (rhinoceros, swine; Figures 26 and 27), the occurrence of beaver, tapir and aquatic turtle fossils in swamps, oxbow lakes and channels, and the iron stain which appears on these fossils. The presence of small desmans in the Pliocene river indicates the antiquity of the erosion valley and the stability of the hydrological regime of the rivers, which is similar in this respect to the regime of the Don and the Volga.

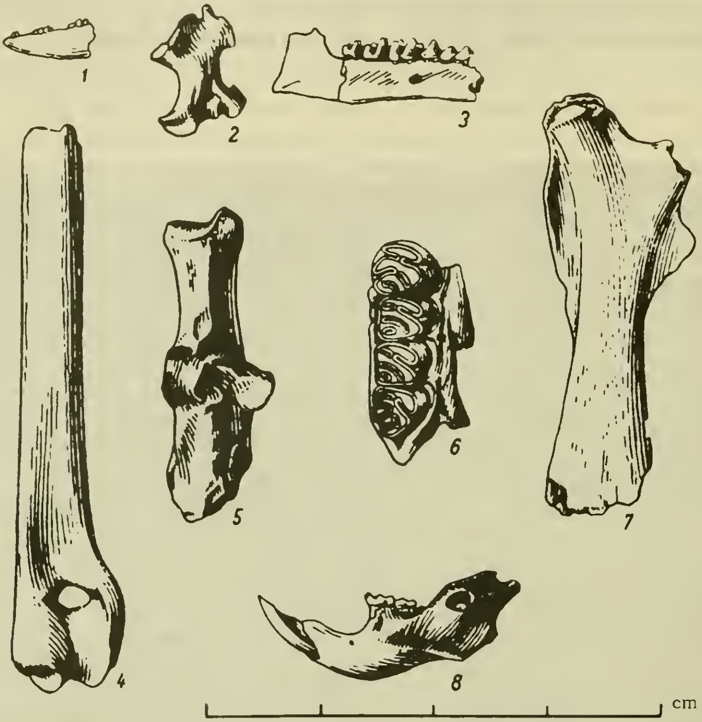


FIGURE 23. Bones of smaller vertebrates from the Kosyakin quarry

1 — jaw of lizard (Lacertidae); 2 — humerus of Talpa sp.; 3 — jaw of Desmana sp.; 4, 5 — humerus and calcaneus of Lepus sp.; 6, 7 — upper molars and femur of Steneofiber sp.; 8 — jaw of Cricetus sp.

The Stavropol complex is not of Upper Pliocene age; Borisyak (1943) has dated it Pontian. The Lower Pliocene age is indicated by the absence of elephants and horses proper. According to Argiropulo (1932, 1940c), the Caucasian Amblycastor is very close to the Upper Miocene species of this genus occurring in Mongolia and North America. The deer in the Stavropol faunal complex are of the Lower and Middle Pliocene types. The
56 Stavropol faunal complex can be tentatively dated as Lower Pliocene on the bases of accepted geological data and the composition of the complex.

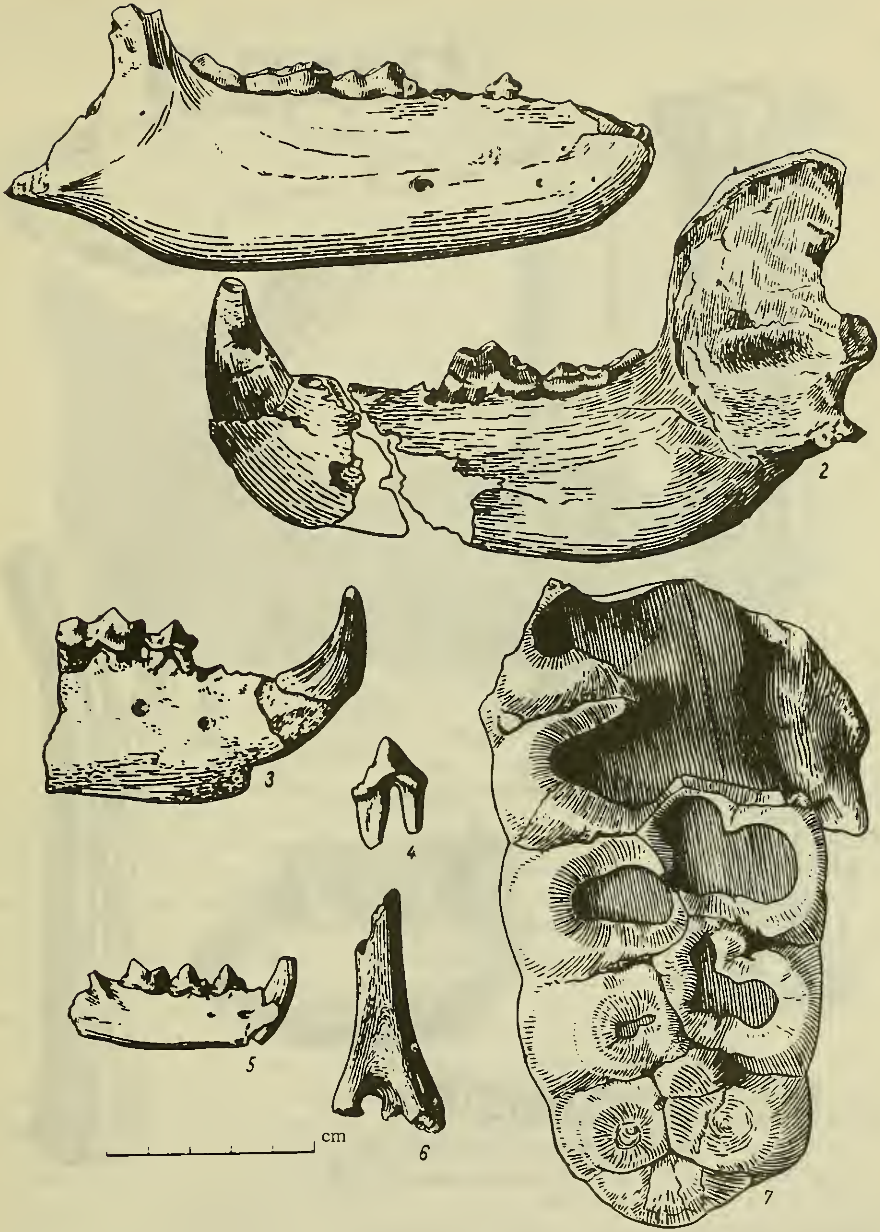


FIGURE 24. Remains of carnivores and proboscideans from the Kosyakin quarry

1, 3 — jaws of Ursus cf. arvernensis; 2 — jaw of Dinocyon cf. thenardi (×½); 4 — premolar of Canidae gen. (×2); 5, 6 — jaw and shoulder of Felis cf. issiodorensis; 7 — M_4 Anancus arvernensis

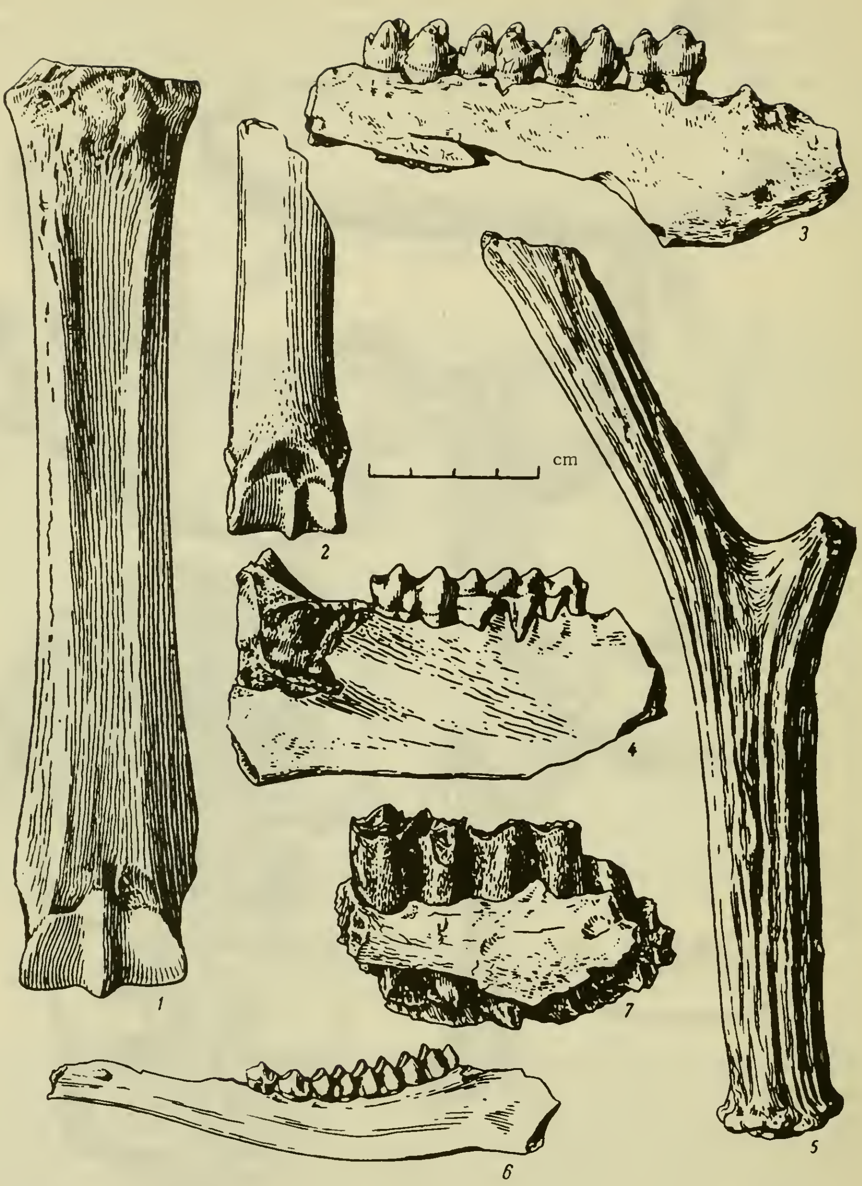


FIGURE 25. Remains of hoofed mammals from the Kosyakin quarry

1, 2 — metapodia of Hipparion gracile and Hipparion sp.; 3 — jaw of Tapirus cf. arvernensis; 4 — jaw of Propotamochoerus provincialis; 5, 6 — horn and jaw of Procapreolus sp.; 7 — jaw of Cervidae gen.

It is younger than either the Taraklian complex of Moldavia (Khomenko, 1914b) or the Pavlodar complex on the Irtysh River and is quite close in age to the Mălușteni complex in Rumania (Simionescu, 1930).

Some geologists correlate the continental clastics, in the foothills of the Ciscaucasus, 700-800 m thick, with the Cimmerian marine sediments. The continental clastics in Kabarda and North Ossetia have been described by Shvetsov (1928), as follows: the continental sequence resembles a moraine and consists of loams, sands and tuff breccias with large boulders of erupted material in some places. The continental beds form a scarp on the northern slopes of the Chernye-Gory Mountains; in the Zmeika ridge the continental beds overlie the Sarmatian clays. The beds were probably formed by mudflows carrying great volumes of poorly sorted material from the
57 mountain slopes. The fossils in the continental beds are land and freshwater mollusks (Helix sp., Paludina sp., Neritina sp.), grasses and leaves, and bones of land vertebrates. M. V. Pavlova has identified an antler (Cervus (?)) and a "rat jaw" in Shvetsov's collection.

FIGURE 26. Jaw of Dicerorhinus orientalis from the Kosyakin quarry

Sands and clays, 1,000-1,400 m thick, accumulated in eastern Transcaucasia in Cimmerian time; those on the Apsheron Peninsula comprise a large oil reservoir, known as the Balakhany productive beds.

There are various opinions on the history of the productive beds. Kolesnikov, in a review of the theories of their origin (Zhizhchenko, Kolesnikov and Eberzin, 1940), concludes that the beds were formed in a "developing tectonic basin," which is to say that they were formed from the clastic products of the erosion of the eastern Caucasian Mountains which accumulated in subsiding shallow-water basins. Land vertebrates are very rare in the productive beds.

In 1932 V. Podgornova discovered fossil mammals in light-colored, fine-grained sandstones in the productive beds to the east of the Lok-Batan volcano south of Baku. According to Bogachev's (1938b, 1941) and our identifications, the following species occur at the locality:

Carnivora

Vulpes khomenkoi Bog.

Artiodactyla

Cervus (cf. Eucladocerus) sp.
Gazella sp.

The sheatfish (Siluris glanis L.) has also been recorded at the locality.

Two complete sets of upper molars and jaw fragments of fox have been found embedded in the light gray, fine-grained sandstone. The bones were considerably permineralized; the replacing substance is straw-colored or pink in fresh fracture. The tooth enamel is black and glossy. The material includes a fragment of gazelle skull with complete sets of upper molars and two complete metacarpals of deer. There is no basis for identifying, as Bogachev did, the Middle Pliocene deer from Lok-Batan with the Quaternary red deer and goitered gazelle. The bones at the locality were probably deposited in the delta of one of the rivers draining the eastern slopes of the Caucasus, a river similar to the present-day Sumgait and Pirsagat rivers.

The layers adjoining the sandstones of the productive beds contain freshwater mollusks (Golubyatnikov, 1925): Planorbis cornu var. manteli Dunk., P. costatus Klein, Limnaea armanensis Noul. and other limnaeids, Unio jasamalicus D. Golub. and Melania glacilicosta Sandb. The alga, Chara sp., also occurs in these beds. It is doubtful that such a collection of species could exist under desert conditions in rivers and lakes of variable salinity. The leguminous plant, Albizzioxylon hyrcanum, which is characteristic of subtropical conditions, is known from the Balakhany beds of the Shiraki Steppe [Leninakan Steppe], west of the Apsheron locality.

58 The fossils occurring in the Balakhany beds indicate that the differentiation of faunal complexes followed the differentiation of the landscapes in the Caucasus from subtropical forests to hot dry semideserts.

(56)

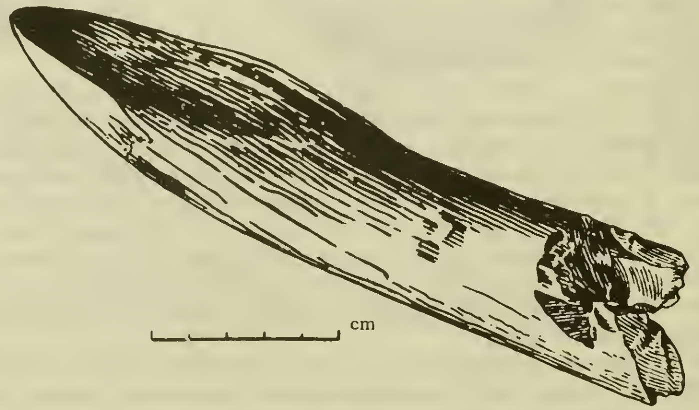


FIGURE 27. Canine (?) of Rhinocerotidae gen. from the Kosyakin quarry

The Middle Pliocene mammals of the southwestern part of the Russian Plain evolved from eastern Mediterranean Miocene faunas. The Middle Pliocene assemblages of mammals in Moldavia and in the Ukraine are particularly important to an understanding of the evolution of the Ciscaucasian fauna. The Moldavian assemblage occurs in gravelly-sandy fanglomerates in the basins of the Salcia, Kagul and Prut rivers; the Ukrainian assemblage is known from limestone catacombs, filled with red clay, in Odessa.

The Middle Pliocene "fauna" of Moldavia consists of ape, rodent, carnivore, rhinoceros, Hipparion, hippopotamus, camel, deer and antelope. Lagomorph and rodent are represented by the Recent genera of hares, pikas, squirrels, beavers, porcupines and mole rats (Khomenko, 1914a, 1915; Borisyak, 1943).

(59)

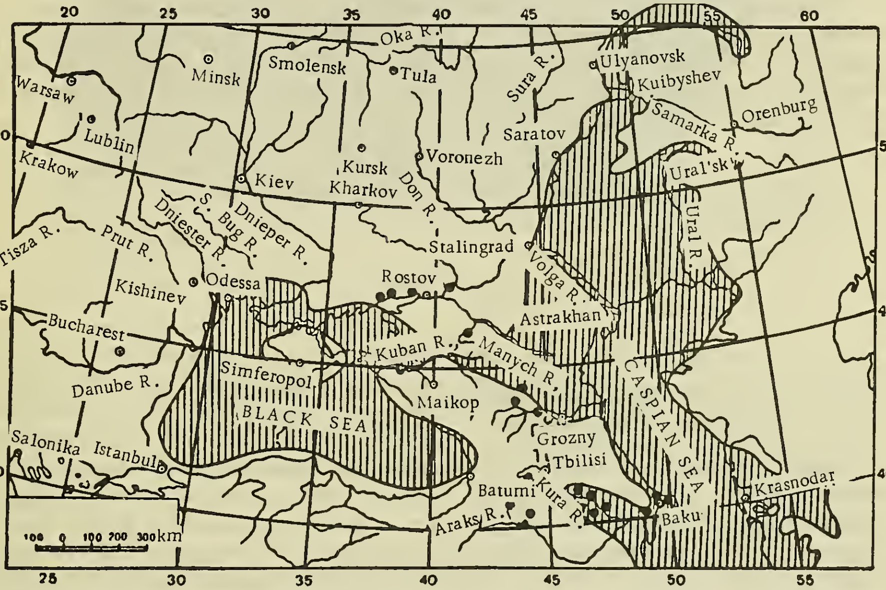


FIGURE 28. Kuyal'nitsk and Akchagyl basins (from Kolesnikov; see Zhizhchenko and others, 1940) Dots indicate main localities

The "fauna" of the catacombs in Odessa consists of nearly 30 species of insectivore, rodent, carnivore, proboscidean, artiodactyl and an ostrich (Gritsai, 1938, 1939; Borisyak, 1943; Pidoplichko, 1954).

The faunal complexes of the areas north of the Black Sea reflect the variability of the landforms: wooded creek and river valleys alternating with steppes. Some of these complexes might have extended southeastward to Ciscaucasia.

Both the Moldavia (Roussillonian) and the Odessa Middle Pliocene "faunas" contain a number of subtropical forms.

The occurrences of ape and hippopotamus in the Roussillonian of the eastern Mediterranean area are evidence of the warming of the climate in post-Pontian time. The climate of the north edge of the Cimmerian basin at the end of the Middle Pliocene was probably similar to the Recent climate of southern Italy, Spain and France, while in Ciscaucasia the climate was probably of a more continental type.

During the Upper Pliocene, the configuration of the Caucasian Isthmus was similar to its present form, but it was intermittently cut off in the north by narrow straits in the Manych region, which temporarily severed the land connection between the Caspian Sea and the Black Sea basins.

In the Black Sea region most of the Upper Pliocene localities are situated along the sea coast. Fossils can probably be found in the zone of contact between deltaic deposits and gravelly fanglomerates of the paleo-Don, paleo-Donets, paleo-Dnieper and other ancient streams of the Kuyal'nitsk and post-Kuyal'nitsk basin (Figure 28).

59 A number of authors in the last and present centuries (Fischer von Waldheim (1809), Eichwald (1850), Nordman (1858-60), Pavlova (1895), Bogachev (1923-24, 1938d), Sherstyukov (1926, 1927) and Grigor (1929)), have noted the following mammals from the Upper Pliocene of the Azov Sea and Kuban River regions:

Carnivora

Hyaena sp.
Meles sp.

Rodentia

Trogontherium cuvieri Fisch.

Proboscidea

Mastodon arvernensis Croiz. et Job.
Elephas lyrodon Weithofer
E. meridionalis Nesti
E. antiquus Falc.

Perissodactyla

Equus stenonis Cocchi

Artiodactyla

Camelus sp.
Cervus sp.
Bos sp.

Upper Pliocene mammals in the Azov Sea region were collected by Gromov (1933, 1936) in 1933-1936 in the gravelly sands near the villages of Morskaya, Merzhanovka and Khapry, and in the Volovaya gulley near Taganrog. Similar fossils were collected by the author from the Leventsovka quarries near Rostov in 1954. Fragmentary iron-stained and well-rounded bones from the Khapry sand indicate that the bones were buried in alluvial fans and in sediments exposed to marine abrasion. Some of the bones are marked by bore holes made by marine invertebrates, showing that they had been deposited in the sea (Figure 29).

60 According to the identifications of Gromov (1948), Borisyak and Belyaeva (1948), and the author, the following species occur in the Azov Sea region:

Carnivora

Canis cf. lupus L.
Canis sp.
Ursus sp.
Hyaena sp.
Machairodus sp.

Rodentia

Trogontherium cuvieri Fisch.

Proboscidea

Mastodon sp.
Elephas planifrons (?) Falc.
E. meridionalis Nesti

Perissodactyla

Hipparion sp.
Equus stenonis Nesti (cf. major Boule)
Rhinoceros sp.
Elasmotherium sp.

Artiodactyla

Sus sp.
Camelus (Paracamelus) cf. kujalnikensis Chom.
Eucladocerus pliotarandoides Alles.
Cervus cf. elaphus L.
Cervus sp.

Fragments of ostrich long bones have also been collected in the region (Struthio sp.).

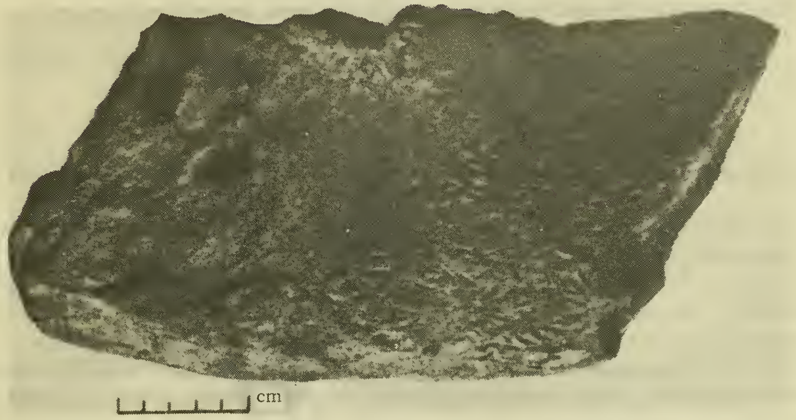


FIGURE 29. Jaw of Elephas meridionalis with borings caused by invertebrates From the Khapry sands on the right bank of the Don River (Orig.)

Although the species listed are of different ages, as pointed out by Bogachev (1923-1924), they may, nevertheless, be assumed to represent one faunal complex. Since the same species also occur farther west, the complex may be considered characteristic of the Upper Pliocene of the southern part of the Russian Plain.

Trans-Kuban Plain

The burials in the gravels of the Trans-Kuban Plain along the Psekups River are in the main similar to the northern Azov Sea localities. The material was collected in 1930-1932 by Gromov (1935b, 1937, 1948) near the villages of Bakinskaya and Saratovskaya on the left bank of the Psekups River. Two floodplain terraces can be distinguished on the bank: the lower terrace of Würm age and the upper terrace of Riss age.

Gromov (1948) has demonstrated the presence of freshwater basins in
61 the foothills of western Caucasia in geological sections which show a variation from fast-flowing stream deposits to swamp deposits.

According to Gromov (1948, p. 56) the following species occur in the lower and middle parts of the sedimentary sequence:

Proboscidea

Elephas meridionalis Nesti — teeth and limb bones

Perissodactyla

Rhinoceros etruscus Falc.	— nearly complete skull and skeletal components
Equus stenonis Cocchi	— metapodia, phalanges
Equus sp. (aff. stenonis)	— limb bones

Artiodactyla

Bison sp.	— broken skull
Bos sp. (Leptobos)	— broken skull
Eucladocerus pliotarandoides Aless.	— skull with a horn and horn fragments
Cervus sp. (Rusa)	— fragments of horns
Cervus sp. (ex. gr. polycladus?)	— fragments of limb bones of a very large deer
Cervus sp.	(larger than elk!)

The material also included the lower part of an ostrich tibia (Strutio sp.).

The above-mentioned material from the Psekups was lost during the war before it could be described.

The material preserved in PIN includes an antler of a deer (Eucladocerus, Figure 30) and a skull of the Etruscan rhinoceros. The material is straw-colored and strongly impregnated with iron.

From the presence in the Trans-Kuban Plain of intact skulls and horns, it can be inferred that during the Upper Pliocene quiet rivers flowed over this area into large bodies of still water. Such landforms could exist only at the stage of more advanced peneplanation of western Caucasia.

East of the Psekups there have been individual occurrences of large Upper Pliocene mammals in the gravel beds deposited in piedmont basins, such as the bones and teeth of elephant (Elephas cf. planifrons Falc. and E. meridionalis Nesti) observed along the Laba and Kuban rivers, in the region of Tshchikskie plavni* (Navozova, 1951), near the villages of Novo-Labinskaya, Nekrasovskaya, and Grigoropolisskaya (Gromov, 1937), and south of Armavir. The occurrences of southern elephant, rhinoceros (Rhinoceros cf. etruscus Jaeg.) and deer (Eucladocerus pliotarandoides Aless.) are more frequent in the ferruginous sand near the village of Voskresenskaya, west of Stavropol, and in the lower part of the river sands in the Girei quarry near the Kropotkin station (Figure 31).

At the time when this faunal complex lived in Ciscaucasia the climate was mild-temperate; broadleaf forests of the Colchis and Hyrcania type covered considerable areas of western Ciscaucasia. Bos, horse and ostrich fossils evidence a progressive development of savannah-type grasslands. The animals inhabiting the piedmont plains were probably often killed by torrential streams and buried in masses of deposited gravel.

In other cases, accumulation of bones in the gravels was caused by the erosion of bone-bearing lenses by later streams. Therefore, the Psekups
62 and the Taman faunal complexes (see below) probably antedated the
formation of the bone-bearing gravels in the Ciscaucasian plains.

Most of the fossiliferous strata in the Psekups, Laba and Kuban areas are usually correlated with the Akchagyl and sometimes with the Apsheron stage of marine sedimentation in the Caspian region.

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* [Periodically flooded areas with Phragmites, Typha and Carex in river deltas and bottomlands in the southern part of the U.S.S.R.]

FIGURE 30. Horn of Eucladocerus pliotarandoides from the gravels on the Psekups

Taman Peninsula

The bone-bearing formations of the Taman Peninsula are slightly younger than the lower beds in the Psekups area. The fossiliferous localities on the Taman Peninsula are the Sinyaya and Kapustina gulleys and Sennaya, Fontalovskaya and Kuchugury (Figure 32). The bone-bearing breccia at Sinyaya gulley was discovered by Gubkin (1914) in 1912. He identified the freshwater sands exposed on the northern coast of the peninsula as of Basal Pleistocene. The sands contain numerous freshwater mollusks of the genera Vivipara, Bythinia, Dreissensia, Unio, and other forms (Figure 33). Broken, sometimes rounded, bones were found to be heavily permineralized, particularly at the Sennaya and Fontalovskaya localities. Permineralized excreta of hyenas, swine and ruminants also occur in the sandy-gravelly beds at Sennaya. The material from the localities mentioned is housed in the ZIN and PIN collections, and has been identified by Borisyak (1914), Belyaeva (1925, 1933a, b), Vereshchagin (1951a, 1957a) and Burchak-Abramovich (1952a). The species identified are given in Table 4 and Figure 34.

A vertebra of a large fish was taken from the ferruginous sand near Sennaya. A seal phalange, resembling those of the Caspian seal (Phoca caspica Gmel.) (Kirpichnikov, 1953) is probably not from the same beds from which land vertebrates were taken at Sinyaya gulley.

A taphonomical and ecological analysis of the species studied suggests that they are part of one faunal complex. The fauna lived on the land which formed between Ciscaucasia and the Danube River during one of the regressions in the post-Kuyal'nitsk (Apsheron) basin.

The presence of horse and bison (species adapted to steppe life), of rhinoceros, forest antelope, deer and elephant (species adapted to forest life), and of
63 beaver (a species adapted to lake and river life) indicates that western Ciscaucasia was a plain with dense vegetation along the rivers. The climate was probably moderately warm. From the morphogenetic point of view, this faunal complex is very close to the Villafranchian complex of Western Europe and the Nehavend complex of southwestern Asia. However, a number of Taman species are indistinguishable from the species of the Khapry complex (beaver Trogontherium, southern elephant, camel) (Vereshchagin,
64 1957a). Similar species also occur in the Apsheron beds of eastern Ciscaucasia and Transcaucasia.

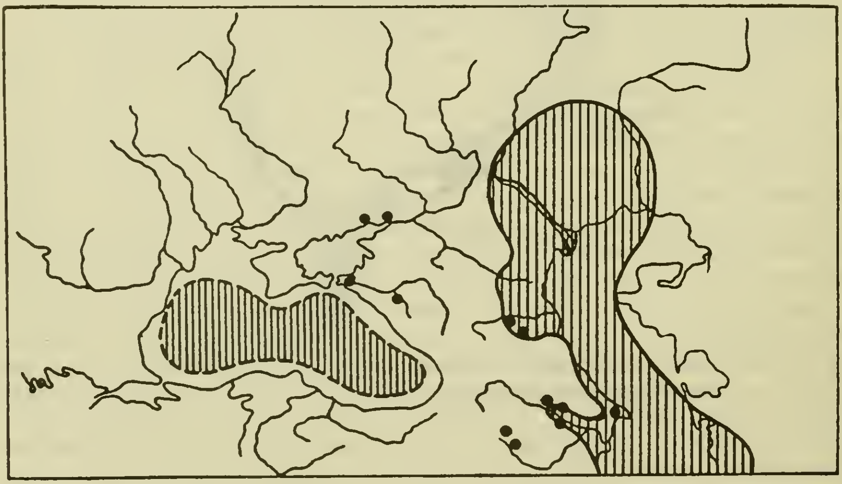

FIGURE 31. Chauda and Apsheron basins (from Kolesnikov; see Zhizhchenko and others, 1940) Dots indicate main localities

The evolution of Upper Pliocene fauna complexes in the Caspian region was studied at localities situated along the margins of the Akchagyl and Apsheron basins of the Caspian depression.

In Akchagyl time the axis of subsidence in the northern Caspian became oriented in a north-south direction, as opposed to its earlier east-west

(63) TABLE 4. Upper Pliocene mammals and number of bones from five localities on the Taman Peninsula

	Number of bones
Carnivora	
Canis tamanensis N. Ver.	2
Panthera sp.	1
Rodentia	
Castor tamanensis N. Ver.	2
Trogontherium cuvieri Fisch.	5
Proboscidea	
Elephas meridionalis Nesti*	803
E. trogontherii Pohl.	
E. antiquus Falc.	
Perissodactyla	
Elasmotherium caucasicum Boris.	66
Rhinoceros cf. etruscus Falc.	5
Equus aff. süssenbornensis Wüst.	54
Artiodactyla	
Sus tamanensis N. Ver.	2
Camelus cf. kujalnikensis Chom.	1
Eucladocerus sp.	22
Megaceros cf. euryceros Aldr.	1
Tamanalces caucasicus N. Ver.	3
Cervidae gen.	41
Gazella sp.	2
Tragelaphus sp.	2
Strepsicerotini gen. (cf. Taurotragus)	18
Bison cf. schoetensacki Freud.	12
Bison sp.	2

* According to Garutt (1958) this is Phanagoroloxodon mammontoides.

FIGURE 32. Cliffs and landslides on the northern coast of the Taman Peninsula, near Cape Litvinov

Photograph by author, 1954

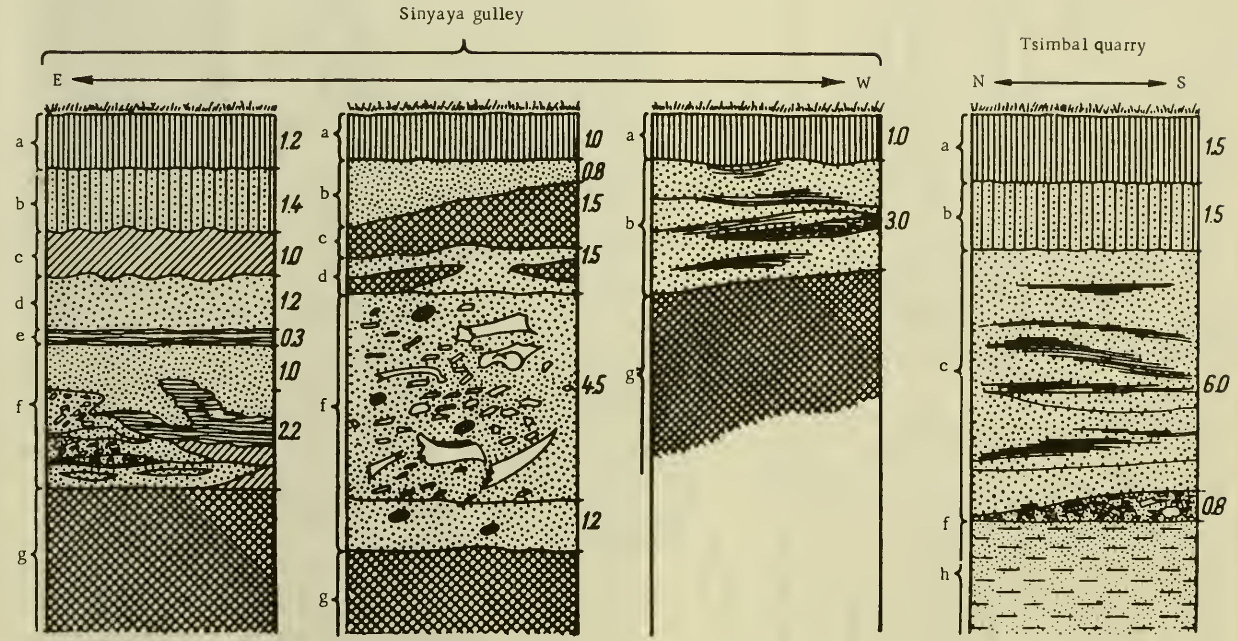

FIGURE 33. Stratigraphic sections at the Sinyaya gulley and Tsimbal quarry

a — loams with humus; b, c—sands, clays and bone-bearing conglomerates; g — brown clays; h — marine sands. Numbers to the right of sections indicate thickness in meters orientation. Akchagyl marine sediments can be traced from eastern Transcaucasia and the foothills of the Kopet-Dag in the southeast to Kazan and Ufa in the north (Arkhangel'skii, 1934; Kovalevskii, 1933; Kolesnikov, (Zhizhchenko, Kolesnikov and Eberzin, 1940)). In Akchagyl time, the rivers draining the Caucasus Range entered the narrow Kura bay which extended almost to Tiflis, and the wide Terek bay which extended to Mozdok. The rivers transported the bodies of dead animals to the plains and to the coastal bays.

During the transgressive maximum, the Apsheron and the Kuyal'nitsk basins were connected by a narrow strait south of the Stavropol Plateau (Gatuev, 1932).

This growth of the relict marine basin at the time of deposition of the productive beds has been explained by Kovalevskii (1933) as the result of marine transgression into the Caspian region. However, his hypothesis 65 on connections with the boreal sea is not supported by recent data on molluscan faunas which occur in the northern part of the basin.

Gradual climatic changes probably persisted throughout Akchagyl time. However, the glaciation of the Greater Caucasus, assumed by Kovalevskii 66 (1936), had not yet begun. A reoccurrence of volcanic activity in the Akchagyl is indicated by thin layers of ash and pumice which appear in the massive loams and gravels of the foothills region. The Akchagyl basin, which covered a great area of the Russian Plain, was a natural barrier on the migration routes between central Asia and Ciscaucasia (Figure 28).

The Akchagyl land flora is known from the shores of the Kura bay, near Naftalan, from Kakhetia and from the Shiraki Steppe. The following species have been identified by Palibin (1936): oriential beech (*Fagus orientalis*), oak (*Quercus* sp.), willow (*Salix alba*), common pomegranate (*Punica granatum*), elm (*Zelkova* [= *Carpinifolia*] *crenata*), lime (*Tilia platyphyllus*), alder (*Alnus glutinosa*), mulberry tree (*Morus andrussovi*), Pitsunda pine (*Pinus pithyusa*), sequoia (*Sequoia langsdorfii*) and many other species.

The list of species given above suggests that the environment of the flora on the shores of the Kura bay was very similar to Recent environments in the foothills of eastern Transcaucasia.

Palibin (1936) and Grossgeim (1936, 1948) believed that there were no tropical plants in the Caucasus in Akchagyl time. The last of the evergreen sequoias and cherry laurels in the Shiraki area probably grew in a humid climate with moderately cold winters.

The earliest occurrence of *Elephas planifrons* and *Equus stenonis* in the Caucasus is in Akchagyl beds, although land vertebrate fossils seldom appear in these beds and the material mainly consists of teeth of mastodon, elephant and horse.

In Ciscaucasia, teeth of *Mastodon arvernensis* Croiz. et Job. and *Elephas planifrons* Falc. were collected on the Malgobek ridge, 40 km south of Mozdok. Teeth and bones of *Elephas planifrons* (?) were also found in the Solenyi gulley near Grozny (Pavlova, 1931).

In eastern Transcaucasia, the Akchagyl conglomerates between the Alazan and Kura rivers (Kudryavtsev, 1932) contain bones of large vertebrates, freshwater mollusks (*Helix* sp., *Planorbis*, *Cyclostoma*) and species of plants known in the Recent. An antler of *Cervus* sp. is known from the Akchagyl of western Azerbaidzhan.

The coarse breccia of the Bedeni ridge in the Tsalka District of Georgia contains fragmented bones of mammals among which teeth of *Elephas* aff.

(67)

FIGURE 34. Fossils of the Taman complex

1 — jaw of Canis tamanensis; 2 — ulna of Panthera sp.; 3 — skull of Castor tamanensis; 4 — upper jaw of Trogontherium cuvieri; 5 — upper jaw and teeth of Elephas meridionalis; 6, 7 — Pm_3 and metacarpus of Equus aff. süssenbornensis; 8 — jaw of Sus tamanensis; 9 — horn of Eucladocerus sp.; 10 — horn peduncle of Tamanalces sp.; 11 — horn axis of Bison sp.

planifrons Falc. and Equus stenonis Cocchi have been identified. The breccia is underlain by a layer of doleritic lava and is covered by lacustrine sands and clays. The lake sediments are overlain by a layer of dolorite (Zaridze and Tatrishvili, 1948). Thus, in that area, the mammals lived and died during a period when the volcanos in the Lesser Caucasus were dormant.

68

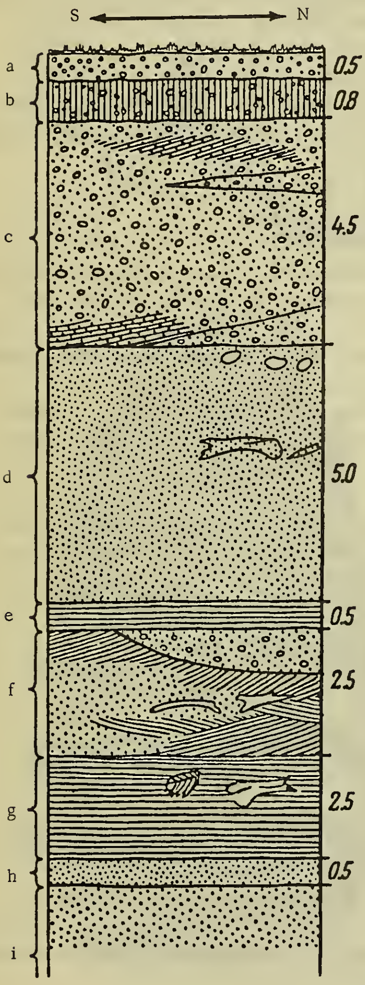

FIGURE 35. Stratigraphic section of bone-bearing sands near Georgievsk

a-c — gravels with obsidian fragments on the high terrace; d-i — light-colored and ferruginous sands with rounded fragments of volcanic ash, bones of elephants and hoofed mammals. Numbers on the right indicate thickness in meters

The next transgression in the Caspian Basin, a somewhat smaller one, is known as the Apsheron sea.

The Kura bay of the Apsheron sea reached the longitude of Kirovabad. The Terek bay was temporarily connected with the Euxinic basin by a strait in the Manych area. The sea reached the latitude of Sarepta and [Lake] Inder in the north.

The climate and landforms of the Caucasus in Apsheron time probably remained the same as in the Akchagyl, and the volcanic activity was of about the same intensity. Torrential mudflows, caused by heavy rains, carried volumes of gravel and boulders from the mountains (Kudryavtsev, 1933); these boulders can now be seen on the Kakhetia Plain.

The land vegetation known from the Apsheron deposits in the Shiraki Steppe consisted of spruce (Picea orientalis) and a number of Recent forms: beech, oak, aspen, apple, willow, filbert, Turkish filbert, walnut (Juglans regia), zelkova, honeysuckle; and Hyrcanian forms: oak (Quercus castaneifolia), alder (Alnus subcordata), maple (Acer ibericum) (Palibin, 1936). Cooling of the climate in Apsheron time resulted in the disappearance of the subtropical evergreens.

The wooded landscape of the shores of the Kura bay was probably similar to those parts of the present-day landscapes of Colchis and Asterabad which are still in a completely natural state.

During the regressions of the Akchagyl and Apsheron seas, arid conditions undoubtedly prevailed in the eastern part of the Caucasian landmass. The development of coastal steppes and semideserts created the environment for dispersal of steppe and desert mammals.

Fossil mammals are more abundant in the Apsheron than in the Akchagyl sediments. The material consists mostly of single limb bones and teeth of proboscideans and perissodactyls. These burials occur primarily in littoral marine deposits formed in quiet bays at various basin levels. Some occurrences are known from continental deposits: from the zone of accumulation at the piedmont "barrier" at a mountain base, and from the travertines in the Pyatigor'e area.

In eastern Ciscaucasia, "traces" of a faunal complex, similar to those of the Psekups and Taman, occur in the travertines and loams of Mount Mashuk, and in the coastal loams of the Apsheron basin. Bones of elephant and hoofed mammals from the travertines are brittle and some contain cavities formed by dissolution, and filled with calcite crystals. From the oldest, Upper Pliocene "travertine complex" in Mount Mashuk, the following forms have been described: *Elephas meridionalis* Nesti, 69 E. cf. *antiquus* Falc., E. aff. *trogontherii* Wüst, Bovinae, Cervinae (Egorov, 1932; Ivanova 1948; Gromov, 1948).

We collected teeth of *Mastodon arvernensis* Croiz. et Job., southern elephant (*Elephas meridionalis* Nesti), horse (*Equus* cf. *stenonis*) and bones of deer (*Eucladocerus* sp.) (Figure 36) from alluvial gray sands below a layer of redeposited basalt fragments and volcanic ash (Figure 35), near the Cossack village of Vinogradnaya and near Georgievsk.

Bones of *Elephas meridionalis* and *Equus* sp. have been found in the Apsheron loams on the slope of Mount Tash-Kala near Grozny (Pavlova, 1931). Two teeth of *Equus stenonis* Cocchi and an antler of a large antelope (*Bubalis* sp.) found near Verkhni Achaluki on the Sunzha ridge are probably also of Apsheron age (Burchak-Abramovich, 1952a).

The following forms from the locality near the village of Vinodel'noe, northeast of Stavropol, are identified by Borisyak and Belyaeva (1948) in the PIN collections:

Proboscidea

Elephas meridionalis Nesti

Perissodactyla

Equus (*stenonis*?) sp.

Artiodactyla

Paracamelus gigas Schloss.

A camel mandible from this locality has been described by Khaveson (1954b, Figure 37).

Teeth of southern elephant from the piedmont gravels near Makhachkala have been recorded occasionally.

Apsheron Peninsula

Fossil marine and land mammals are very abundant in the limestones of the Apsheron stage on the Apsheron Peninsula near Binagady, Shikhovo and Baku.

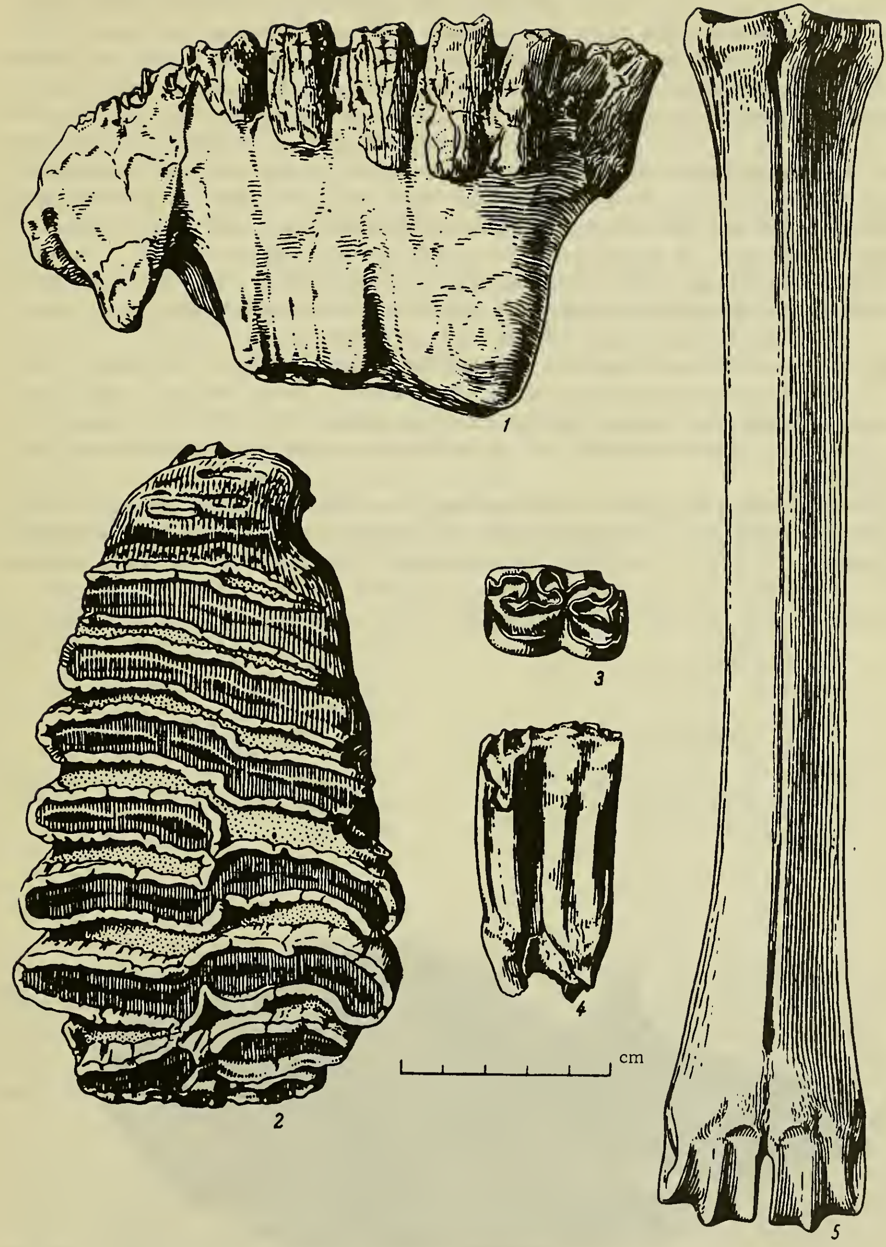

FIGURE 36. Fossils from the river sands in the Georgievsk quarry

1, 2 — M^5 of Elephas meridionalis and worn surface of tooth; 3, 4 — worn surface and inner surface of Pm_3 of Equus stenonis; 5 — metacarpus of Eucladocerus sp.

According to Bogachev (1923, 1938a, 1940d), the fauna includes porpoise (Delphinus delphis L.), an unusual predacious marine pinniped similar to otter and seal (Necromites nestoris Bog.) and perissodactyls (Hipparion crassum Gerv., Hipparion sp.). The humerus of a seal, indistinguishable from that of Phoca caspica Gmel., has been found under a 22-m-thick bed of Apsheron limestone near Baladzhar. The presence of Black Sea porpoise (Delphinus delphis L.) in the Caspian region can be accounted for (Bogachev, 1939a) by migration from the Mediterranean in Akchagyl time, i.e., at the time of migration of the mollusks, Mactra, Cardium and Potamides. According to Bogachev, the dolphin became extinct in the Caspian at the end of the Apsheron because of advancing glaciation.

The same can be said of the incompletely studied Necromites which, according to Bogachev (1940d), is similar to Semantor macrurus Orl. from the Pliocene deposits of eastern Siberia.

Farther west, fossils occur in the clayey ridges of Kabristan and in the two or three parallel ridges of hills which extend from the Iora and 71 Kartalinia plateaus to the Gerdyman-Chai canyon in the east. The hills are made of clays and loams with gravelly intercalations totalling 400 m in thickness.

The material collected by geologists in the Kondzhashen, Palan-Tikyan, Karadzha, Boz-Dag, Chuzgun-Tapa and other ridges has been identified by Bogachev (1938c), Burchak-Abramovich (1951a, 1952c), and the author.

Rodentia

Trogontherium cuvieri Fisch.
Muridae gen.

Proboscidea

Anancus arvernensis Croiz. et Job.
Elephas meridionalis Nesti

Perissodactyla

Equus sp.
Rhinoceros cf. etruscus Falc.
Rhinoceros sp.

Artiodactyla

Cervus sp.
Eucladocerus sp.
Bison sp.

FIGURE 37. Jaw of Paracamelus gigas from Vinodel'noe

It is possible that the upper jaw of Stegodon sp. in the collections of the Natural History Museum in Baku came from some Upper Pliocene deposits in eastern Transcaucasia (Bogachev, 1935).

The most abundant Upper Pliocene species from the Apsheron beds of Transcaucasia are, as a whole, very similar to the post-Kuyal'nitsk fauna of eastern Ciscaucasia. The mastodons occurring in the Apsheron beds were either the last survivors of the eastern Mediterranean group, or they were redeposited from older beds.

Upper Pliocene index mammals have been identified from near Leninakan and Erzurum in the Armenian-Anatolian highlands of southern Transcaucasia. The fossils probably occur in the gravelly-pebbly sands deposited by streams in small, inland, freshwater lakes.

As early as 1899, Abich mentioned an accumulation of fossil bones in Upper Tertiary calcareous marls and conglomerates underlying the layer of tuff and lava on the slopes of a fortified hill near Leninakan. Academician I. F. Brandt has identified "Mastodontidae, Cervidae and Bovidae" in that material.

74 Bogachev (1923-1924) mentioned the finds of Elephas armeniacus Falc. in gray volcanic sands near Leninakan. The species is probably identical with E. meridionalis Nesti.

In later collections from that area Burchak-Abramovich identified bones of Elephas sp., Rhinoceros mercki Jaeger, and Equus stenonis Cocchi (Avakyan, 1948).

The following list (which requires revision) is given by Bogachev (1938c) for species occurring in the Upper Pliocene diatomite near the village of Nurnus on the Zanga River:

Carnivora

Mustela filholi Gaudry
Putorius sp.

Lagomorpha

Lepus sp.

Rodentia

Gerbillus sp.

Perissodactyla

Hipparion sp.
Rhinoceros etruscus Falc.

Artiodactyla

Tragocerus sp.

The diatomite, 7 m thick, occurs between andesitic lavas below and basalt above (Gambaryan, 1934), indicating that a freshwater basin existed in the middle Zanga region in a period between two strong volcanic eruptions. Intercalations of pumice and ash in the diatomite bed show that the volcanic activity also continued during the deposition of the bed.

Occurrence of gerbil bones indicates that xerophilous vegetation thrived along the southern margins of the Armenian Highland in Upper Pliocene time. The stratigraphy of the fossil localities and the species composition of the Upper Pleistocene Transcaucasian fauna indicate that in Apsheron time the climate was temperate, and the volcanos were very active. These data also reflect to a certain degree semi-arid to arid conditions in the southern and eastern parts of the country.

Pleistocene elements are traceable in the Upper Pliocene faunal complex of the Caucasus, particularly in the Taman Peninsula.

(72)

TABLE 5. Stratigraphic distribution of the main localities of Tertiary mammals in the Caucasus

Epoch	Division	Stage	Localities: Black Sea Area and Ciscaucasia
Pliocene	Upper	Chauda beds	Taman Peninsula: Sinyaya gulley, Sennaya, Kuchugury
		Gurie beds	Stavropol area: Voskresenskaya, Trans-Kuban Plain: Psekups, Bakinskaya
		Kuyal'nitsk	Taman Peninsula: Kapustina gulley
	Middle	Cimmerian	Zmeika ridge: Darg-Kokh
	Lower	Pontian	Stavropol Plateau: Kosyakin quarry
Miocene	Upper	Meotian	North Azov coast: Novocherkassk, Tuzlovka
		Sarmatian	Stavropol area: Burlatskoe, Blagodarnoe, Petrovskoe
	Middle	Konka Karagan Chokrak Kuchugury Helvetian	Stavropol area: Belomechetskaya
	Lower		
Oligocene			

(73)

Stage	Localities: Caspian Area and Transcaucasia	Predominant Groups of Species
Apsheron	Terek Range: Malgobek, Grozny, Achaluki Apsheron Peninsula: Binagady, Khurdalan, Shikhovo Armenian Highland: Leninakan, Nurnus	Taman wolf, southern elephant, Trogontherium, Equus stenonis, Cervus pliotarandoides, Taman bison
Akchagyl	Iora Plateau: El'dar, Dzheiran-Cheli Kirovabad Plateau: Karasakhkal, Naftalan Iora Plateau: Palan-Tikyan	Mastadon arvernensis Aceratherium Hipparion Cervus pliotarandoides
Productive beds	Apsheron Peninsula: Lok-Batan	Fox, deer, gazelle
Pontian		Dinocyon, Mastodon arvernensis, hamster, Dicerorhinus, tapir, Hipparion, roe deer
Meotian Sarmatian	Kartalinia Plateau: Dzhaparidze Gori valley: Arkneti Iora plateau: El'dar, Udabno Kartalinia Plateau: Kyasaman, Kotsakhuris-Kedy	Hyena, long-snouted mastodon, Aceratherium, Hipparion, giraffe, gazelle
Konka Karagan Chokrak Helvetian		Amphicyon, swamp mastodon, Paranchitherium, Anchitherium, giant swine, antelope
	Dzhavakhetia: Akhaltsykh	Benaratherium Chalicotherium Anthracotherium Tragulids

The Neogene faunal complexes of the Caucasus are not endemic. The Oligocene "fauna" of the Lesser Caucasus is related to the central Asian and European "faunas" of the same period.

The Middle Miocene "fauna" of Ciscaucasia, known from Belomechetskaya, is also related to the Miocene "faunas" of Eurasia and North America. This "fauna" migrated over temporary land bridges from the north and south, although the trend from the south was more pronounced.

In the Upper Miocene, Sarmatian, the Hipparion complex migrated to the Caucasus from the south over land which joined the island of Caucasus with Asia Minor.

The local fauna of the mountains has probably evolved since the Miocene. Some of the surviving, endemic elements of the highland fauna are undoubtedly descendants of Upper Miocene forms.

75 Evolution of the Pliocene faunal complexes in the piedmont and the plateaus can be traced mainly to migrations from the north and south. The hot, dry climates of the Pliocene produced a more pronounced southern influence on the evolving fauna.

It is only at the very end of the Pliocene that the northern faunal elements became important. So-called Pleistocene genera and species appear during the general cooling at the end of the Pliocene. Evolution of endemic species in the Pliocene occurred mainly in the highland regions and left relicts on the peneplain.

The paleontology of the Caucasian land mammals does not support the hypothesis of a "Pontian landmass" in the Black Sea Basin connecting western Caucasia, the Crimea and Asia Minor (Andrusov, 1918; Vul'f, 1944; Puzanov, 1949). This hypothesis has also been discarded by geologists (Muratov, 1951). However, it is more than likely that dry land existed in the Upper Pliocene where the Sea of Azov now lies (Vereshchagin, 1957).

A stratigraphic summary of Caucasian localities of Tertiary land mammals is given in Table 5.

Many forms of the Upper Pliocene Taman complex survived in the Caucasus and continued to evolve through the Lower and Middle Pleistocene.

76 *Chapter II*

DEVELOPMENT OF CAUCASIAN LANDSCAPES AND MAMMALIAN FAUNA IN THE QUATERNARY

THE PLIOCENE — PLEISTOCENE BOUNDARY IN THE CAUCASUS

The specific features of evolving landforms in this area between two ancient continents make the identification of the Pliocene-Pleistocene boundary difficult.

The variety of zoogeographic zones and the complexity of their boundaries developed in the Upper Pliocene as well as in the Recent.

Therefore, any study of the geomorphology based upon single occurrences of plants and animals in continental deposits often reflects only local conditions.

This problem, as it concerns the European continent, is still under discussion by geologists and biologists (Zhirmunskii, 1936; Nikolaev, 1947, 1950). We agree with Nikolaev that the Pliocene-Pleistocene boundary must be identified on the basis of all available data of the various disciplines, rather than on isolated criteria.

A variety of geomorphological changes caused by the interplay of tectonics and climate have been proposed as the markers of the Pliocene-Pleistocene boundary. Such markers are sea level fluctuations, orogenic and erosional cycles, glaciations, evolutionary changes of plants and animals, and morphogenetic stages of fossil lineages.

The lower boundary of the Quaternary has been variously placed — in the Upper Sarmatian by geologist Kovalevskii (1936) and botanist Grossgeim (1936); at the end of the Akchagyl by geologists Reingard (1931, 1936a), Gerasimov and Markov (1939) and paleontologist and geologist Gromov (1948); and in the Upper Apsheron by geologists Pavlov (1936), Mirchink (1936b) and Vardanyants (1948).

The Russian zoogeographers Menzbir (1934) and Serebrovskii (1935) did not resolve the question when they applied Western European stratigraphic concepts to the Caucasus.

The hypothesis of Kovalevskii, Grossgeim and Shvetsov (1928) that the
77 Pliocene continental glaciations in the Caucasus correlate with the Günz and Mindel glaciations is no longer accepted.

Gromov (1948) inferred from the geomorphological and paleontological data that, some time at the Tertiary-Pleistocene boundary, the climate became more severe which, however, did not imply an extensive glaciation. He considered the Khapry and the Psekups faunal complexes (see Chapter I) characteristic of the transition from the Pliocene to the Pleistocene in

Ciscaucasia and the southern part of the Russian Plain, and placed the Taman complex at the base of the Quaternary.*

At that time the following forms were considered indicative of early preglacial time on the Caucasian Isthmus: Elephas trogontherii (E. wüsti M. Pawl.), Bison schoetensacki Freud., Elasmotherium caucasicum Boris., Cricetus cricetus L., Spalax microphthalmus Güld. The faunal break was expressed in the disappearance of mastodon, elephant (Elephas planifrons and E. meridionalis), Hipparion and Etruscan rhinoceros, coupled with the appearance of bison. Thus Gromov's biostratigraphic criteria of the upper margin of the Tertiary are similar to those of West European authors: the Khapry and Psekups complexes coinciding with the Günz and Günz-Mindel glaciations, and the Taman complex with the Mindel glaciation of the West European glaciological scheme.

The first erosional cycle in the Quaternary occurred in the Günz. The cycle is represented by gravels of the Kuban River terrace which are 175 m thick.

Similar paleontological considerations have been put forward by Pidoplichko (1940c, 1952, 1954) for the northern Black Sea coast and the Ukraine.

New paleontological data have confirmed that pronounced qualitative changes in the flora and fauna of the Caucasian Isthmus occurred only at the end of Apsheron time. These changes are indications of a mildly warm or temperate climate.

Silicified wood of broadleaf species — oak (Quercus sp.), beech (Fagus sp.) and elm (Ulmus sp.**) — has been recorded from Upper Pliocene freshwater beds near Kuchugur on the Taman Peninsula, and in the lower part of the alluvial sands in the Girei quarry on the Kuban. It is quite possible that subtropical species did not exist in the Caucasian flora of this period. An abundance of terrestrial mollusks (Chondrula, Helix) and freshwater mollusks (Corbicula, Anodonta, Bithynia, Micromelania and other species) in the post-Kuyal'nitsk continental beds of the Taman Peninsula and in the Upper Apsheron beds of eastern Transcaucasia, is evidence of a temperate climate.

It was in Upper Apsheron time that mastodon and Hipparion became extinct in the foothills of the northern Caucasus. The forms which then appeared were horse (Equus cf. stenonis, E. aff. süssenbornensis), Elasmotherium caucasicum, camel (Paracamelus) and bison (Bison sp.).

78 The morphogenesis of the Caucasian elephant (Elephas meridionalis — E. trogontherii) was in a transition stage during the Upper Apsheron (Vereshchagin, 1957a).

The picture is similar in the continental deposits of the Transcaucasus, particularly so in the Armenian Highland. However, the chronological correlation with the Ciscaucasian localities is uncertain, despite the similarities in the composition of the faunal complexes and in the morphogenetic stages.

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* When Gromov wrote this, the Taman complex was poorly known; in point of fact, it is very similar to the Psekups and Khapry complexes (Vereshchagin, 1957a).

** Identified by A.I. Zubkov.

Thus at the end of Apsheron time, new cycles of erosion and mountain formation commenced on the Caucasian Isthmus; the flora developed a temperate or, in some places, a xerophilous aspect, and the vast areas from which the seas receded came to be inhabited by ungulates of a type adapted to the steppe, or even to the desert.

Taking into account that this continental phase undoubtedly covered a very long period, we agree with Pavlov (1936) in placing the beginning of the Anthropogene in the Caucasus at the end of the Apsheron sea regression and at the beginning of the Baku sea transgression.

THE PROBLEM OF THE CAUCASIAN CLIMATES AND LANDSCAPES IN THE PLEISTOCENE AND THEIR BEARING ON THE EVOLUTION OF FAUNAL COMPLEXES

The chief considerations in studying the development of the climates and landforms of the Caucasus in post-Apsheron time are the following:

1. Tectonic cycles and the dynamics of the land relief created by river erosion.
2. Fluctuations of the sea level and the land connections between the Ciscaucasus and the Russian platform.
3. The extent and number of glaciations as related to the tectonics and climatic fluctuations.
4. Changes in flora and formation of vegetation zones.

These factors have been studied in the Caucasus on an empirical basis, disregarding the paleontological material. A summary of these studies would be germane to the overall problem of the history of the fauna.

Dynamics of land relief. In the Pleistocene the dynamics of the relief of the Caucasus was highly complicated. The peneplanation of the ancient mountains of the Greater and Lesser Caucasus at the end of the orogenic period of the Top Pliocene (Apsheron age) is a fact accepted by geomorphologists.

Remains of an ancient peneplain are in fact observable in the Main Range, e.g., in Abkhazia, Svanetia and Kabarda, and particularly in Dagestan. At the end of the Pliocene, the poorly drained, boggy alpine plateaus of the present Dagestan highlands were probably no higher than 500-800 m above sea level. The peneplain is considered to be of either Apsheron or Baku age; Mirchink (1936a) regards it as Upper Apsheron-Lower Baku. Some ridges in the region of Vodorazdel'nyi and the Bokovye ridges presumably did not rise over 1,000-1,500 m above the level of the Apsheron sea. Plant and animal fossils from these plateaus would have been
79 of great interest in the study of the faunal complexes. Unfortunately, their preservation was probably precluded by the action of rapid drift and erosion.

According to Nikolaev (1941, 1949) the relief of the inner plateaus of the Greater Caucasus is much older than Apsheron time. The relief of the Armenian Highland (Paffengol'ts, 1948, 1950) can be traced as far as the time in the Lower Quaternary when Lake Sevan was formed by the lava flows from the Bogu-Dag volcano which dammed the deep erosional valley of the paleo-Zanga River.

Nikolaev (1941, 1949) places the maximum uplift of the Greater Caucasus, following a series of oscillating, tectonic movements, at 3-4 km, which was reached in "post-Upper Pliocene" time. On the basis of their studies in Dagestan and Ossetia, Reingard (1939) and Vardanyants (1933b, 1948) hypothesized that the central part of the Main Range is a horst, which was uplifted by 1,000-1,500 m. The figure of 3-4 km is probably the sum of the uplift of the Central Range and the subsidence in the Black Sea and Caspian Sea depressions.

The most recent tectonic movements have been detected in the central Caucasus, in the Stavropol area and on the Taman Peninsula. The laccoliths in the Pyatigor'e area, which stand out in the surrounding relief, "underwent a relatively greater uplift than the surrounding areas." Ronov (1949), working by a "volume method," stated that the uplift of the Greater Caucasus in the Pleistocene was nearly 2,000 m.

Thus, by a general consensus, the relief of the Caucasian mountains resulted from arching, or, in some places, from horst uplift, and from a concomitant subsidence in the piedmont plains and in the Black Sea and Caspian Sea depressions.

Because of these tectonic movements, the younger terraces in the foothills were formed close by older, denudational terraces, which, in the plains, disappeared completely under the younger ones. This overlapping of terraces is very important in a stratigraphic correlation of terrace deposits and in fossil dating.

The uplift of the Caucasian mountains inevitably resulted in glaciations (which are discussed in more detail below) and in the formation of a rocky relief with numerous cuestas and talus in the faulted areas. The new topography allowed an expansion of plant and animal species adapted to a rocky terrain. The higher relief also promoted a greater ecological and morphological differentiation which was reflected in the formation of new habitats and in the division of existing ones.

The slopes of the ridges which rose during the Pleistocene were actively eroded by rivers. Mountain streams deepened their valleys, stage after stage, forming terraces which correspond to the mountain-building cycles. Rivers cut through the young rising ridges forming narrow canyons in the process.

Such post-Pliocene canyons occur on the northern slope of the Main Range (along the Baksan, Chegem, Cherek and Urukh rivers); in eastern Transcaucasia (along the Geok-Chai, Tur'yan-Chai, Alazan, Kura and Mtskheti rivers); on the southeastern spurs of the Karabakh Mountains (along the Araks River), and in Talysh (along the Vazaru-Chai river).

80 The differential uplift of the mountain ridges combined with river erosion produced sheltered valleys, screened by ridges, which captured atmospheric precipitation and resulted in the development of temperate, arid areas in the highlands. These were a refuge for plants and animals adapted to drought. During the Pleistocene such areas existed in Dagestan, in the longitudinal mountain valleys of Ossetia and Kabarda, in the Gori depression on the Kura River, in the upper part of the Pambak River valley on the Armenian Highland, and in the Zuvanda depression in Talysh. These areas are still inhabited by xerophilous animals: suslik, hamster and steppe vole.

Karstic niches and caves which were created in limestone terrain by river erosion became habitations for some predator species and, later, for man.

A thick mantle of gravels and loams formed in the piedmont during the Pleistocene from the transport of clastic material by rivers from the mountains. Such deposits cover the Trans-Kuban and Terek-Sunzha valleys, the Kusary and Kirovabad plains in Transcaucasia, and the terraces on the Black and Caspian seacoasts.

These piedmont plains were inhabited by mammals associated with the forest-steppe and with moderately humid climatic conditions. The piedmont plains were also the paths of migration from north to south, and vice versa, of those species which lived on the lowland plains.

Vulcanism has had a pronounced effect on the relief and hence on the areas of species distribution in the highlands and on the piedmont plains (Apsheron and Taman peninsulas). In the Armenian Highland the lavas covered great areas of the plateau, sometimes nearly 50% of a whole area (Maruashvili, 1946). Volcanism affected the distribution of animal species both directly and indirectly. For example, the absence of forests in western Armenia is, according to some geobotanists, the result of the volcanic activity and lava flows of the Pleistocene (P. Yaroshenko, 1941).

The orogenic cycles were probably closely related to fluctuations in sea level during the Quaternary.

Fluctuations of sea level. The transgression of the Baku sea, which followed the Apsheron regression, was characterized by an abundance of Didacna. The next stage, the Khazar sea, was characterized by the archaic Didacna surachanica Andr. The equivalent in the Black Sea Basin was the Neo-Euxine sea. The Khazar sea was followed by the brackish Khvalynsk sea which extended far to the north leaving brackish-water mollusk fauna near Ural'sk and Kazan. The Khvalynsk sediments
81 correlate with the beds of the Ancient Black Sea. The last major transgression in the Caspian depression (Khvalynsk sea) is usually thought to correspond to the last stage of glaciation of the Caucasian Range. The Khvalynsk sea receded into the postglacial Caspian, in which later transgressions were only minor and did not extend much beyond the present coastline (Kovalevskii, 1933; Figure 38).

The major Pleistocene transgressions considerably reduced the coastal terraces on the east and west coasts of the Isthmus.

Sea erosion of the piedmont barrier, as in eastern Transcaucasia, or of the coastal plains restricted the areas of distribution and migration of animals on the plains. The alluvial plains were also affected by marine erosion: the Yeisk-Kuban, Kuma-Terek, Rion and Kura-Araks plains, which, at various times, were inhabited by faunas of diverse origins.

The Manych strait formed during the transgression must have restricted the migration of animals from the Russian plains at least to the extent that hibernating animals could not have migrated over ice-covered country.

During the regressions the low-lying areas remained covered by broad salinas and marshes with residual lagoons and lakes. Desalinization of these areas progressed rapidly in western Ciscaucasia where steppes
82 developed. In eastern Ciscaucasia, desalinization proceeded at a slower rate. There semideserts developed, inhabited by jerboas, gerbils, saigas and goitered gazelles. Residual lakes and lagoons became plavni overgrown with nymphaea and bulrushes. Colchis developed a marsh-type vegetation consisting of alder, nymphaea, sedge and sphagnum. The longevity of such marshy tracts depended on the hydrological regime of the feeding rivers and the rate of alluvial fill. The fauna of these marshes included such hydrophilous animals as otter, water rat, European beaver and boar.

FIGURE 38. The Caucasus and the Caspian in the Upper Pleistocene

1 — old freshwater sediments in the Volga Basin; 2 — Aral-Caspian marine transgression; 3 — region of Quaternary glaciation (from Kovalevskii, 1933)

Extent and number of glaciations. Climatic fluctuations and glaciations in the Caucasus could have been the most important factors in the development of the fauna.

Data on Caucasian glaciations is based on the geomorphology of the area and on the relationships between the glacial and orogenic cycles and the sea level stands. Correlation of these data has been complicated by the attempts of Russian geologists to identify Caucasian glaciations with the European glacial stratigraphic scheme developed for the Alps. There has been almost no original stratigraphic work done to date on the glaciations in the Caucasus that is free of this "Western glaciological hypnosis." Geomorphological studies show those peculiarities which distinguish the development of the Caucasus during the Pleistocene from the development of the Alps.

Academician Pavlov (1925) believed that the end of Apsheron time in the Caucasus coincided with the Pliocene (Günz) glaciation, and that it was marked by the uplift of ranges causing a formation of mountain glaciers and intensive deposition of the gravels which are common in the upper part of the Apsheron suite. According to Pavlov, the Mindel glaciation correlates with the upper Baku and the Riss glaciation with the Upper Khazar, while the

Khvalynsk corresponds to the time when the Würm glaciers waned. Essentially this correlation is still valid.

Reingard (1937, 1947b) recognized four or five major stages of glaciation in the Caucasus. The first (Günz), which glaciated as far as the piedmont, occurred in the transition from Akchagyl to Apsheron time, and is represented only by scattered gravel deposits. The Mindel glaciers extended 80 km north on the piedmont plain of the central Caucasus during the Apsheron-Baku transition period. This glaciation was followed by the long second interglacial, during which thick sequences of diluvial loams accumulated from transport of clastic material from the mountains. The third glaciation, the Riss, was the most extensive and its erosional effects in the valleys were the most pronounced. During the interglacial which followed, the glaciers remained only on the mountain peaks. During the fourth and the last glaciation, the glaciers covered only the mountain valleys, and subsequently receded in four stages, with one advance which occurred in the Middle Ages of our era.

83 According to Reingard, the rise in the level of the Caspian Sea was related to the decrease in evaporation at the time of glaciation. Initially, the sea level rose slowly. Later, during the melting of the glaciers, the rise was more rapid, attaining its maximum in the second half of the glacial phase. At that time, the Black Sea level had not yet reached its maximum (Figure 39).

According to Gerasimov and Markov (1939), the entire glacial history of the Caucasus can be subdivided into two periods. During the first period (Akchagyl-Apsheron), one or two glacial phases occurred in central and eastern Caucasia as the result of the uplift of the mountains. In the second period (the second half of the Quaternary), two glacial phases developed in the Greater Caucasus, "the mountain framework formed by the Lower Quaternary tectonic movements." The authors doubted any synchrony between these and the alpine glaciations, although they were certain of "basic changes in climate which occurred several times, along with a number of glaciation (3-4) in the Caucasus."

A record number of ten glaciations beginning with the Upper Miocene has been given by Kovalevskii (1936).

84 Three or four glacial phases in the Caucasus have been suggested by Vardanyants (1948). However, he tended to accept Gromov's (1935b) subdivision into two glacial epochs corresponding to the Riss and Würm of Europe: the Riss corresponding to the Early Khazar, and the Würm to the Early Khvalynsk, with corresponding stages of retreat following each (Figure 40).

In the Black Sea Basin the periodically established connections with the ocean were controlled by the uplift and subsidence in the Bosphorus-Dardanelles region and modified the processes of glaciation and transgression. A stratigraphic summary of Vardanyants' is given in Table 6.*

A number of marine basins periodically connected the Aral, Caspian, Black and Mediterranean seas, and their waters interchanged with the fresh waters of the Caspian through the Manych strait. Increase in salinity of the basins was due to the penetration of the Mediterranean water eastward in post-Tertiary (Karangat and Ancient Black Sea) time.

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* Other geologists, for example Popov (1955), correlate the Khvalynsk time with the Neo-Euxine beds, the Khazar time with the Karangat beds, etc.

It seems strange that the views of geologists on the extensive glaciations in the Caucasus were supported, rather than opposed, by biologists.

(83)

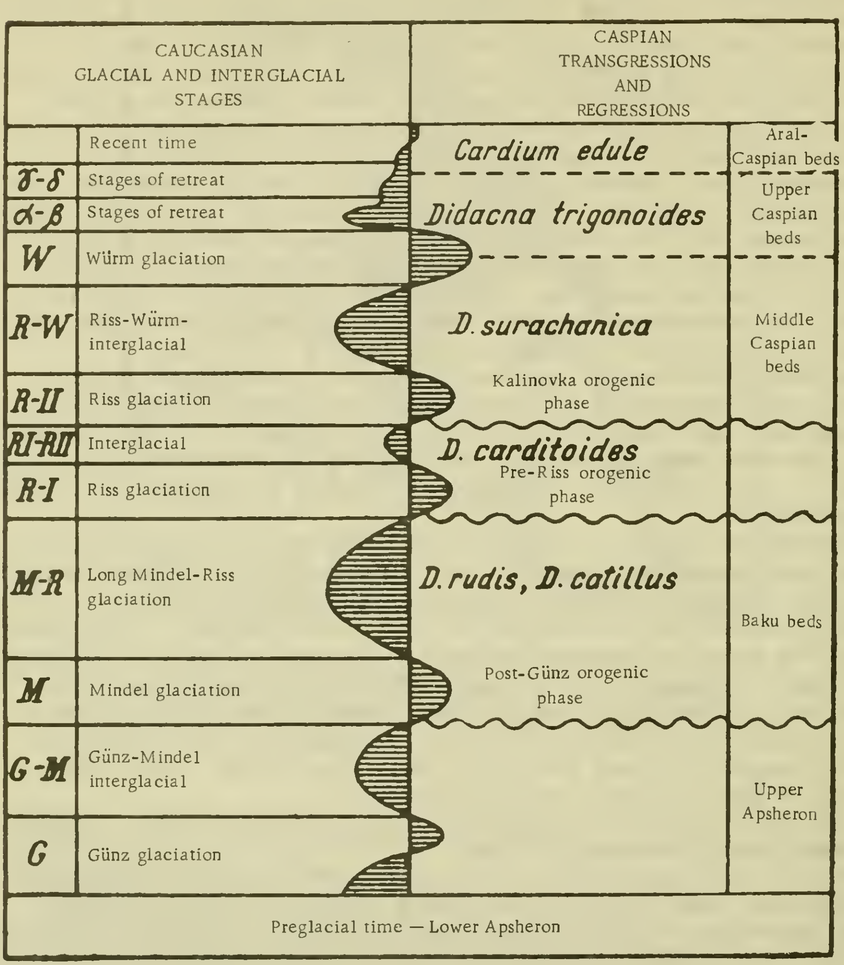

FIGURE 39. Relationships between glaciations, orogenic phases in the Caucasus and fluctuations of the Caspian Sea level (according to Reingard, cited in Bogachev, 1940)

Formation of vegetation zones. According to the botanists
Kuznetsov (1909) and Medvedev (1915) and the zoologists Satunin (1910)
86 and Dinnik (1911), there was only one glacial phase during which the
Caucasian fauna and flora were saturated with northern forms, and the
mountain animals and plants had to seek refuge on the plains.

From an analysis of Recent Caucasian flora, Grossgeim (1948) has inferred a number of hot interglacials, in order to account for the presence of xerophilous southern plants at a number of places in the Caucasus. Geobotanists Maleev (1946) and Kolakovskii (1947b), who studied the origin of the eastern Mediterranean flora (in particular, that of Colchis), also

FIGURE 40. Glaciation in the Caucasus during the pre-Khazar orogenic phase

1 — inferred outline of the sea; 2 — areas of glaciation (from Vardanyants, 1948)

accepted the notion of several glacial epochs and warm interglacials. They connected the occurrence of mesophilous broadleaf forests to the pluvial glacial periods, and the reduction of mesophilous flora, with concomitant development of semixerophilous and thermophilous vegetation, to the arid interpluvials. These conclusions are based either on studies of discontinuities in plant distribution, or on the geological literature (Vereshchagin, 1949c). An interplay of many factors, other than climatic, is responsible for discontinuities in the distribution of species. Even the penetration of northern plants (e. g., sphagnum and sundew) far into the south — to the Greater Caucasus, the marshlands of Colchis and the Lesser Caucasus highlands — cannot be correctly evaluated unless all the factors which control species distribution are known. The use of phytocenotic transformations to detect climatic changes is open to question even when applied to a period of time as short as the historical epoch (e. g., Sinskaya, 1933; Fedorov, 1952). The Pleistocene climatic changes cannot be evaluated from the fossil plant record alone because the number of known macroscopic plants is small. However, the available paleobotanical and geobotanical evidence indicates that the flora of the Caucasus in the Middle Pleistocene resembled the Recent flora and the plant habitats had the essential aspects of the Recent. The arboreal vegetation at the end of the glacial epoch was also similar in type and in distribution areas to that of Recent time (Grossgeim, 1936, 1948).

The valley glaciers of the past, as, for instance, those on the slopes of western Caucasia, were much larger than those of the Recent. This is

(85) TABLE 6. Stratigraphic summary of post-Tertiary history of the Black Sea, the Caucasus and the Caspian Sea (from Vardanyants, 1948, p. 23) and connections via the Bosphorus and the Manych region

<table>
<tr><th>Bosphorus</th><th>Black Sea</th><th colspan="2">Caucasus</th><th>Manych</th><th>Caspian Sea</th></tr>
<tr><td></td><td>Recent sediments</td><td colspan="2">Bühl stages</td><td>Open (?)</td><td>Post-Khvalynsk layer</td></tr>
<tr><td>Closed</td><td>Subsidence, regression, decreasing salinity</td><td colspan="2">Uplift, glaciation (Bühl or Neo-Würm)</td><td>Closed</td><td>Regression</td></tr>
<tr><td></td><td>Ancient Black Sea beds</td><td colspan="2">Würm stages</td><td>Open</td><td>Khvalynsk layer</td></tr>
<tr><td>Open</td><td>Subsidence, influx of seawater</td><td colspan="2">Uplift and glaciation (Würm)</td><td>Closed</td><td>Regression</td></tr>
<tr><td></td><td>Neo-Euxine beds</td><td colspan="2">Riss-Würm</td><td>(?)</td><td>Khazar layer</td></tr>
<tr><td>Closed</td><td>Subsidence, regression, decreasing salinity</td><td colspan="2">Uplift and glaciation (Riss)</td><td>Closed</td><td>Regression</td></tr>
<tr><td></td><td>Karangat beds</td><td rowspan="3">Mindel-Riss</td><td colspan="2">Open</td><td>Upper Baku (transitional beds)</td></tr>
<tr><td>Open</td><td>Subsidence, influx of seawater</td><td>Uplift</td><td>Closed</td><td>Regression</td></tr>
<tr><td></td><td>Uzunlarskoe and Ancient Euxine beds</td><td></td><td>Closed</td><td>Middle Baku
Lower Baku</td></tr>
<tr><td></td><td>Chauda beds</td><td colspan="2">Uplift and glaciation (Mindel)</td><td>Closed</td><td>Regression</td></tr>
<tr><td></td><td>Krasnodar horizon?</td><td colspan="2">Günz-Mindel</td><td>Closed</td><td>Upper Apsheron</td></tr>
<tr><td>Closed</td><td>Regression and decreasing salinity (?)</td><td colspan="2">Uplift and glaciation (Günz)</td><td>Closed</td><td>Regression</td></tr>
<tr><td></td><td>Guri beds</td><td colspan="2"></td><td>Open</td><td>Lower and Middle Apsheron</td></tr>
</table>

indicated by the occurrence of glacial troughs and terminal morainic ridges in the valleys of the Laba, Zelenchuk, Kuban, Baksan and other rivers in the area (Figure 41).

The glacial troughs occur in the upper parts of the valleys, far short of the Skalistyi ridge. It is clear that there were no basic differences in the environments of the faunal and floral complexes between the time when the valleys were covered by glaciers, and the Recent. The vegetation of the highlands descended, although it was not completely displaced, to the
87 piedmont plains.* During the period of maximum glacial advance, there was adequate living space for mountain animals on the meridional and lateral mountain ridges near the glaciers. Even at present, mountain forests

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* Even Grossgeim (1936, p. 203), allied as he was with Kovalevskii, was compelled to recognize this fact.

(coniferous, broadleaf and mixed) and mountain animals exist close to the glaciers, as on the Cherek, Urukh and Rion rivers (Figure 42).

The gravel beds and large boulders in the piedmont plains were more likely the result of mudflows, caused by floods and volcanic activity, than relicts of hypothetical glaciations.

The evolution of mammalian faunal complexes must be related to the snow factor and to the latitudinal shift of the climatic zone on the Russian Plain caused by the northern European glaciation. However, the depth and duration of the Pleistocene snow cover have not been studied, and can only be inferred from examples of distribution and migration of some mammals in the Recent.

FIGURE 41. Glacial trough and terminal moraine, overgrown with pine, in the Tseya ravine in North Ossetia

Photograph by author, 1947

The occurrence of boreal plant species in the Caucasus can only be accounted for by the proximity of the Riss glacier tongues to the Caucasian Range (Medvedev, 1915; Grossgeim, 1936, 1948). In other words, it is assumed that tundra and taiga existed in the Manych area and in the Salsk
88 steppes. Results of recent palynological and paleontological studies indicate that steppes always existed between the lower Don and the lower Volga rivers.

We will evaluate the paleontological and zoogeographical data in the Caucasian stratigraphy after we review the Pleistocene localities. It should be noted that the hypothesis of extensive continental glaciation in the Caucasus implies that the evolution of all the highly specialized forms (mountain goat, snow mouse and other forms) took place within a very short time — the postglacial period.

The glacial stratigraphic scheme, particularly the hypothesis of continental glaciations in the Caucasus, should be reviewed with reference to biological data.

(88)

FIGURE 42. Glacier and forest in the upper reaches of the Rion

Photograph by author, 1957

Absolute geochronology of the Quaternary. Application of the absolute time scale of the Quaternary to the Caucasus did not produce new results. Most Russian authors accepted the estimates of Soergel (1925) and Milankovich (1939) of 600,000-650,000 years as the duration of the glacial epoch. In estimating the time of origin of the Aral-Caspian sea at 23,000 B.C., of the Khazar sea at 13,500 B.C. and of the Khvalynsk sea at 3,400 B.C., Kovalevskii (1933) condenses the entire history of man and the evolution of the Caucasian fauna into a very short period of time. Later investigators have found that the Quaternary orogenic processes and 89 glaciations in the Caucasus lasted much longer — 500,000-600,000 years according to Vardanyants (1948) or even 1,000,000 years according to Nikolaev (1949) and to Ronov (1949). These estimates, which are of great importance in the calculation of the rates of evolution, speciation and development of the fauna, will undoubtedly be amended in the course of future studies of the physicochemical composition of rocks, bones and sediments. The only Caucasian stratigraphic stage with a satisfactory paleontological record is the Upper Pleistocene — presumably the time when glaciation reached its maximum extent.

MODE OF OCCURRENCE OF FOSSIL MAMMALS AT THE PLEISTOCENE LOCALITIES

Pleistocene localities are more amenable than those of the Tertiary to studies of the conditions of animal death and deposition.

In the Caucasus Quaternary mammal fossils occur in marine terraces along the coasts of the Black, Azov and Caspian seas, in river and lake terraces, in the surface loams and in caves.

Only a few occurrences of mammals in marine and lagoonal sediments are known in post-Apsheron strata. This is probably due to the latest tectonic processes, since it is unlikely that the variability of the animal world in the Pleistocene was any less than in the Tertiary.

The bodies of animals which had died from various causes (see Introduction) accumulated at river mouths and estuaries. Smaller accumulations formed in the alluvial sediments of the middle and lower parts of rivers. All such sites in the lower parts of the valleys of the Kuban, Terek, Rion and Kura rivers are at present in the zone of tectonic subsidence, in which sediments continue to accumulate. Consequently, most of the sites remain concealed by the sedimentary cover and can be discovered only in the processes of drilling and quarrying.

Exceptions to this usual mode of occurrence are found in those sites which were at the head of coastal bays, provided the bays were in the area of the later uplift of the foothills. Such localities are found in the middle parts of the Kuban (Kropotkin, Nevinnomyssk), on the Terek River (near Mozdok and Kotlyarevskaya), on the Rion (at the longitude of Kutaisi and Zestafoni), and on the Kura (in the Mtskheti-Tbilisi area).

It is possible that several fossiliferous layers occur at localities in a "zone of undulation" (i.e., longitudinal depressions and swells) because favorable hydrological conditions prevailed over several epochs.

Most of the Pleistocene mammals are found as intact or fragmented skeletons in continental deposits of various origins (alluvial, lacustrine, diluvial, eolian) in caves, travertines and asphalt pools, on the plains and in the foothills of the Caucasus Isthmus.

Although life was precarious in the mountains and avalanches, falling
90 rocks, slippery, ice-covered surfaces and hunger brought frequent death to the animal communities, the chances were poor for the preservation of their remains. The fine-grained alluvial sediments of mountain rivers did not offer much likelihood of preservation either. Such sediments are usually thin and tend to shift with time (Shantser, 1951). Fossil vertebrates do not occur, as a rule, in the terminal and lateral moraines of mountain valleys, because of the attrition of bones in the process of moraine deposition.

The diluvial sediments at the foot of the mountains, far from the valleys of large rivers, do not contain fossil accumulations, since skeletons were usually destroyed during the slow deposition of the sediment.

Skeletons of animals carried by torrential streams onto the plain areas stood a better chance of preservation in the thick mud and conglomerates formed by the streams. Mudflows continued to cause destruction and death among animals throughout the Quaternary; they have been vividly described by Ivanovskii (1911) for the Araks River valley, and by Muratov and Gvozdetskii (1948) for the Khasaut valley in the northern Caucasus. Mudflows are also known to have occurred in the rivers of eastern

Transcaucasia, for example, in the Demir—Aparan-Chai ravine.

Mudflows are produced by such factors as heavy rains and volcanic eruptions which melted the firn and ice. The flows, which were more frequent and powerful in the Pleistocene, killed masses of animals.

Heavy snow and surface ice were probably common causes of violent death among the Pleistocene animals of the plains, just as they are among the Recent animals. On the plains beyond the river valleys bones were rarely preserved and then only in the gulleys and diluvial loams.

Disposal of food remains by primitive man at campsites and in caves added a new factor to the accumulation of Pleistocene fossils. The prey carried by predatory animals and owls also contributed to the bone accumulations of many species at the same cave sites.

This type of death assemblage occurs most frequently in the mountains and is the main source of information on the history of the mountain fauna.

The sections which follow are devoted to the discussion of the major localities by regions.

PLEISTOCENE BONE-BEARING LOCALITIES

Western Ciscaucasia

Following the deposition of the bone-bearing Psekups gravels and conglomerates on the Taman Peninsula, no rich, diversified mammalian accumulations are known for quite a long time. The Lower and Middle Pleistocene fossil record consists mostly of teeth of Elephas meridionalis and E. trogontherii.

91 On the Kuban Plain, i.e., on the right bank of the latitudinal section of the Kuban, fossil mammals occur at great depth in the sediments of ancient rivers which ran off the Caucasian mountains.

The remains were deposited on the edges of floodplains of the plavni or liman type fed by mountain streams, probably beyond the zone of deposition of coarse clastics.

The clays and sands of the Kuban Plain (e.g., those in the Krasnodar area) contain bones of large Middle Quaternary mammals of Khazar time, along with wood and freshwater mollusks (Unio, Paludina) (Pravoslavlev, 1932). The overlying beds are loess loams with occasional intercalations of volcanic ash. In addition to mammals and plants, these beds contain terrestrial mollusks (Buliminus tridens Müll.), which are indicative of a steppe environment.

Bones of "Bos, Equus, Cervus, Elephas" have been recorded by Pravoslavlev and Ansheles (1930) from the 50-m-thick loams near the Cossack village of Temizhbekskaya.

A number of fossils from other localities were identified by the author in 1952 in the Krasnodar Museum. These include the teeth and skull fragments of an early mammoth, Elephas trogontherii — E. primigenius, from the village of Dinskaya, and remains of a long-horned bison, Bison priscus longicornis, from the village of Krylovskaya on the middle Chelbas. The skeleton was buried in the silty sand of a stagnant-water basin. The bones were only slightly permineralized and resembled alabaster in their appearance. Bones of

Bison priscus longicornis and mammoth were preserved under similar conditions near the village of Skobelevskaya. The bones were found in a silty marsh bed 16.5 m beneath the loess. Elongated grooves, the tracks of boring invertebrates (Trichoptera larvae ?!), occur on the surfaces of the bones. The occurrences of B. priscus longicornis indicate the Middle Pleistocene, Khazar age of these localities.

Five nearly complete skeletons of small cave bear (Grigor, 1926), described by Borisyak (1930, 1931) as Spelaearctus rossicus, were found near Krasnodar at a depth of 14 m in the sandy loams of the second alluvial terrace of the Kuban. The death and deposition of the animals have been attributed to mudflow by Borisyak.

Girei Quarry. The stratigraphy of the alluvial sediments of the Kuban Plain has been worked out by Gromov (1948) from the sections in the quarries near the village of Girei and the Kavkazskaya railroad station in the town of Kropotkin.

Sandy loams and sands 2 m thick, and greenish loam 1.5 m thick with vertical plant roots have been exposed by quarrying in the 10—15-m-thick Würm terrace of the Kuban. Crossbedded gravels with sand lenses and gravel beds up to 3.5 m thick were exposed in the lower part of the quarry. Bones of mammoth occur at the base of the 3.5-m-thick sequence, which is underlain by a clay bed 0.8 m thick with plant remains (Figure 43), and a sand bed 3 m thick. The sand is underlain by gravels containing bones of bison, deer, and elephant.

92 The following species occur in the gravel beds (Gromov, 1948): Elephas wüsti, E. aff. trogontherii, E. primigenius, Rhinoceros mercki, R. antiquitatis, Bison priscus cf. longicornis, B. priscus deminutus*.

According to the observations of the geologist Kolbutov, the bones of E. wüsti and R. mercki came from the lower gravel bed, which overlies the clays with lignitized wood. The age of these fossils is close to those of the Tiraspol' gravel. The mammoths from the sands and gravels higher in the section are of Riss age, and thus contemporaneous with the "fauna" at the Il'skaya paleolithic locality (Gromov, 1948). The material represents three faunal complexes: 1) post-Khazar with Elephas primigenius, 2) Khazar with E. trogontherii, 3) pre-Khazar with E. wüsti.

According to Gromov, the age of most of the bones from the Girei quarry is Khazar, i.e., Early Riss or Riss-Mindel.

Our studies in 1952 of the locality at Girei revealed the following stratigraphic sequence from top to bottom: surface loams; ancient alluvium, 12-13 m thick; Sarmatian blue clay, 5-6 m of which were exposed by the Recent Kuban River erosion (Figure 44).

Fragments of large tree trunks, often coated with ferruginous silt, saturated with water and charred in appearance, are common in the lower part of the sands and clays at a depth of 10 m. The following trees, which
93 are characteristic of the present foothills, have been identified: oak (Quercus sp.), beech (Fagus sp.), and poplar (Populus sp.). Bones occur in the gravels overlying the wood-bearing sands. Most of the bones are well-rounded, heavily permineralized and iron-stained.

(92)

FIGURE 43. Gravels and sands (stripped of loam surface) in the Girei quarry

Photograph by author, 1952

We identified elephant teeth from the Girei quarry, now in the Krasnodar Museum, as follows: Elephas meridionalis — two molars with enamel 3.5-4 mm thick; E. trogontherii — three molars with enamel 2.4-2.8 mm thick; E. trogontherii primigenius — one tooth with enamel 1.8-2.2 mm thick. The bone material in the teeth of the meridionalis and trogontherii species is pink-tinged beige and resembles marl. The state of preservation is comparable in both species. A tooth of an early mammoth with 8.5 enamel lobes over 10 cm on M^3 is in a better state of preservation: in fracture the bone material is white, black-veined and slightly iron-stained. The collections also include bone fragments of deer (Cervus elaphus) and a marl-like fragment of a horn stem of Bison cf. schoetensacki.

The sandy-gravelly sequence at Kavkazskaya contains an assemblage consisting of animal remains which have been eroded and redeposited by lake sediments of different ages. As a whole, the Elephas meridionalis — E. trongotherii complex is possibly somewhat younger than the Taman faunal complex (see Chapter I). In all probability, there were no antelope in the younger complex: the bison were larger than the Taman species, and the deer were less diversified than those in the earlier complex.

The bones of mammals which are infrequently found in the upper parts of the loess and in the fossiliferous soils underlying the loess on the water divides of northwestern Ciscaucasia are attributed to a later time. The Middle Pliocene localities in the lake sediments near Krylovskaya and Skobelevskaya are exceptions to this dating. Mirchink (1936b) has correlated the upper

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* The material was lost during the war.

part of the loess in Ciscaucasia with the Würm glaciation, and the fossil soils with the Riss-Würm interglacial.

The Basal Quaternary of the Trans-Kuban Plain is represented by the middle part of the Psekups gravels with E. meridionalis, Equus stenonis and unidentified Bos (Gromov, 1948).

94 The meridionalis and trogontherii elephant species are usually dated as the Lower or Middle Pleistocene. These occur, as a rule, in the highest terraces of the left tributaries of the Kuban. A tooth from the mandible of Elephas trogontherii was found near the village of Pregradnaya on the Bolshoi Zelenchuk (ZIN collection).

The Trans-Kuban Plain collections in the Krasnodar Museum include elephant molars of a species intermediate between Elephas trogontherii and E. primigenius. The tooth enamel is 1.8-2.4 mm thick; it forms 7-8 lobes over 10 cm of the upper surface. The iron stain on the bones indicates that the remains of the elephants were buried in fine-grained river and lake sands, which subsequently became marshland. As for their state of preservation, these teeth always look younger than the teeth of E. meridionalis from the Psekups and Taman; the dentine and cement are dense and light beige and yellowish in color. In the gravel quarry near the village of Nekrasovskaya on the Laba, the following forms have been identified: tooth of an elephant of the type intermediate between E. meridionalis and E. trogontherii; lower molar of Equus aff. süssenbornensis; fragment of a horn of the deer, Eucladocerus sp.; and a fragment of a horn of a giant deer, Megaceros euryceros. The faunal composition, the mode of preservation and the iron stain on the bones at this locality resemble some deposits on the Taman Peninsula.

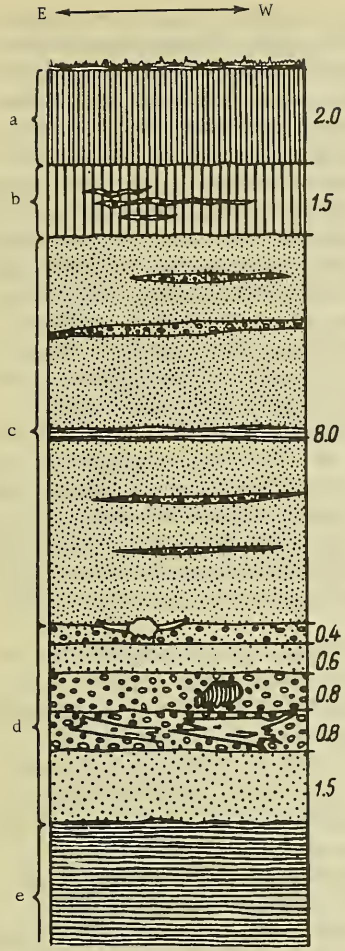

FIGURE 44. Section through bone-bearing gravels and sands in the Girei quarry

a — surface loams; b — sandy loam with gravelly intercalations; c — river sands with layers of gravels and clays; d — gravels and sands with mammalian bones and tree trunks; e — Sarmatian blue clays. On the right — thickness in meters

More recent collections by the Krasnodar Museum from the gravel quarry near the village of Ivanovskaya include molars of true mammoths with enamel 1.4-1.8 mm thick and 12 lobes over 10 cm. A molar of a mammoth was also found on the Pshish River. Teeth of Elephas meridionalis and E. trogontherii from the vicinity of the village of Novo-Labinskaya on the Laba River are in the Maikop Museum collection.

The museum material is difficult to place stratigraphically because of inadequate labelling and the peculiarities of the mode of deposition on the piedmont plain (see above). On the plain, cones of silt debris, formed out of mudflow and carrying the bodies of animals, were deposited one on top of the other. However, these deposits were later eroded by rivers which redistributed the bones in aggradation terraces. In this way, faunas of quite different ages occur in the same river terraces, and, for this reason, Mirchink's (1936b) attempted synthesis of the geomorphological and paleontological data on the river terraces of the southern Russian Plain and of Ciscaucasia can be accepted only with great reservation. On the basis of the occurrence of Elephas planifrons teeth, Mirchink dated the 175 m terrace near Cherkessk Pliocene in age. The 100-125 m terrace belongs to the Mindel glaciation period, according to Reingard. On the Kuban Plain, this terrace is overlain by two loess strata. Two layers of osseous soil, correlated with the "Paludina sands" near Taganrog, Bessergenovka and Yeisk, occur here. The 50 m terrace near Cherkessk has been correlated by Mirchink, without paleontological evidence, with the moraines near the village of Khumarinskoe and the lower loess horizon occurring on the water divides of western Ciscaucasia. The loess, according to Mirchink, is of Riss age. It is likely that the loess in Ciscaucasia correlates with the gravels at the base of the
95 second terrace in the lower Volga. Fossils of the Khazar faunal complex occur in these gravels.

Il'skaya Paleolithic site. The activities of Paleolithic man in western Ciscaucasia are traceable through flint tools which occur on the shoals of the Kurdzhips and Belaya rivers near Maikop and Fortep'yanovka. The area probably had many summer encampments. The caves in the foothills, mentioned in local accounts, have not as yet been investigated by paleontologists. The Fanagoriiskaya cave, a narrow, cold crevice cut through the limestone conglomerates by the upper Ayuk rivulet west of the village of Goryachi Klyuch, was unsuitable for large animals.

The Il'skaya site was discovered in 1898 by Debaille (see Volkov, 1899). This is an open site on the right bank of the Il', the left tributary of the Kuban, 40 km southwest of Krasnodar. The site, now in deforested foothills, was rediscovered in 1925 by Zamyatnin (1934) who carried out excavations in 1927-1928, and who was followed by Gorodtsov (1940) in 1930 and 1936-1937.

Paleolithic remains occur in the lower of two beds of fossil soils in diluvial loams located on the second 10-14 m terrace of the Il' under the dolomite cliffs.

The archaeologists mentioned above have described numerous tools found at the site made of dolomite and, occasionally, of flint. Because of the poor finish of the dolomite tools, Zamyatnin dated the site Mousterian, but the more refined finish of the flint tools led Gorodtsov to date the site Solutrean. The geological dating of the terraces is Riss-Würm, Early Riss (Gromov, 1933, 1948).

According to Gorodtsov, the community abandoned the site when the surface of the Riss terrace became bogged at the onset of diluvial processes. At the same time oil seepage from the dolomite displaced the water at the site and preserved the strata containing Paleolithic tools and bones. The state of preservation of the bones varies at the Il'skaya site. Some fragments "jingle" and are so thoroughly permineralized that they only stick slightly to wet fingers; their specific gravity is almost equal to that of Pliocene bones. These bones are usually strongly stained with the iron oxide which fills the pores, or are covered with particles of silty fine-grained sand of a type characteristic of swampy springs on river floodplains. The enamel of the teeth is completely black. Those bones which were preserved in oil are younger in appearance. All the collected bones are food remains — the epiphyses on the bones are broken off, and the diaphyses split as though bone marrow has been extracted. Fragments of jaws and individual teeth of bison are particularly abundant and bones of young mammoths, showing teeth impressions of large carnivores, also occur at the site.

When the asphalt which adhered to the teeth of the bison was dissolved with benzine, the remains of birch mice, small snakes, beetles and grasses became visible.

96 Table 7 and Figure 45 give the species and their number in the Zamyatnin and Gorodtsov collections, as identified by Gromova (1932a, 1937) and by the author.

TABLE 7. Mammals from the Il'skaya site

Species and higher taxa	Number of bones	Number of individuals
Ursus spelaeus	2	2
Canis aff.. lupus (small form)	19	4
C. lupus	1	1
Crocuta spelaea	24	7
Elephas primigenius	210	5
Lepus aff. europaeus	15	1
Sicista cf. caucasica	2	2
Muridae, not determined below generic level	9	2
Equus caballus	13	5
E. cf. hidruntinus	23	3
Sus scrofa	1	1
Cervus elaphus	33	4
Megaceros euryceros	37	4
Bison priscus	2,401	43
Saiga tatarica	38	2
Artiodactyla, not determined below generic level	549	—
Total	3,377	86

The absence of woolly rhinoceros, elk and mountain goat is probably not accidental. These animals were rare and difficult to hunt.

Elasmotherium and camel, common in the Middle Pleistocene of the Volga River region, either did not exist on the Trans-Kuban Plain, or, at most, were extremely rare.

Bison remains account for 87% of the bones at the Il'skaya site. The species, according to Gromova, is one of the forms showing reduction in size: Bison priscus deminutus.

In fact, relatively small molars and carpal bones (of cows?) occur along with bones of large bison, which are indistinguishable from those of Khazar age of the middle and lower Volga. The proportion of large bones is small,

(98)

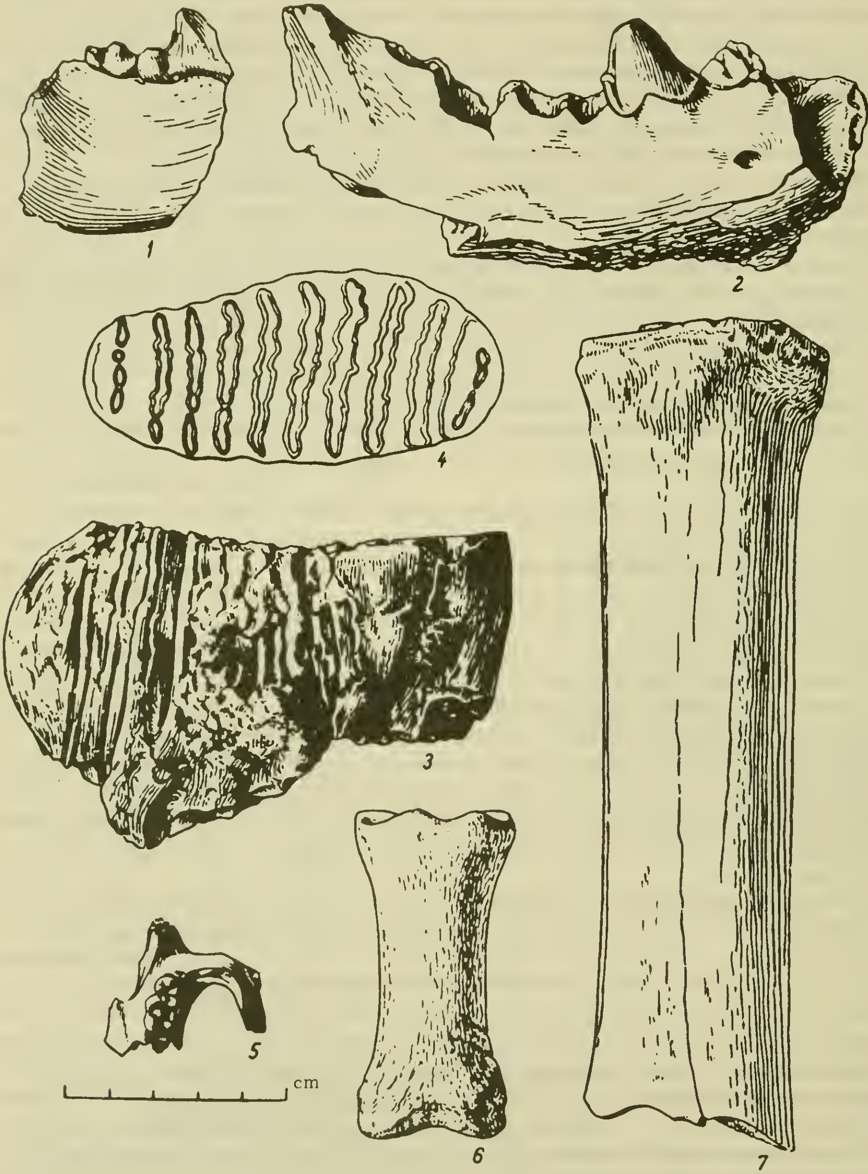

FIGURE 45. Mammal remains from the Il'skaya site

1 — jaw of Canis lupus; 2 — jaw of Crocuta spelaea; 3, 4 — M_4 of Elephas primigenius showing worn surfaces; 5 — upper jaw of Sicista cf. caucasica (×8); 6 — phalange of Equus hidruntinus; 7 — metacarpus of E. caballus;

but the determinant here may have been the selectivity of the ancient Trans-Kuban hunters rather than any morphogenetic factor. It is possible that hunters might have killed cows in preference to bison.

The surroundings of the site were probably meadow- and forest-steppes, which were inhabited by large herds of bison, horse and deer.

The climate and landscape of the Trans-Kuban region in the Upper Pleistocene can be best inferred from the presence of saiga and boar. Saiga did not live on the left bank of the Kuban in historical time, because of the damp summers and snowy winters which prevailed there. Boar, however, survived until recently by descending to the forested plain after heavy snowfalls in the mountains. Thus it can be seen from the evidence at the Paleolithic site that the Trans-Kuban area was more of a steppe than it is at
97 present; the climate was drier, and there were no catastrophic snowfalls. However, the saigas could migrate from the north into the foothills only over ice- and snow-covered ground, as they do now in eastern Ciscaucasia.

(99)

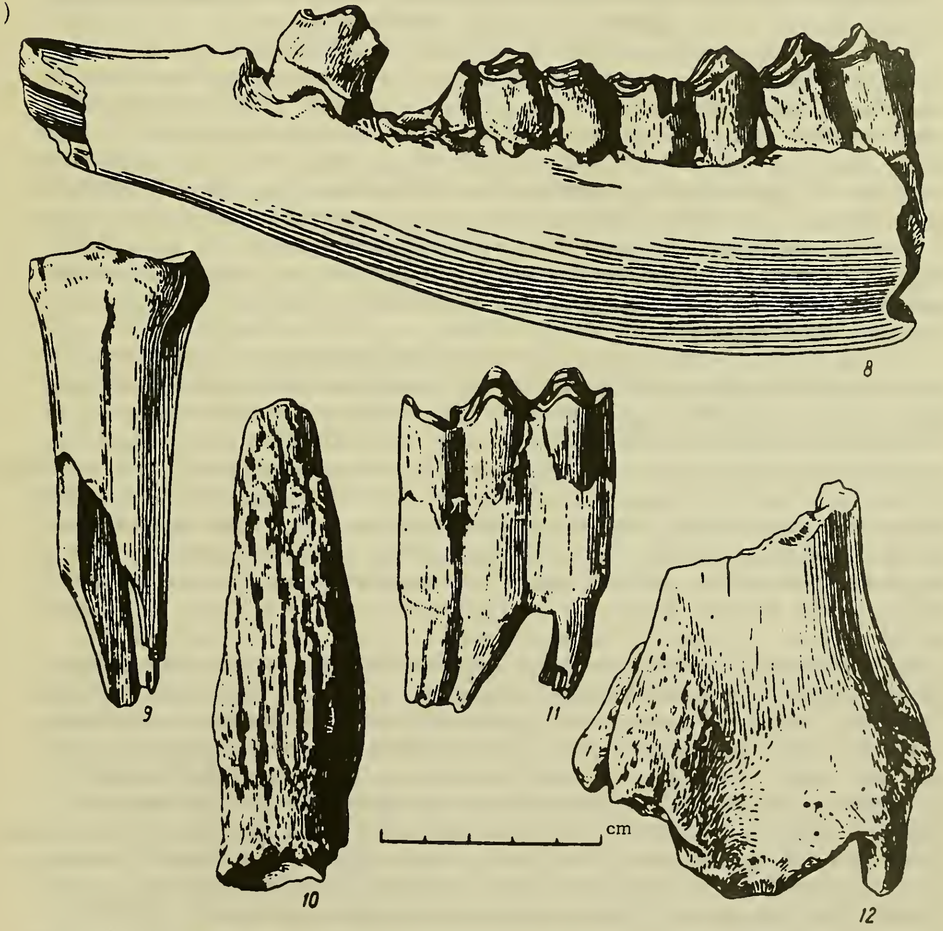

FIGURE 45 (continued)

8 — jaw of Megaceros euryceros; 9 — metacarpus of Cervus elaphus; 10 — horn stem of Saiga tatarica; 11, 12 — M_3 and epiphysis of shank bone of Bison priscus.

The negligible number of boar bones is probably accounted for by the much higher altitude of the mountain forests at that time. The absence of rock and mountain animals — mountain goats, sheep and boreal mammals — is also highly indicative.

The absence of mountain goats, however, cannot be used in dating this site and estimating the extent of glaciation in the Caucasus. Even during the maximum extent of glaciation, these animals could have lived along the margins of the mountain glaciers near the Semashkho and Oplenen peaks, 60-70 km from the site, and well outside the regular hunting grounds of the Il'skaya hunters. The mountains close to the site were low and gently sloped. The absence of the arctic fox, reindeer and ox indicates, most likely, that these species did not reach the northern Caucasus.

The elephant bones at the Il'skaya site belong to a mammoth of a late type (tooth enamel thickness: 1.3-1.4 mm). At least two adults and three young, at the stage of tooth growth — M^3-M^4, were found.

New collections of the bones of smaller species, which are preserved at the site in asphalt crusts, would contribute much to the understanding of the evolution of the Quaternary fauna in the Caucasus.

Fragments of insect chitin which fell into the oil pools at the site and were thus preserved, were examined at our request by Bogachev, who identified eighteen beetles, one ant and one wasp (?). Of the beetles, the most common are water scavengers and water beetles (Dytiscus sp. nov., Agabus sp., Illibius sp., Hydroporus sp., Colymbetes fuscus L.); others are ground beetles (Carabus sp. nov., Platysma sp., Amara sp., Bembidium sp.), leaf beetles (Gastroidea sp., Donacia sp.) and Coprinae (Aphodius subterraneus L.). The steppe forms are represented by Tentyria nomas Pall. Many of the species differ considerably from the Recent forms, which indicates the antiquity of this fauna.

Among the 20 grasses preserved in chunks of bitumen, collected by Zamyatnin and studied by Kipiani, the following predominated: Cruciferae gen. et sp., Compositae gen. et sp., Lepidium perfoliatum, Polygonum aviculare, Euphorbia cf. palustris, cf. Statice, Chenopodium sp. et cf. Atriplex. There were also occasional remains of Alisma sp., cf. Carex, Scirpus sp., Plantago sp., and other forms. No macroscopic remains of arboreal species were recorded. The species listed are ancient, weedlike types, characteristic of sunny habitats and some of them of a shallow-water environment. Cherdyntsev has set the age of the Il'skaya site from the carbon-dating of the bones at 39,000 years.

In our opinion, the Il'skaya fauna indicates the beginning of the Upper Pleistocene and the extensive development of steppes in the foothills region.

In 1957 Formozov carried out exploratory excavations at the entrance to a cave in the Belaya River ravine near the village of Dakhovskaya. He collected eighty fragments of poorly preserved bones and some tools of the Mousterian type from the 3-m level. We have identified the bones as follows: Canis sp. (10/2), Vulpes sp. (17/4), Ursus spelaeus (3/2), Crocuta spelaea (1/1), Meles meles (7/2), Panthera spelaea (4/1), Felis cf. silvestris (2/1), Lepus europaeus (3/1), Cricetus cricetus (3/2), Elephas cf. primigenius (14/1), Cervus elaphus (5/2), Megaceros euryceros (5/2), Capra cf.

caucasica (2/1), Bison priscus (19/3).* This fauna is characteristic of ecological assemblages of the Middle-to-Upper Pleistocene transition. As a whole, it is quite similar to the Il'skaya assemblage. Some small forms of wolf and fox are particularly interesting.

Central Ciscaucasia

On the Stavropol Plateau and in the Pyatigor'e area Pleistocene mammals occur mainly in diluvial loams covering the water divides and filling old
100 gulleys. Older, Lower Pleistocene fossils occur in deposits of ancient streams and marine and lake bays on the surrounding plains. The Lower Pleistocene material is represented by Elasmotherium sibiricum from the vicinity of Divnoye in the Manych depression (Pavlova, 1916), and by Equus cf. stenonis teeth from loess loams near the village of Mirnyi (Khomenko, 1913a). The following finds can be dated Middle Pleistocene, Khazar: horn of Megaceros hibernicus, found by Khomenko in diluvial clays in the Kalaus cliffs; Saiga prisca (= S. tatarica) from diluvial clays in the Koronkoyar gulley, 35 km south-southwest of Stavropol; Equus caballus fossilis, in diluvial clays of the Shatyr mound, and remains of Bos sp. from sands at the bottom of a well in the stream bed of the Mutnyanka.

The collection of elephant teeth in the Stavropol Museum includes three lower molars (7 lobes over 10 cm; enamel thickness 2.5-2.8 mm) of Lower Pleistocene Elephas trogontherii. The museum collections also contain six fragments of long-horned bison skull and one fragment of skull of a primitive bull (Bos primigenius) which was found in the Stavropol area. Most of the material was collected from beds underlying the loess loams and can be dated Middle Pleistocene.

New materials were collected by Gnilovskii in 1941 on the Kuban-Yegorlyk canal on the western edge of the Stavropol Plateau. The following specimens were collected from a 6-m depth of the first terrace of the Yegorlyk: two fragments of mandible, a lower carpal epiphysis and a heel bone (bitten through by some carnivore) of Paracamelus cf. gigas; fragmentary bones of short-horned bison; and fragments of neck vertebrae, horn, forelimb bones and astragalus of Bison cf. schoetensacki. The bones are chalky in appearance, with light iron oxide stains along the cracks.

The following bones were collected from a 9-m depth in the alluvial bed overlying the Maikop clays in the first Yegorlyk terrace: fragments of upper molars of bulls (Bos sp. or Bison sp.) and an upper molar and first phalanx of a small horse (Equus sp.). The bones, which are iron-stained and not rounded, occur on the erosional surface and are probably Lower or Middle Pleistocene.

Ryabinin's (1918) collections from the Udel'naya steppe of the upper Kalaus are of Upper Pleistocene and partly Holocene age. The material was collected from the upper part of the loess loams exposed in the left bank of the Malyi Kiyankul' gulley, at the upper end of the Pervaya Ternovaya gulley, and in the Kalaus stream bed near the opening of the

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* The numerator indicates the number of fragments; the denominator, a possible number of individuals.

Malyi Yankul' gulley. At the Malyi Yankul' locality numerous mammal bones occur at a depth of 2.5 m in the structureless brown, sandy, gypsiferous clay with small, limey concretions. Ryabinin has identified the following forms: "Equus caballus fossilis, Sus scrofa fossilis, Bos taurus fossilis, Saiga tatarica fossilis and a horn similar to those of goitered gazelle (Gazella subgutturosa)." Mesolithic tools (of the Solutrean or Magdalenian cultures," according to Ryabinin) collected at the locality indicate the last part of the Pleistocene or even the transition to the Holocene.

101 Thus, the fauna of the margins of the Stavropol Plateau does not support the hypothesis that mountain mammals of the Caucasus migrated to the plains during the maximum glacial advance. No boreal species have been recorded in the area. Studies of the caves on the southern and western slopes of Mount Strizhament (Vereshchagin and Gromov, 1953b) would contribute to the knowledge of the steppe and forest-steppe complexes of the Stavropol area of the Upper Pleistocene.

Bones of a mammoth have been recorded from gravel quarries near Yessentuki in the region of the Pyatigor'e laccolith on the Kabarda sloping plain (Karpinskii and Dreier, 1904). Eikhwal'd (1850, p. 190) reported finding near Kislovodsk the complete jaws of a primitive form of Equus caballus covered with tuff.

Travertines of the Pyatigor'e area. Travertines were deposited in post-Pliocene Pyatigor'e by mountain springs, which changed course after each mountain-building cycle. Animal remains were shifted and scattered by carnivores over the slopes until they became covered by sediment. Layers of lime-tuff formed on the bones upon contact with water rich in calcium-carbonate.

Travertines were deposited on almost all the laccoliths — Lysaya, Zheleznaya, Zmeika and Beshtau. However, only the travertines of Mount Mashuk have been subjected to paleontological study (Ivanova, 1948; Mirchink, 1936b; Gromov, 1948).

According to Ivanova, there are four stratigraphic complexes of travertines: the first of Pliocene age (see Chapter I), the other three of Pleistocene and Holocene age.

The travertines of the second complex (Mindel and Mindel-Riss age) occur in patches on the northern and eastern slopes. Teeth and jaw fragments of Elephas aff. antiquus have been found in these travertines. The travertines of the third complex cover a larger area to the northeast. These travertines have been correlated with the 55-m Riss and Riss-Würm terrace of the Podkumok, where numerous bones of deer (Cervidae) occur. The fragments of Lepus sp. and Capreolus sp. teeth, collected by Kobutov in the Boichenko quarry, probably come from the travertines of the third complex. The material is Upper Pleistocene in appearance.

The travertines of the fourth (Upper Pleistocene to Recent) complex occur in the first and second terraces on the southern slope of a mountain near Pyatigorsk, which extends to the stream bed of the Podkumok. According to Gromov (1948), the teeth of an advanced type of Equus sp. and of Elephas primigenius found in the gravels and loams of the second (Würm) terrace originally came from the travertines.

The Pleistocene collections in the Pyatigorsk Museum include a sample of dolomitized travertine with a calcitic mold of a horn of a small bison (Bison sp.). Also in the museum is a fragment of the upper jaw of a mammoth with the third milk tooth, collected from quarry No. 1 on the northern slope of Mount Mashuk. The fresh appearance of the bone is very unusual among fossil findings in the south and suggests that the Pyatigor'e mammoth died as recently as the Holocene. The fragment of mammoth upper molar found in the travertines near the Medovyi waterfall in the 102 vicinity of Kislovodsk, the mammoth teeth found in the sands and loams near the village of Kamenskaya, and those found at a 12-m depth in the banks of the Yutsa River are all older in appearance. The museum collections also include two jaws of woolly rhinoceros (Rhinoceros tichorhinus) and six skull fragments of primitive bison. The state of preservation of this material is Upper Pleistocene.

All these fossils from the alluvial and diluvial sands and loams of the sloping Central Ciscaucasian Plain give only a very schematic picture of the ecological assemblages of the mammoth fauna which lived near the mountains. In the Lower Pleistocene the region was undoubtedly a steppe. At the end of the Pleistocene, however, the region became forested, at least in Pyatigor'e as indicated by occurrences of deer and gazelle bones in the travertines of the third complex of Mount Mashuk, and by the occurrences of post-Pliocene "flora." Krasnov has identified 14 species of grasses and trees from the travertines of the Pyatigorsk area — species which are also characteristic of Recent broadleaf forests of the foothills: beech (Fagus sylvatica), filbert (Corylius avellana), white beech (Carpinus betulus), elm (Ulmus campestris), oak (Quercus robur), Norway maple (Acer platanoides) and other forms. The "flora" from Mount Zheleznaya, which is similar in composition, though somewhat later in age, was identified by Palibin (1913) as follows: willow (Salix alba and other species), linden (Tilia cordata), ash (Fraxinus excelsior) and medlar (Mespilus germanica). No boreal elements have been recorded at these Upper Pleistocene or Lower Holocene localities; on the contrary, the southern elements are more abundant in the floras.

Eastern Ciscaucasia

Most of the plain in eastern Ciscaucasia was covered by the Caspian transgression, which accounts for the scarcity of Pleistocene mammals in the sediments of the plain.

The semideserts and steppes in the lower reaches of the Kuma, Terek and Sulak were in the zone of subsidence. The postglacial marine and river sediments of the area are at present below the base of river erosion. As a consequence, the only known fossiliferous localities with Pleistocene mammals are situated farther west on the high terraces along the shores of Pleistocene bays, on the piedmont plain and in the foothills.

The sloping plains of eastern Ciscaucasia are covered by diluvial sediments and the alluvium of the Terek, Sunzha, Sulak and other rivers. The relief of this area is more complex than that of western Ciscaucasia as a result of uplift of the Terek and Sunzha ranges during the Tertiary and erosion and further peneplanation during the Pleistocene. These ridges now separate the Vladikavkaz [Ordzhonikidze] and Sunzha plains from the alluvial plains of the western Caspian region.

As early as 1886, Pohlig mentioned mammoth bones from the Sunzha valley in the Caucasian Museum collection in Tbilisi. Mullaev (1929) described a tooth of Elephas trogontherii from the post-Tertiary beds on the Ursdon River near the village of Karagach in the southwestern corner of the Vladikavkaz Plain. Scapula fragments of E. trogontherii from the 5-m level of the Mozdok sand quarry are in the collections of the
103 Pyatigorsk Museum. Teeth of E. trogontherii of an early type from the Grozny Region are in the collections of the Grozny Museum. All the fossils came primarily from Lower Quaternary alluvial sediments.

Gromov (1948) recorded two skulls of Bison priscus deminutus and a fragment of a Megaceros sp. skull from the first terrace of the Terek near Mozdok. The cranial cavities of the bison skulls were filled with volcanic ash. This fact establishes the time of the fossils as the time of deposition of the volcanic ash which occurs under the gravels of the first terrace and on the face slope of the second Riss terrace on the eastern slope of Mount Mashuk.

It seems possible that, in the last outburst of volcanic activity of the Kazbek and Elbrus in the Upper Pleistocene, animals were sometimes killed and buried in the ash deposited by torrents. Of the fossils from the Kuma valley below Budennovsk, a lower molar of a mammoth is included in the collections of the Pyatigorsk Museum. The Upper Pleistocene fossils are represented by fragments of Sus scrofa ferus mandibles collected by the geologist Plamenevskii in the alluvial sediments of the first (Würm) terrace on the right bank of the Terek above Ordzhonikidze.

Generally speaking, the evolution of landforms and faunal complexes was similar in eastern and western Ciscaucasia. The same large mammals occur in the Lower and Middle Pleistocene — Elephas trongotherii, giant deer, primitive bison and — in the Upper Pleistocene — boar.

Forests were probably well developed in the Upper Pleistocene along the lower northern slopes of the Caucasus, and even in Dagestan. Whitebeam (Sorbus aria) and European hornbeam (Carpinus betulus) have been identified by Palibin (1913) as "post-Tertiary" species from the foothills near Makhachkala. These species also occur in the area at the present time.

Very few fossil mammals are known from the piedmont and inner parts of Dagestan, or from the marine terraces of the western coast of the Caspian Sea, from Sulak to the Apsheron Peninsula. The collections in the museum at Makhachkala contain tooth fragments of Elephas trogontherii of an early type (enamel thickness 2.5-3.0 mm) from the ferruginous gravels of the Manas River. A tooth fragment of a more recent elephant, with features of Elephas primigenius, and the atlas of an elephant from the vicinity of the village of Unty are in the same collections.

Investigations of Paleolithic sites and excavations of caves and sheltered areas in the Apsheron limestone above Makhachkala and inner Dagestan would contribute to a better understanding of the evolution of Middle and Upper Pleistocene fauna in this part of the country.

Western Ciscaucasia

In western Ciscaucasia the Pleistocene mammals occur mainly in cave deposits, kitchen middens and food remains of carnivores.

Other types of deposition are seldom found. Several factors account for this: a lack of sedimentation and a rapid stream-flow which destroyed the bones, a humid climate which induced rapid decay of bone material, and the rapid 104 subsidence of the sea bottom in coastal areas which precluded the formation of deltas.

Some occurrences are known from terraces and from small reed and sphagnum marshes and lakes which still exist in the region of Sochi, Pitsunda, and Ochamchiri. Some of these localities were later uplifted and exposed by river erosion. There are extensive alder and sphagnum marshes along the lower Rion and Supsa (Poti, Kobuleti) in the area of the Colchis depression which is at present rapidly subsiding under the load of river deposits. Without artificial excavation, whatever fossil mammals occur in those beds will remain there for centuries to come, practically inaccessible to study.

The tooth of Elephas primigenius Blum. in the Sochi Museum (mentioned by Gromov, 1948) might have been introduced into the area.

Ryabinin (1937) has described a fragment of the right half of the mandible of a large cat, similar to Felis cf. spelaea, found in 1935 6 km north of Sochi. The mandible was taken from the gravels of the third marine terrace (Karangat) and originally dated Riss-Würm. More recently it was identified as Early Riss (Vardanyants, 1948). Shells of Cardium, Tapes and Mactra occur in the same terrace.

The Black Sea coast of the Caucasus was favored by Paleolithic hunters for its propitious conditions for big-game hunting: numerous narrow valleys and canyons, coastal terraces which carried the free migration of ungulates both from the north and from the south, and many caves inhabited by bears.

The uplift of the spurs of the Bolshoi Range in the Pleistocene saved the cave deposits from river erosion. Paleolithic sites occur along the foothills from Sochi and Tuapse in the north to Kutaisi and Batumi in the south and the east. Paleolithic deposits probably continue along the northern coast of Asia Minor.

Zamyatnin (1937a) has described and mapped 43 Paleolithic localities in Abkhazia. He subdivided the sites into three chronological groups: 1) pre-Mousterian, 2) Mousterian, 3) Upper Paleolithic. Most of the sites, however, are represented by only a few flint tools.

Efimenko and Beregovaya (1941) have listed 15 open sites and 14 cave sites in western Georgia.

Fossil mammals are known only from cave deposits in the gorges of the Khosta, Kudepsta, Mzymta, Tsebel'da, Rion, Kvirila and other smaller rivers.

Caves on the Black Sea coast

In 1936-1938 Zamyatnin (1940) excavated the Navalishinskaya and Akhshtyrskaya caves in the Sochi and Adler area in the Krasnodar Territory.

Navalishinskaya cave is near the village of Navalishino, 12 km
from the sea, on the right bank of the Kudepsta. Two cultural layers were
found in the cave: the upper layer (Upper Paleolithic) with bones of hamster
and redeposited bones of cave bear; the lower layer (Mousterian,
Aurignacian), with bones of elk, goat, hamster, cave bear, wolf, birds
105 and shells of *Anodonta* and *Helix*. According to Zamyatnin, the cave
was merely a seasonal shelter of early man.

The mammals from the cave were identified by Gromov (1948), as shown in Table 8.

TABLE 8. Species and number of bones of mammals from the Navalishinskaya cave

Species	Middle Paleolithic	Upper Paleolithic
Canis lupus	1	—
Ursus spelaeus	165	229
Cricetus cricetus	—	1
Alces alces	—	1
Capra sp.	1	1
Total	167	232

The Shirokopokosskaya cave (which Gromov called Navalishinskaya II) is located near Navalishinskaya I. It contained Upper Paleolithic tools, cave bear bones and a few bones of red deer (Gromov, 1948).

Bones of cave and European brown bear were excavated in 1946 in the Vorontsovskaya cave in the Khosta ravine (collection of the Krasnodar Museum). The state of preservation of the cave bear bones is not uniform: in fresh fracture the mandible bone is brownish and free of organic matter. The radius and femur are dark brown, and show little loss of organic matter; when scraped, they exude an odor of fresh bones. It seems that the cave bear lived in postglacial times.

Akhshtyrskaya cave is located on the right bank of the Mzymta River 100 m above the river bed at the point where the river leaves its narrow canyon, near the village of Akhshtyr, 15 km from Adler (Figure 46), and is, at present, inhabited only by bats (mostly horsehoe bats). The entrance to the cave faces south and a corridor 4.35 m high, 2 m wide and over 100 m long leads to the cave, which was probably much lower in Paleolithic time. In front of the corridor is an overhead ledge and two entrances with two platforms. The eastern platform has been excavated by Zamyatnin (Figure 47). From the west the cave can be approached over a narrow, easily defended trail on the cliff. Zamyatnin assumed that it was intermittently inhabited by man over several millennia. Because of the elevation of the platform dwelling site, the inhabitants probably threw away most the bones and tools into the river. In the intervals between man's occupancy, bears and bats lived in the cave. Two narrow crevices, which were also inhabited by bears, are located farther west and down the cliff.

According to Gromov (1948) the big cave was formed during the formation of the 60-80 m terrace on the Black Sea coast, which was raised 112 m near the Akhshtyr anticline.

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FIGURE 46. Mzymta gorge below the Akhshtyrskaya cave

Photograph by author, 1954

Two phases can be distinguished in the geological history of the cave. In the first phase two perpendicular faults formed: one, a normal fault, the other, a displacement along the bedding planes of the limestone. These two faults resulted in the formation of the cave which then, in the second phase, was continually enlarged by dissolution of the ceiling. During this period detritus, loam and fragments of stalactites continued to accumulate on the floor.

Gromov assumed that detritus accumulated with cooling of the climate, whereas decomposition of the detritus into loam occurred in a warmer and more humid climate, but the faunal data which follow do not support these assumptions.

Zamyatnin (1940) has identified five cultural layers in the cave from the Middle Paleolithic (Lower and Upper Mousterian) to the Recent. He correlated the Lower Mousterian of the Akhshtyrskaya cave with the beds at the Il'skaya site in Ciscaucasia and with the Kiik-Koba cave in the Crimea.

The excavations produced over 3,000 identifiable fragments of bones, mostly from the Middle Paleolithic layers. The material includes bats, carnivores, rodents, ungulates and birds.

Remains of large animals, fragments of epiphyses and diaphyses, are typical food remains. Bat bones and excreta have accumulated in the cave into present time. Eagle owls probably carried in the hamster bones which were found in the cave.

Most of the cave bear bones are metapodia, phalanges, isolated teeth and 107 fragments of limb bones. Exploratory excavations in the sheltered section of the cave produced complete bones: femora, tibiae, fibulae, humeri, radii, ulnae, and skull fragments of bears which probably died of natural causes.

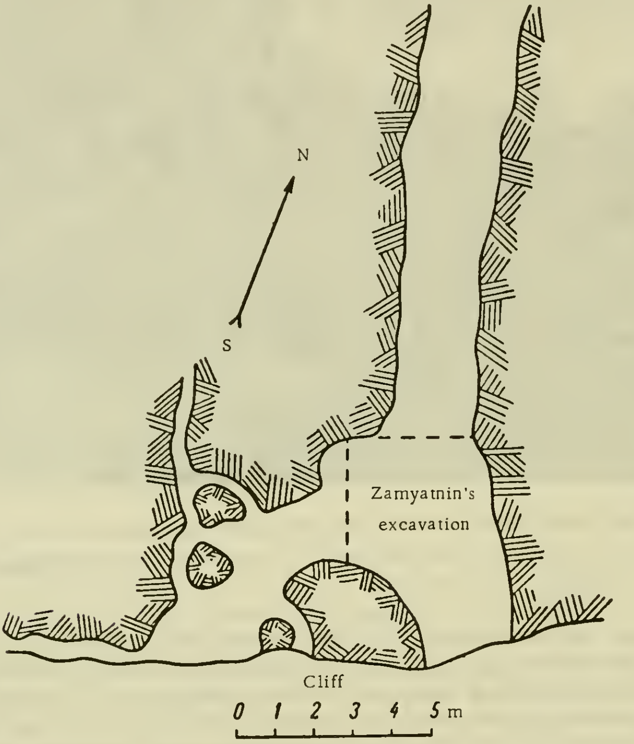

FIGURE 47. Diagram of the frontal part of the Akhshtyrskaya cave

The matrix on the bones of Mousterian and Upper Paleolithic specimens is indistinguishable to the eye, but specimens in varying states of preservation occur within the same bed. The bones are pinkish yellow to light brown in color. The enamel of the teeth is either the natural color or darker with black cracks, and the roots are yellow, brick or brown. The Mousterian bones are darker, with some surfaces spotted with dendrites; numerous dendrites may have coalesced resulting in a dark brown color over the entire bone. In fracture, the bones are usually light beige. They are light in weight and free of permineralization.

The composition of the mammalian fauna of the cave is given in Table 9 and Figure 48 (author's identification).*

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* Our count of bones and individuals in the ZIN collections differs somewhat from Gromova's: bones from the Lower and Upper Mousterian were combined, since there is no noticeable difference in the composition, number and type of preservation.

108 A cervical vertebra of an eagle was found in the Mousterian beds. Bones of the goshawk Astur gentilis L., of the magpie Pica pica L. and of small sparrows (Passeriformes) were collected from the Upper Paleolithic beds.

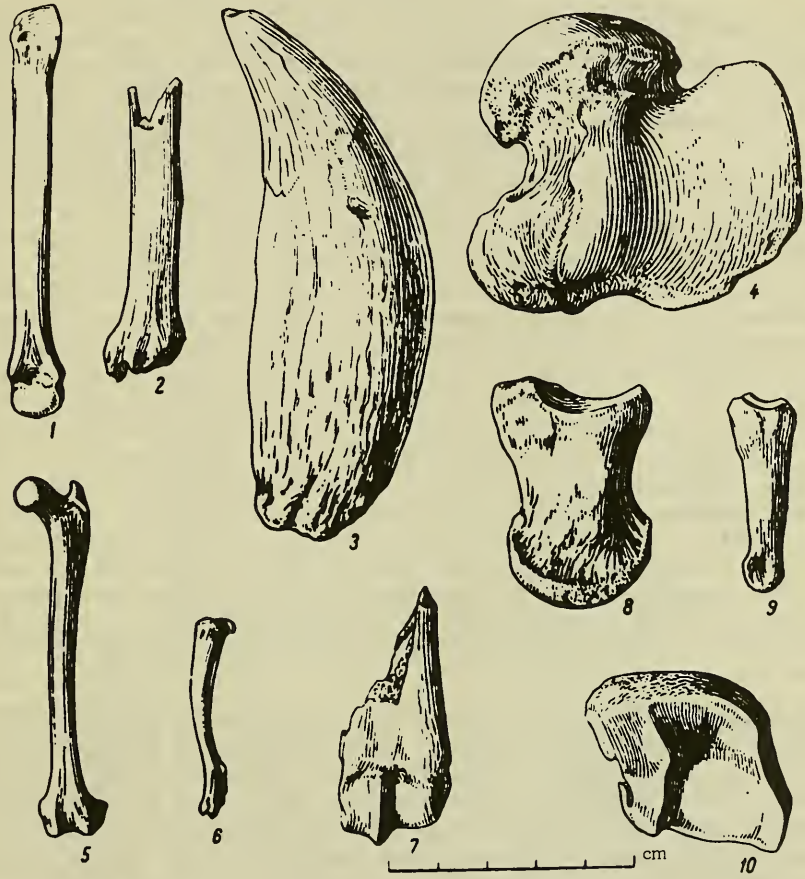

FIGURE 48. Mammal remains from the Mousterian beds of the Akhshtyrskaya cave

1 — metacarpal of Canis lupus; 2 — shank of Vulpes vulpes; 3, 4 — canine and astragalus of Ursus spelaeus; 5 — femur of Martes sp.; 6 — shank of Cricetus cricetus; 7 — carpal of Sus scrofa; 8 — second phalange of Cervus elaphus; 9 — first phalange of Capreolus capreolus; 10 — carpal of Alces alces

The number of bones in the Upper Paleolithic beds is much smaller than in the Mousterian beds. The smallest possible number of cave bears is 39, as estimated by the number of phalanges. This was evidently a species easy to hunt in the canyons where it lived. The European brown bear is represented only by a molar from the Upper Paleolithic.

Next in descending order of quantity are mountain goat, deer and boar.

Remains of mountain and rock ungulates are fairly rare: the evidence of mountain goat has been mentioned, but there is no evidence of chamois.

109 The Upper Paleolithic shows a slight increase in the number of boars, which may indicate not only an increase in species population in the vicinity of the cave, but also the gradual extinction of the cave bear, which forced the hunters to look for other game.*

TABLE 9. Mammals from the Akhshtyrskaya cave

Species	Middle Paleolithic		Upper Paleolithic		Total individuals
	number of bones	number of individuals	number of bones	number of individuals	
Rhinolophus ferrum-equinum	—	—	1	1	1
Vulpes vulpes	9	1	3	1	2
Canis lupus	9	1	—	—	1
Ursus arctos	—	—	1	1	1
U. spelaeus	2,946	32	543	7	39
Martes cf. foina	1	1	1	1	2
Felis cf. silvestris	1	1	2	1	2
Cricetus cricetus	1	1	—	—	1
Sus scrofa	2	1	7	3	4
Alces alces	—	—	3	1	1
Cervus elaphus	18	3	4	1	4
Megaceros euryceros	2	1	—	—	1
Capreolus capreolus	—	—	2	1	1
Bison priscus	9	2	—	—	2
Capra caucasica	6	2	9	4	6
Total	3,004		576		68

The absence of wild sheep in the Upper Pleistocene of the Black Sea coast supports the notion that forests and mesophilous vegetation covered the area, as inferred from the composition of the Akhshtyrskaya "fauna."

It seems unusual that bison and giant deer bones were found only in Mousterian beds, since the bison has survived in this region to the present. Elk and gazelle appear only in the Upper Paleolithic beds, though these species existed in the Caucasus at least from the time of the Lower Pleistocene. Gromov's (1948, p. 262) theories of climatic changes which he predicated on the presence or absence of these species are, therefore, untenable. The number of specimens of ungulates and carnivores (except for the cave bear) is too small to furnish a basis for sound conclusions on faunal and climatic changes.

The paleogeographic study of the animals from the Akhshtyrskaya cave must include the ecology of the species and the hunting traditions of the primitive tribes.

The highly diversified terrain and the forests of the Black Sea coast were not suitable ground for mammoths, horses, giant deer, saigas,

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* Gromova (1948) has identified a lower metatarsal epiphysis and the second phalanx of a ram as the small, wild "Ovis cf. ophion." Further examination shows that the bones are contemporary Holocene in appearance and their identification as Mousterian is incorrect; they are probably bones of a domestic sheep which fell into the excavation from post-Paleolithic beds.

110 primitive bison and steppe bison. The species occurring near the dwelling site were hunted for food.

The topography of the Black Sea coast in the Pleistocene was such that the vertical zonation of the vegetation remained stable, despite climatic changes. This accounts for the homogeneity of the fauna in the Akhshtyrskaya cave throughout the Middle and Upper Paleolithic.

The assemblages of mammals from the Navalishinskaya and Akhshtyrskaya caves are not universal. Nevertheless, they clearly indicate the existence in the western Caucasus of a boundary between the distribution areas of the steppe and forest-steppe species of the Russian Plain. Only the eurytopic hamsters crossed this barrier. No northern species are recorded from the western Caucasus and the northwestern foothills; nor were there any southern elements from the dry upland steppes of Asia Minor.

Farther south along the Black Sea coast, Pleistocene mammals occur in the caves near Sukhumi (Krongel'm, 1873). They were recently discovered in the Ablaskira cave and in the grottoes in the Tsebel'da canyon.

Ablaskira cave is located on the western slope of one of the spurs of the Panavskii (Kodor) ridge, 2 km northeast of the village of Otak and 35 km from Ochamchiri. The Achkhitizgo River flows out of the cave entrance at an elevation of 265 m above sea level.

Paleolithic remains occur in wall niches not far from the entrance. The cave has been described by Satunin (1910) and Maruashvili (1938b).

Seventy-five fragments of bones of two adult cave bears and one young were collected in the cave by Sadovskii in 1946. The bones were collected in the section 50-400 m from the entrance in the clay and gravel of the stream. The material consisted of tibiae, humeri, metapodia, phalanges and a nearly complete cranium of a very short-snouted adult specimen. Like the animals found in the deeper part of the Akhshtyrskaya cave, these died from natural or accidental causes, rather than at the hand of man. In fracture, the bones are chalky white; they disintegrate easily under pressure, are not permineralized and their surface is free of dendrites. There are no data on the conditions of bone accumulation, the time of deposition of the clays on the cave floor or the time of human settlement in the cave.

The grottos near the village of Tsebel'dinskoe in the Tsebel'da ravine were surveyed by the archaeologist Solov'ev in 1941. Paleolithic tools and bones collected in the Kholodnyi grotto and in Kei-Bogaz are now housed in the ZIN. The animal fossil material consists of fragments of teeth and of tubular and plate bones, which were transported partly by Paleolithic hunters and partly by eagle owls. Identification of the species in the collection is given in Table 10 and Figure 49.

The state of preservation suggests that most of the bones are of Upper Pleistocene age; only a small part of the collection (the rodent bones in particular) may be of Holocene age. The bones represent the local faunal complex of mountains and forests. The southern limit of the common hamster is in the area of these southern caves.

111 Caves of Imeretia

The northeastern part of the Colchis Plain is a low plateau composed of limestones overlain by Oligocene sands and silts. The tributaries of

TABLE 10. Mammals from the Paleolithic sites at the Kholodnyi grotto and Kei-Bogaz

Species	Number of bones	Species	Number of bones
Ursus spelaeus	3	Sus scrofa	75
U. arctos	1	Cervus elaphus	60
Martes sp.	6	Capra caucasica	58
Felis silvestris	1	Bison priscus	8
Arvicola terrestris	2	Total	234
Cricetus cricetus	20		

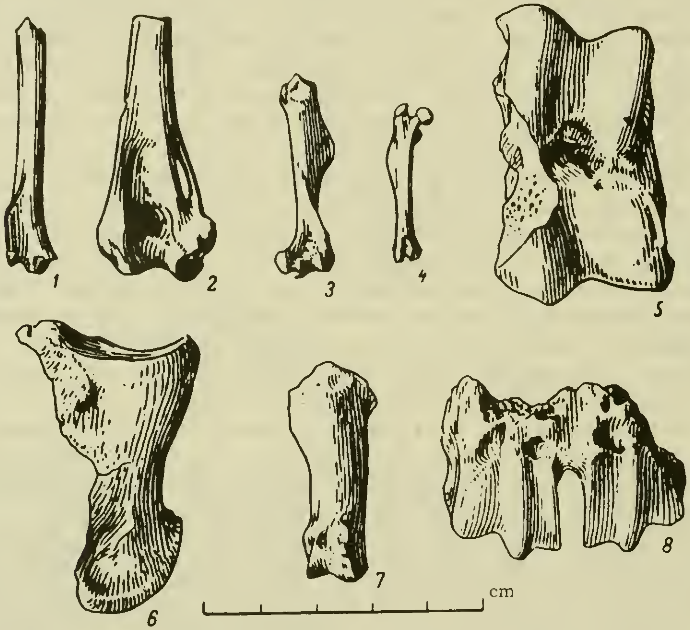

FIGURE 49. Mammal remains from the Kei-Bogaz grotto

1 — humerus of Martes sp.; 2 — humerus of Felis silvestris; 3 — humerus of Cricetus cricetus; 4 — femur of Arvicola terrestris; 5 — astragalus of Sus scrofa; 6 — second phlanx of Cervus elaphus; 7 — first phalanx of Rupicapra rupicapra; 8 — epiphysis of metacarpal of Capra caucasica

the Rion cut canyons 50-60 m deep through the plateau. Over several millennia numerous caves (dated Upper Paleolithic) were formed in the walls of these canyons, and were inhabited by prehistoric hunters, cave bears and eagle owls.

112 The first discoveries of the Paleolithic in western Transcaucasia were made in the first half of the last century. The Swiss Favre collected stone tools in 1863 from "Jason's Grotto" in the Sakazhia cave near Kutaisi (Zamyatnin, 1957).

FIGURE 50. Entrance to the Sakazhia cave

Photograph by author, 1954

Burnt and split bones were collected by the engineer Bernatskii (1884) in one of the caves near the village of Rgani in the Chiaturi area. Some of the bones were sent to Rudolf Virchow in Berlin, and some were left in Tbilisi, where they were studied by Anuchin (1887). Bernatskii's collection consisted mostly of bones of cave bear.

Zamyatnin has dated all the Imeretian cave sites investigated thus far as Upper Paleolithic. The earliest sites were uncovered by Krukovskii in the Chiaturi area: the Khergulis cave near the village of Vachevi and the overhang, Taro-Klde, near the village of Shukruti. The "3rd layer" in the Khergulis cave contained Mousterian and Upper Paleolithic flint tools, and split bones and teeth of cave bear (Ursus spelaeus), horse (Equus caballus), Caucasian goat (Capra cf. caucasica) and bison (Bison cf. priscus).

Krukovskii's exploratory excavation at the Taro cave produced Upper Paleolithic cutting tools, Mousterian points, teeth of cave bear, bones of

Asia Minor hamster (*Mesocricetus* aff. *auratus*) and teeth and split bones of Caucasian goat and bison.*

According to Zamyatnin, the middle group of the Paleolithic sites includes the following caves: Sakazhia, Uvarovo, Bnele, and Devis-Khvreli. The Sagvardzhile cave on the Dzevrul rivulet belongs to the same group, although only preliminary data have so far been published on the many cultural layers of this cave (Kiladze, 1953; Gzelishvili, 1953).

Sakazhia cave is on the left wall of the ravine of the Tskhali-Tsiteli rivulet (the right tributary of the Kvirila), near the Motsameti Monastery,
113 3 km from Kutaisi. The cave, which was formed near the surface of the
faulted limestone plateau, is now approximately 300 m above sea level and 50 m above the present stream bed. The arched entrance is 5 m high, broadening at the top, and leading into a corridor which turns left (Figures 50, 51).

Even though few of the earlier boxtrees and hornbeams remain, the setting of the cave against the cascading river and fallen rocks is still very picturesque. The cave dwellers could hunt their game on the marsh plain of the Rion and in the nearby mountains.

Indications are that these caves were not inhabited by eagle owls or bears, except possibly, in the latter case, for very brief periods.

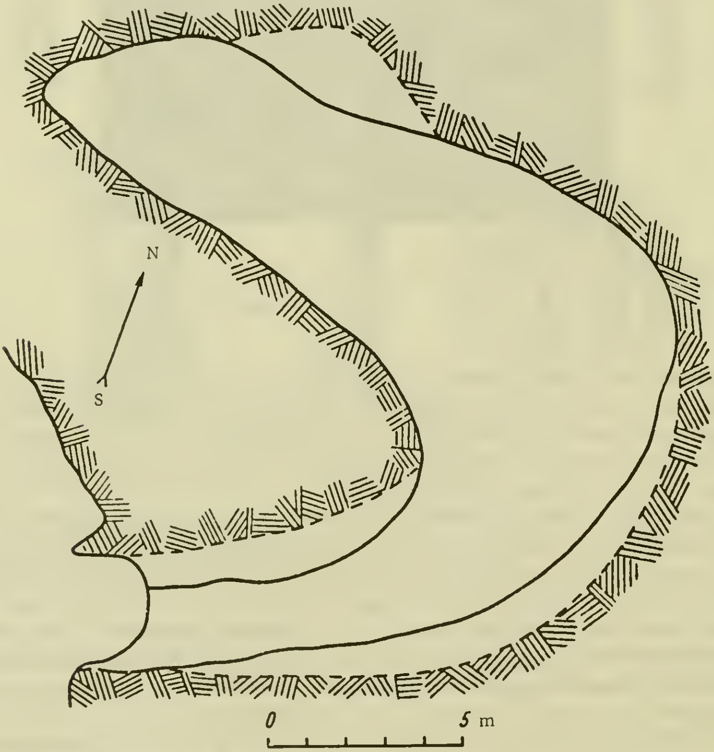

FIGURE 51. Diagram of the Sakazhia cave

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* The bones have been identified by the author from drawings by S.N. Zamyatnin.

The Sakazhia deposits are 2 m thick. The cave was excavated in 1914 by Shmidt and Kozlovskii who dug in the straight corridor, and in 1936 by G.K. Nioradze. In 1954 the author collected some bones and flint tools at the far end of the cave where some deposits still remain.

The several thousand flint tools and fragments, which include many cutting edges and knifelike tools (Figure 52), establish the age of the culture as Solutrean (Nioradze, 1953; Zamyatnin, 1957). The collection includes many points and arrowheads made of the diaphyses of horse and bison
114 metapodia. It seems strange that the dating of the thick cultural layer is

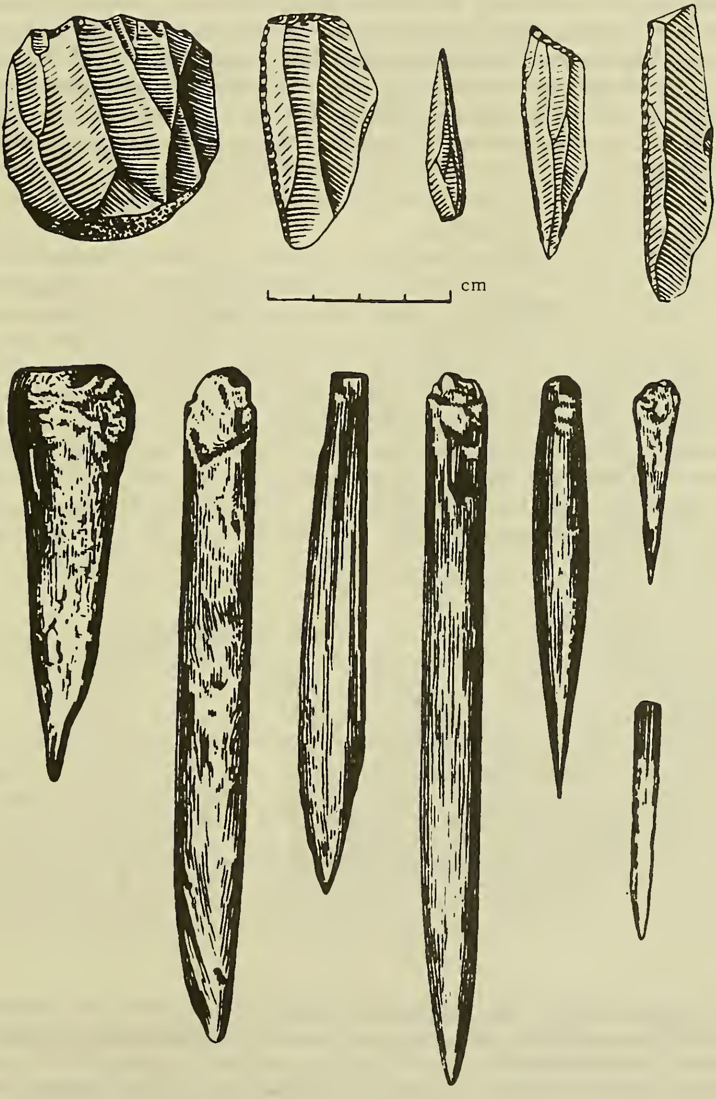

FIGURE 52. Sakazhia cave flint tools (from Zamyatnin, 1957) and bone tools (from Nioradze, 1953)

so narrow, since the cave was undoubtedly used as a habitation into post-Solutrean time. Bones of domestic animals which occur in the collection are probably derived from the upper layers.

Upper Paleolithic food remains are represented by teeth, phalanges, jaw fragments and epiphyses and diaphyses of skeletal bones. There are 115 472 specimens in Shmidt's collection, 130 in the author's and over 16,000 in Nioradze's. *

Most of the bones, however, were not identifiable, because they were split into fragments. Single bones (heel bone and radius of Felis spelaea) bear the tooth impressions of large carnivores. The enveloping matrix suggests Upper Pleistocene age. The fragments are mostly gray with a slight yellow, free of dendrites and fossilized, but not permineralized The tooth enamel is a natural color with only occasional darkening. The canines of a European brown bear appear to be younger — of Holocene age.

Belyaeva (1940c) and Gromov (1948) published lists of 18 species identified from a few teeth and phalanges in the Nioradze collection. The results of the author's studies of both collections are given in Table 11.

TABLE 11. Mammals from Sakazhia cave

Species	Number of bones	Number of individuals
Vulpes vulpes	5	2
Canis lupus	13	3
Ursus spelaeus	35	5
U. arctos	11	3
Panthera spelaea	12	3
Felis cf. lynx	1	1
Martes cf. foina	3	1
Meles meles	2	1
Chionomys roberti	1	1
Castor fiber**	1	1
Hystrix cf. hirsutirostris	1	1
Equus caballus	102	8
E. hidruntinus**	1	1
Sus scrofa	75	7
Cervus elaphus	140	10
Capreolus capreolus	6	2
Alces alces	5	1
Bison priscus	1,488	32
Capra caucasica †	166	25
Rupicapra rupicapra	8	2
Total	2,076	110

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* Shmidt's collection is kept in Odessa, Nioradze's in Tbilisi.

** The data on occurrences of these two species are taken from Gromov and Belyaeva, since they do not appear in any available collections.

† In this and the following tables of Imeretian deposits, the goat species is represented by the west Caucasian form, rather than the east Caucasian, contrary to erroneous identifications by Gromov (1948) and Gromova (1948).

In addition to the bones listed in the table, ungulates and carnivores of intermediate size (goat, boar, chamois, wolf) are represented by at least 8,800 fragments of diaphyses, and larger animals (bison, deer, 118 horse, cave bear, Panthera spelaea Goldf.) by at least 6,000 fragments. A few fragments of human bone were also found in the cave.

The diversity of the landscape was reflected in a highly variegated species composition: bison, goat, deer, horse, boar and cave bear. Because the cave was advantageously located between mountain and plain, the Sakazhian dwellers were able to hunt boar, elk and beaver on the Rion marsh plain, bison (their chief prey), deer and horse on the Imeretian Plateau, and goat and chamois in the rocks of the Rion ravine.

In the Uvarovo and Baratashvili grottos in the same canyon, Shmidt collected nearly 30 teeth of Caucasian goat, 12 teeth of bison, 12 bone fragments of cave bear, 2 deer teeth, 1 horse tooth, 1 fibular tarsal bone of a wolf, 1 fragment of the pelvis of a beaver and a number of Upper Paleolithic tools. The state of preservation of this material is similar to that of material found in the Sakazhia cave.

The Bnele cave collection consists of a few bone fragments, identified by Smirnov (1923-1924), together with bones from the younger site at the Gvardzhilas cave.

The Devis-Khvreli cave is located 4 km from the Kharagouli station on the right slope of the Chkherimela rivulet ravine in the Cenomanian crystalline limestones. The cave entrance, which faces southwest, lies 340 m above sea level and 80 m above the Chkherimela rivulet bed. In 1926 Nioradze excavated a section of the cave 25 m long, 4.5 m wide and 6.5 m high, which revealed four layers: 1) upper layer, with Recent animals; 2) brown layer, with animal remains; 3) cultural layer; 4) clayey bed. Nioradze (1933) has identified the site as Upper Aurignacian, whereas Zamyatnin dates it Upper Magdalenian. The bone collection consists of food remains and bones in eagle owl pellets. The species, identified by Gromova (1929) and M. V. Pavlova, are listed in Table 12. (The number of bones available to Pavlova is unknown.)

TABLE 12. Mammals from the Devis-Khvreli cave

Species	Number of bones	Species	Number of bones
Canis lupus	?	Capreolus capreolus	2
Ursus spelaeus	?	Alces alces	1
U. aff. arctos	20	Bos or Bison	?
Mesocricetus cf. auratus	?	Capra cf. caucasica	22
Sus scrofa	30	Rupicapra rupicapra	3
Cervus elaphus	1		

As a whole, the fauna resembles the fauna of the Sakazhia cave. The smaller number of species recorded is due to the smaller scale of excavation. It is unusual that no equine bones should have been recorded at a site located in the center of a dry plateau. Near the spurs of the Rachin 119 ridge are sites belonging to intermediate and late faunal complexes which are described below.

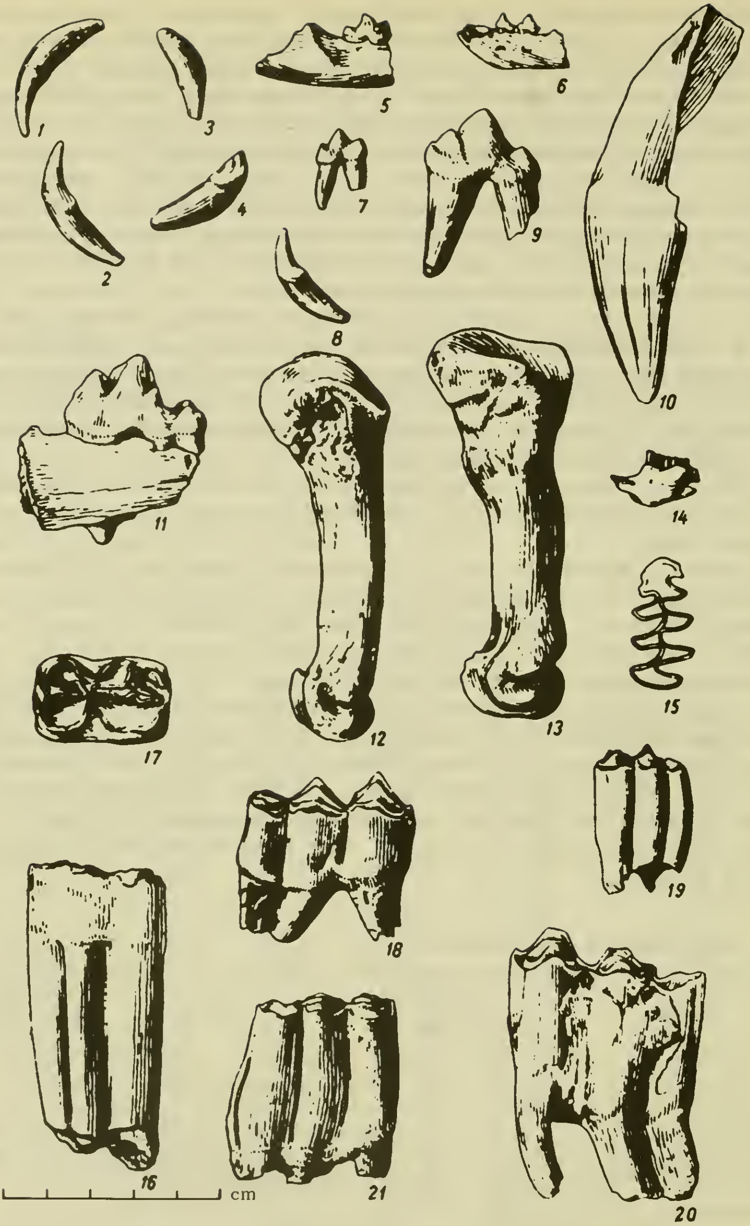

FIGURE 53. Mammal remains from the Sakazhia cave

1, 2 — canines of Vulpes vulpes; 3, 4 — canines of Meles meles; 5, 6 — jaw of Martes sp.; 7 — Pm$_3$ Felis lynx; 8 — canine of Felis silvestris; 9 — Pm$_4$ and 10 — canine of Panthera spelaea; 11 — M$_1$ Canis lupus; 12, 13 — metacarpal and metatarsal of Ursus spelaeus; 14 — jaw (× 2) and 15 — first molar (× 10) of Microtus cf. roberti; 16, 17 — Pm$_3$ and its worn surface from Equus caballus; 18 — M$_3$ Cervus elaphus; 19 — M$_3$ Rupicapra rupicapra; 20 — M$_3$ Capra caucasica; 21 — M$_3$ Bison priscus;

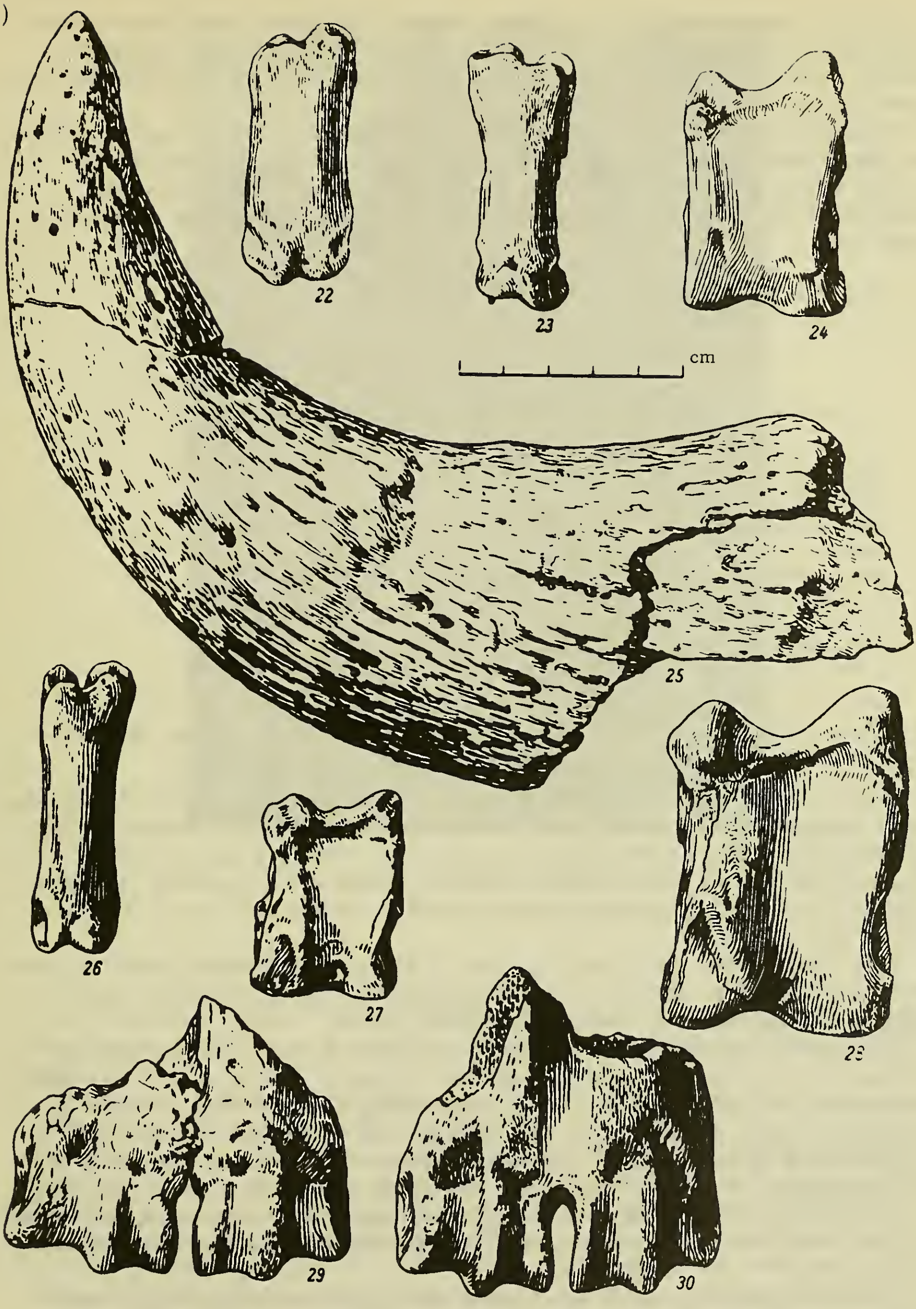

FIGURE 53 (continued)

22 — first phalanx of Sus scrofa; 23, 24 — first phalanx and astragalus of Cervus elaphus; 25, 28-30 — horn, astragalus, metacarpal and metatarsal epiphyses of Bison priscus; 26, 27 — first phalanx and astragalus of Capra caucasica

In 1934 Zamyatnin (1937b) collected Upper Paleolithic tools from beneath limestone overhangs on the right bank of the Kvirila near the village of Mgvimevi in the Chiaturi area. In 1940 Kiladze (1944) continued excavating under one of the overhangs.

The bones from Mgvimevi are highly fragmented and free of organic matrix and permineralization except for a calcitic crust found on some bones.

The bones collected by Zamyatnin and Kiladze were identified by Gromova (1948) and later by the author. The list of species is given in Table 13.

TABLE 13. Mammals from the vicinity of Mgvimevi*

Species	Number of bones	Number of individuals
Canis lupus	3	2
Ursus spelaeus	1	1
Panthera spelaea	1	1
Mesocricetus cf. auratus	3	1
Equus caballus	21	3
Bison priscus	57	4
Capra cf. caucasica	37	
Ovis cf. ammon	3	3
Caprovinae (not identified more precisely)	40	
Total	166	15

* The numbers include material received by the ZIN osteological laboratory after the 1948 publication.

The game animals in order of importance were bison, goat and ram, the latter represented by a noteworthy species of large argali. Horses were also abundant. The presence of cave bear and Panthera spelaea indicates the age as Pleistocene, possibly Topmost Pleistocene. The lack of deer, boar and gazelle specimens is due to the limited scope of the excavation.

The Gvardzhilas cave is one of the Upper Paleolithic sites. It was partly excavated in 1915-1916 by the engineer Krukovskii (1916), and in 1953 by Kalandadze and Tushabramishvili (1955).

The cave is located in the ravine of the Chirula rivulet, the right tributary of the Kvirila, near the village of Rgani. The wide oval entrance faces south; it is located on a small protruding platform nearly halfway up the right wall of the canyon. Several grottos are located somewhat higher on the opposite wall. The length of the cave is 30 m, the width at the entrance is 19.5 m and the height approximately 4 m (Figures 54, 55).

According to Krukovskii, the calcitic ceiling of the cave collapsed three or four times and two ancient cultural layers were buried beneath the fallen rubble.

120 The tools from this cave are mostly cutting and scraping edges made of pink chert. Many bone implements were also collected: points, darts, awls (Figure 56). From the flint tools, the site was dated as Top Paleolithic, Magdalenian-Azillian.

FIGURE 54. Gvardzhilas cave

Photograph by S.N. Zamyatnin, 1926

Krukovskii collected nearly 150 bone fragments and teeth of carnivores, ungulates and rodents; 14 species have been identified by Smirnov (1923-1924).

The collections made by Kalandadze and Tushabramishvili contain over 4,600 bones; the author's contains 78 bones.

All the bones of large animals are typical food remains of Paleolithic hunters: broken epiphyses, diaphyses, skulls and teeth. A small number of bones of insectivores, rodents and birds are derived from eagle owl pellets. The bones appear very fresh with a yellowish beige color
121 and nearly intact organic matrix. Much of the enamel has retained its natural color showing only an occasional rusty tint or darkened crack. When the bones are scraped, they smell of dampness. Many show tooth impressions of field mice. The state of preservation shows that the bones cannot be older than Top Pleistocene and they are more likely to be of Lower Holocene age.

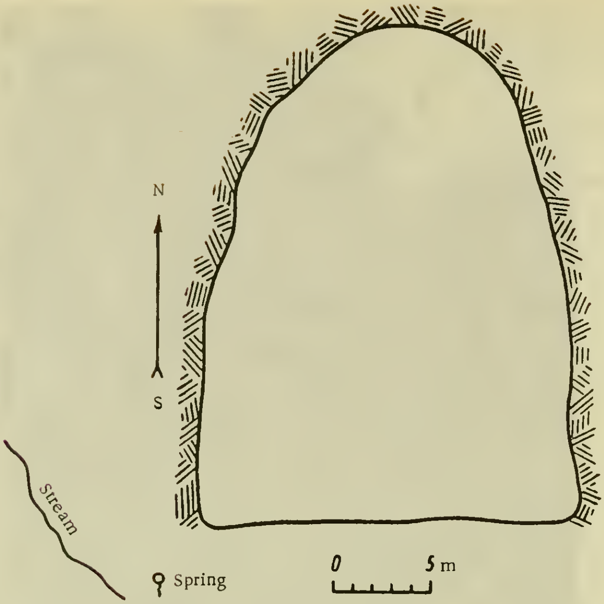

FIGURE 55. Diagram of the Gvardzhilas cave

The list of identified species from all the collections is given in Table 14. The collections from the two layers are combined for purposes of the count, since there are no differences between their species compositions.

Nearly 900 fragments of diaphyses from Tushabramishvili's collection can with difficulty be identified as large ungulates, bison and deer; of which not less than 550 belong to wild goats, chamois and roe deer. In addition, the collection contains 2,970 unidentifiable fragments of small ungulates and carnivores (Figure 57).

The sizable collection of Gvardzhilas cave material clearly indicates a considerable transformation of the ecological composition of regional mammals which occurred there [in the Colchis] at the Pleistocene-Holocene boundary. Horse, sheep and, probably, porcupine vanished from the plateau and, of the southern steppe-plateau forms, only the Asia Minor hamster remained. Since there are no reasons to suppose that the tastes and hunting habits of the primitive tribes changed at this time, it can be assumed that the disappearance of these species resulted from the afforestation of the highland.

Smirnov, Gromov (1948) and Pidoplichko (1951) regarded the Gvardzhilas cave mammals as a stratigraphically and ecologically uniform assemblage. These authors attributed the downward shift of the altitudinal zones to the advancing glaciers of the Greater Caucasus. They cited as support the fact that primitive hunters did not hunt goats and chamois further than a day's march away with a heavy load, i.e., 15-20 km. And they also considered that Prometheomys schaposchnikovi Sat. (a present inhabitant) of alpine meadows) could not have existed in the cave environs in a zone of xerophilous vegetation such as exists there today.

Our observations indicate faulty reasoning on their part. The distribution of game animals, in particular that of Caucasian goat, was wider than at present. And even now, suitable ground for wild goat is to be found in rocks 122 6 km from the cave along the upper Chirula. In April 1954, the author observed one eagle owl which regularly flew each evening from its day shelter below the Gvardzhilas cave to the nearest subalpine meadows and the forests of the Rachin ridge. This owl probably preyed on hamsters in the dry cave environment and hunted Prometheomys in the subalpine meadows and forests.

It is evident that a discussion of the Gvardzhilas cave assemblage need not consider the shift of zones nor the mosaic structure of the landscape; neither should it preclude the possibility of two ecologically different types of animals coexisting in the same landscape zone: the alpine and mesophilous Caucasian goat and Prometheomys and the xerophilous Asia Minor hamster.

The finds of Prometheomys and hamster remains indicate a Pleistocene faunistic connection between the western part of the Greater Caucasus and the Lesser Caucasus along the Imeretian Plateau and the western slope of the Surami Range.

TABLE 14. Mammals from the Gvardzhilas cave

Species	Number of bones	Number of individuals
Talpa aff. caucasica	1	1
Erinaceus aff. europaeus	2	2
Vulpes vulpes	1	1
Canis lupus	6	2
Ursus arctos meridionalis	6	2
U. arctos caucasicus	5	1
U. spelaeus	6	2
Gulo gulo	1	1
Mustela nivalis caucasica	1	1
Mesocricetus aff. auratus	17	8
Prometheomys aff. schaposchnikovi	5	3
Sus scrofa	3	2
Capreolus capreolus	2	1
Cervus elaphus	34	5
Capra cf. caucasica	254	13
Rupicapra rupicapra	1	1
Bison bonasus (caucasicus?)	235	8
Total	580	54

The Upper Pleistocene faunal complex of northeastern Colchis is known by the remains of game animals and eagle owl victims from five cave sites. The complex has some features which are like and some which are unlike the faunal complex of the Black Sea coast. The similarities are in the occurrences of the mountain-forest ungulates and carnivores: wolf, fox, bear, European wildcat, marten, boar, roe deer, deer, elk and bison, and in the complete absence of the indicator species of the Eurasian plains, i.e., mammoth and primitive bull.

As opposed to the Black Sea faunal complex, a number of migrants from the high steppes of southwest Asia are present in the Colchis complex. These include the Asia Minor hamster, porcupine, argali, horse and Equus hidruntinus.

123 These species migrated from the south into western Transcaucasia. Their migration was facilitated by the presence of a karst relief (i.e., dry soil) and, to a lesser degree, by the arid climatic phase which occurred some time in the Middle Pleistocene.

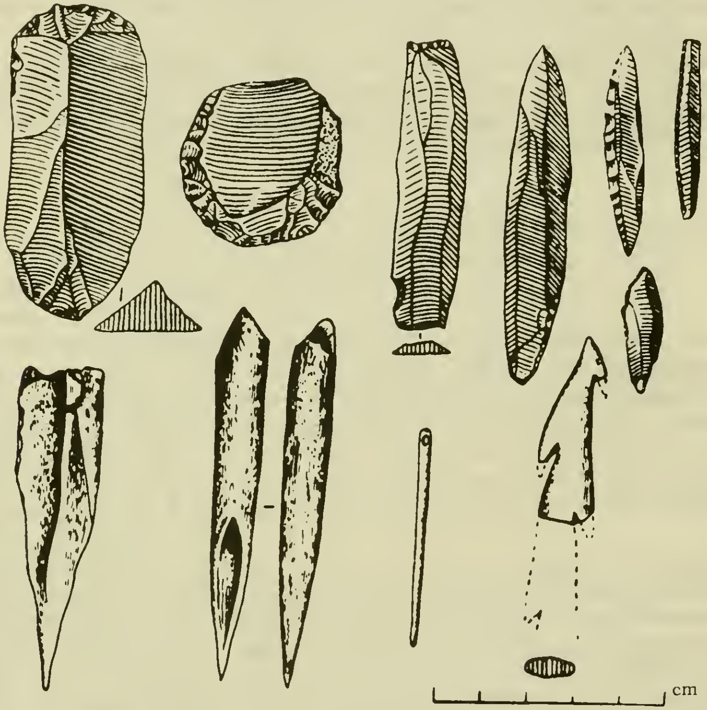

FIGURE 56. Flint and bone tools from the Gvardzhilas cave (from Zamyatnin, 1957)

Forest animals (boar, elk, roe deer) were abundant in the complex, occurring mainly on the marsh plain of Colchis. The European beaver was an ancient relict.

The alpine species of the highlands were much more widely distributed than in present time.

The Kodor and Tsebel'da ravines formed "ecological barriers" for some northern (European) species and for the highland species of southwest Asia. These two faunas converged in Upper Pleistocene time in the region of the barrier.

Thirty species of mammals of Upper Pleistocene age are known from Paleolithic sites and other localities in western Transcaucasia. The species are distributed as follows:

Insectivora	2
Chiroptera	1
Carnivora	13
Lagomorpha	1
Rodentia	7
Perissodactyla	3
Artiodactyla	13

It is significant that mammoth, *Bos primigenius* and northern forms (e.g., reindeer, arctic fox, blue hare) are missing from the complex. 125 And yet there are no warm-climate southern forms in the complex either. The main difference between the western Transcaucasian and the western Ciscaucasian complexes is the presence in the former of forest and mountain species. This indicates that the contemporary fauna and landforms were developed in western Transcaucasia by Middle Pleistocene time.

The transition to the Holocene (postglacial) fauna in western Transcaucasia was probably more abrupt than the changes which occurred during the Middle and Upper Pleistocene. At the end of the Upper Pleistocene the following changes took place in the fauna: the extinction of cave bear, cave cat and cave hyena; the southern retreat of southwest Asian upland xerophilous species (hamster, porcupine, argali); and a decrease among local forest and mountain species (bison, goat, chamois, roe deer). However, the fauna which has survived into the present has preserved the features of a forest fauna.

The climatic change in western Transcaucasia since the Middle Pleistocene probably evolved in different ways than in other regions because of the montane character of the local topography and of regional climatic peculiarities.

The paleogeographic picture we now have will undoubtedly be augmented by further studies of the karst in Imeretia, Abkhazia and the Krasnodar Territory.

A special search for Lower and Upper Pleistocene cave sites must also be undertaken.

Central Transcaucasia

The regions of the Surami water divide, the upper Rion, Bol'shaya Liakhva and the Gori depression are of great interest to paleontologists and zoogeographers as the probable migration route of Neogene and Quaternary mammals from southwest Asia. Pleistocene mammals occur in Paleolithic caves and in diluvial deposits.

In 1952 Lyubin (1953) was the first to find Lower Paleolithic tools in the Bol'shaya Liakhva valley and at Metekhskaya Prona near Dzhidzhoita, Morgo and Lashe-Balta, at an altitude of nearly 1,500 m. The tools from Lashe-Balta (hand axes, flakes, cores) are made of andesite and other quartzitic rocks. All the specimens had been washed out of a high terrace (probably the 60 m terrace) and rounded and redeposited by streams. As in Abkhazia, the bones, which were probably originally deposited in the terraces together with the tools, were not preserved. The value of the paleontological material from the lower layers of the caves is therefore all the greater.

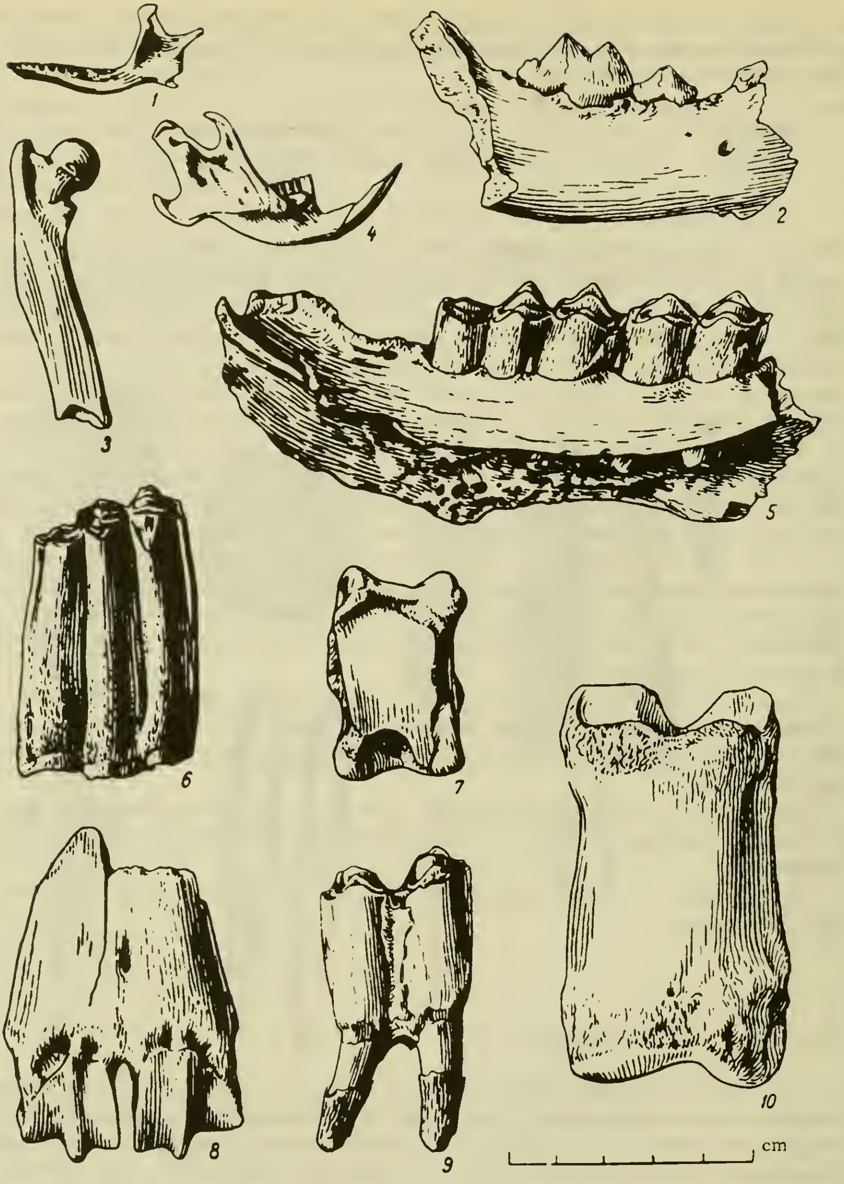

FIGURE 57. Mammal remains from the Gvadzhilas cave

1 — jaw of (×2) *Talpa caucasica*; 2 — jaw of *Gulo* aff. *gulo*; 3 — femur (× 2) of *Mesocricetus auratus*; 4 — jaw of *Prometheomys schaposchnikovi*; 5 — jaw of *Cervus elaphus*; 6-8 — M_3, astragalus and metacarpal of *Capra caucasica*; 9-10 — M_2 and first phalanx of *Bison bonasus*.

Caves of Mount Chasovali-Khokh, Paleolithic and younger beds in caves of the Kudaro region in South Ossetia, were discovered by Lyubin in 1955. The four most important caves were located in the right wall of the Dzhodzhora rivulet ravine above the villages of Kvaisi and Chasovali. The caves are in the dolomite, 1,700 m above sea level and 300 m above the riverbed (Figure 58). Much material was collected from the upper cave, Kudaro I, which is dry and slopes gently to the north from two entrances facing south and east (Figures 59, 60). The excavations in 1955, 1956 and 1957 exposed clay beds, 2.5 m thick, with blocks of limestone. Iron-,
126 Bronze-, Copper- and Neolithic-Age tools and pottery occur in the upper part of the beds. Middle and Lower Paleolithic tools occur in the lower part of the section. The flakes, hand axes and points are made of quartzite and are in part Mousterian and in part Acheulean. All the beds contain bones brought into the cave by men and owls. The Lower Paleolithic bones are mostly devoid of organic matter; they are light brown in color, and have dendritic surfaces. Some bones were rounded like pebbles in a small stream which flowed through the cave in wet seasons. Fragments of limb bones, teeth, phalanges and metapodia of carnivores and ungulates predominate. The material is difficult to identify to the species level.

FIGURE 58. Mount Chasovali-Khokh (caves indicated by arrows)

Photograph by author, 1957

Upper Paleolithic tools and well-preserved bones were found at a depth of 3 m in excavating the clayey-lime beds in front of the entrance to the Kudaro III cave. Table 15 and Figure 61 show the many mammalian species which have been identified from these bones; up to 1958, 40 identifications from the Pleistocene had been made.

Collections from the Paleolithic beds of Kudaro I include: 42 bones of birds, 3 bones of lizards (Lacerta sp.), 43 bones of toads (Bufo sp.), 22 bones of frogs (Rana sp.) and over 30,000 bones of fishes, primarily of Salmonidae.*

The abundance of fish bones in the Lower Paleolithic beds might indicate that the beds were deposited under water, possibly in the paleo-Dzhodzhora River, which might have carried the bodies of animals and abraded the bones.

127 TABLE 15. Paleolithic mammals from Kudaro caves

	Kudaro I Lower and Middle Paleolithic	Kudaro II	Kudaro III Upper Paleolithic
Talpa sp.	1	—	—
Neomys sp.	1	—	—
Chiroptera, not determined below the generic level	27	—	—
Macaca sp.	4	—	—
Canis cf. lupus	27	2	10
Cuon sp.	3	—	—
Vulpes cf. vulpes	33	—	1
Crocuta spelaea	1	—	—
Ursus spelaeus	2,979	45	97
Martes cf. foina	9	—	—
Mustela cf. nivalis	1	—	—
Meles cf. meles	11	—	—
Gulo cf. gulo	11	—	—
Panthera spelaea	3	—	9
P. pardus	9	—	1
Carnivora, not determined below the generic level	18	—	—
Lepus cf. europaeus	12	—	—
Marmota sp.	10	—	—
Hystrix cf. leucura	18	—	—
Allactaga cf. williamsi	2	—	—
Mesocricetus aff. auratus	56	—	—
Microtus aff. majori	16	—	—
M. aff. gud	5	—	—
Prometheomys aff. schaposchnikovi	13	—	—
Muridae, not determined below the generic level	52	—	—
Rhinoceros sp.	6	—	—
Sus scrofa	2	—	—
Cervus cf. elaphus	213	—	20
Capreolus aff. capreolus	36	—	—
Capra cf. caucasica	55	—	11
Ovis cf. ammon	26	—	11
Ovis or Capra, not determined below the generic level	189	—	—
Bison priscus	5	—	—
Small bone fragments of ungulates and carnivores — Artiodactyla-Carnivora	13,013	—	135

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* In a communication on the 1955 excavation (Vereshchagin, 1957b) the intermaxillary bone of a salmon was erroneously identified as a bone of a large lizard.

(128)

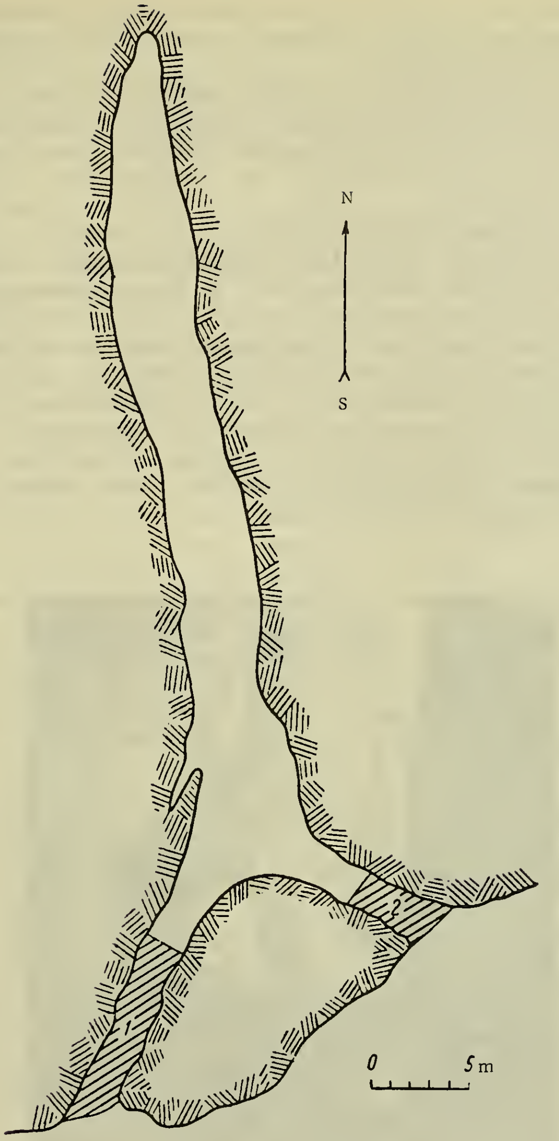

FIGURE 59. Diagram of Kudaro I

1, 2 — excavations of 1955-1958

As a whole, the Kudaro I fauna is indicative of dry plateaus and includes widely distributed forms (wolf, fox, cave bear, badger), Caucasian mountain forms (panther, marmot), and southwest Asian forms (hamster, sheep, porcupine). The indications of the migration of southwest Asian upland-steppe forms to the Caucasian mountains and of the survival of apes through the end of the Pliocene are matters of particular interest. Porcupines, sheep, a few goats and chamois indicate that the relief was quite uniform and the climate warm and dry.

128 Comparison of this site with the Upper Paleolithic sites of Imeretia suggests that mountain goat and other mountain forms existed in isolated areas of Caucasia which were undergoing differential uplift during the Pleistocene. In the Lower Paleolithic the upper reaches of the Rion were uplifted as much as 500 m.

The Upper Pleistocene fauna of central Transcaucasia is represented by single mammoth teeth. One of the teeth of Elephas primigenius from the Dusheti area has been described by Burchak-Abramovich (1946). The tooth of a small mammoth was also found in the town of Gori in the first terrace of the Kura River; according to Gabuniya (1952a), it belongs to an Upper Pleistocene or Lower Holocene mammoth. It is probably of the same age as the late mammoths of the Pyatigor'e area.

The presence of mammoths in the Upper Pleistocene of Transcaucasia is not proof of a migration of "northern" forms to the south, but rather is probably indicative of an endemic evolution of the proboscideans, such as occurred in the western Mediterranean.

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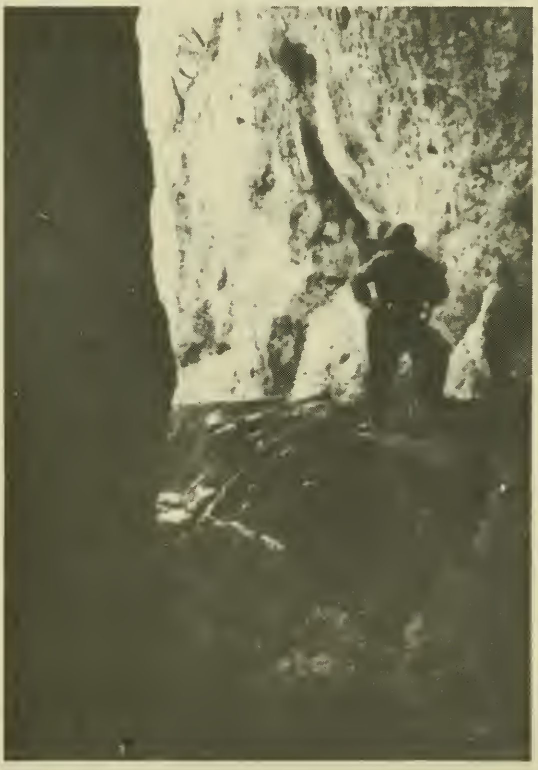

FIGURE 60. Excavations at southern entrance to Kudaro I

Photograph by author, 1956

Eastern Transcaucasia

In post-Tertiary time eastern Transcaucasia was plain country surrounded by mountains in the north, west and south, and the sea in the east.

During the Pleistocene the seas transgressed at least three times over the eastern part of the plain, considerably reducing the living space of the land animals.

129 The known localities of Quaternary mammals are on the marine terraces of the Apsheron Peninsula and on the foothill river terraces in the western part of the plain. Bone accumulations in caves are almost unknown in eastern Transcaucasia.

Lower Pleistocene mammals occur in littoral sediments of the Baku sea on the Apsheron Peninsula. Skull fragments of a young rhinoceros (Rhinoceros cf. mercki), large horse (Equus sp.) and hyena (Crocuta sp.) were collected at a depth of 2 m in coarse, shelly limestone with Didacna rudis Nal. and D. surachanica Andr. near the Kishly railroad station, north of Baku. (The skull of the hyena was previously identified as Hyaena striata (Bogachev, 1925a, 1938b), which is impossible for the Lower Pleistocene.) A fragment of mandible and a tooth of Elasmotherium from the 12-m level in No. 19 oil well near the village of Binagady are in the PIN collections. This material comes from an ancient Caspian terrace with Didacna surachanica Andr. The southern part of the terrace underlies kir* beds which contain the Binagady faunal complex (discussed below).

A lower jaw of a colt (Bogachev, 1938c), identified by Gromova (1949) as Equus aff. süssenbornensis, was collected in oil-bearing gravels of the ancient Caspian terrace which overlies the oil-bearing beds at Khurdalan on the Apsheron Peninsula.

Fossil mammals are more common in Middle and Upper Pleistocene beds than in the Lower Pleistocene. However, their dating is sometimes difficult because of the poor state of stratigraphic knowledge and the discontinuities of the Caspian terraces. Most of the material comes from the Apsheron Peninsula.

The preservation of material in this region was promoted by considerable changes in the relief caused by tectonic, erosional and eolian activity. The ancient, transgressing and regressing Caspian waters in some cases obliterated 131 and in others enhanced the work of the forces operating on the land.

Following the major transgressions of the Caspian, cones of mud volcanos appeared on the Apsheron Peninsula. As a rule, all the deposition sites of post-Baku fossils occur in oxidized oil shows, i.e., bitumens and asphalts.

Many animals died in oil and liquid asphalt which preserved the bodies in a perfect state. The bituminous beds, because of their plasticity, protected the bones from erosion by water and wind.

In most cases, Pleistocene fossiliferous sites were formed through the compound action of freshwater and oil or asphalt seeps on accumulations of mammal remains.

The best known are the Binagady and Kir-Maku fossiliferous localities, although fossil mammals also occur at other places, including: a jaw of a camel (Camelus sp.) found in a ditch at Surakhany; skulls and horns of red deer (Cervus elaphus) collected in the bitumens on Artem Island (Bogachev, 1924, 1932); maxilla of a horse of the "Asian type"

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* Kir, or bitumen, was and still is used in covering and sealing flat roofs.

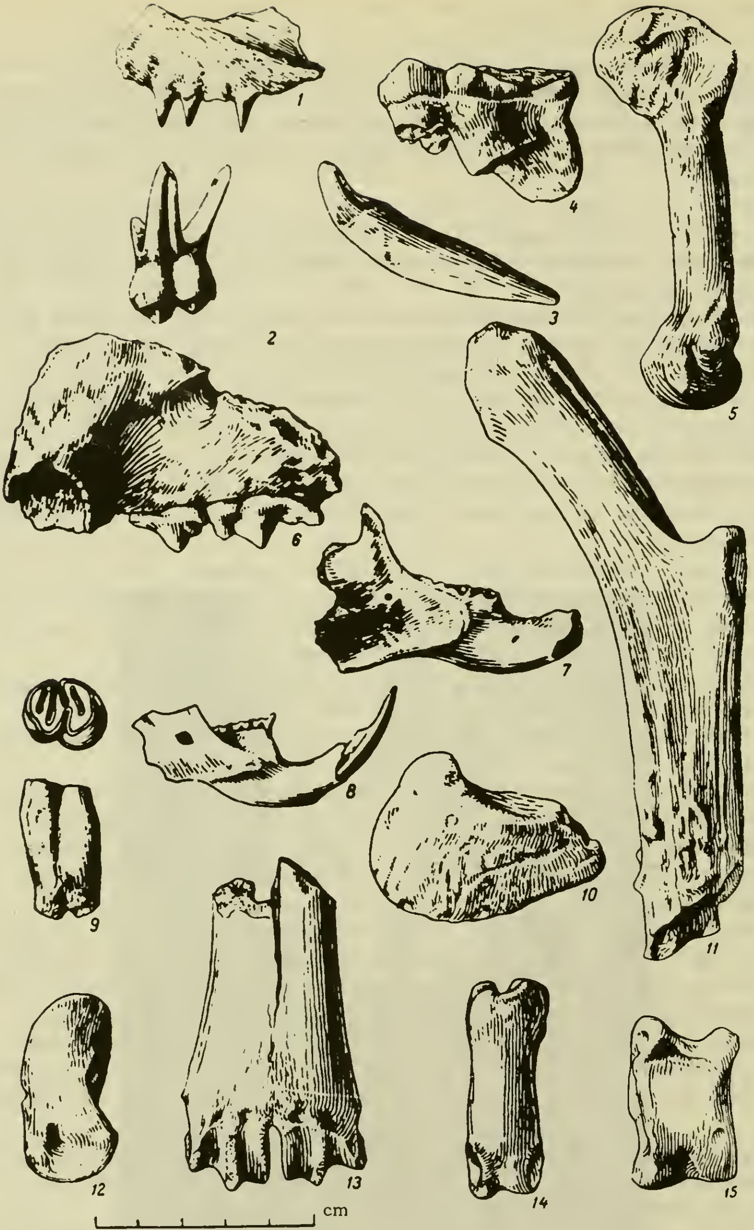

FIGURE 61. Vertebrates from the Paleolithic beds of Kudaro I

1 — intermaxillary (× 2) of salmon Salmo sp.; 2 — M^3 (×2) of Macaca sp.; 3-5 — milk canine (×2), M_2 and metatarsal of Ursus spelaeus; 6 — upper jaw of Panthera pardus; 7 — jaw of Marmota sp.; 8 — jaw (× 2) of Mesocricetus aff. auratus; 9 — side and worn surface of tooth (× 2) of Hystrix sp.; 10 — phalanx of Rhinoceros sp.; 11 — horn of Capreolus cf. capreolus; 12 — first phalanx of Cervus cf. elaphus; 13-15 — metacarpus, first phalanx and astragalus of Ovis cf. ammon

(Equus cf. caballus) found in the clayey breccia of Mount Bog-Boga in Balakhany, 15 km northeast of Baku; bones of a horse known from the ancient Caspian terrace on the Tertiary hills near the village of Ali-Bairamly; remains of one Bos, recorded from the Baba-Zanan Tertiary hills near Sal'yany (Bogachev, 1938c).

Binagady

The Binagady fossils are important in the study of the Quaternary fauna of the Caucasus. The occurrences at that locality of plants, mollusks, insects, reptiles, birds and animals of all ecological and morphological types allows a detailed reconstruction of the ancient Apsheron landscape.

The locality was discovered in 1938 by a student, Mastan-Zade, who was studying the Apsheron bitumens. The first excavations were organized by Bogachev in 1938 (Azerbaidzhan branch of the Academy of Sciences of the U.S.S.R.). The excavations continued until 1941 with the participation of Kasabova and Sultanov and were resumed in 1946 under the supervision of Burchak-Abramovich.

The primitive mining of kir over many centuries left holes and pits of various sizes in the bone-bearing area (Figure 62) which seriously interfered with the excavations.

In order to obtain a clear stratigraphic picture the locality must be excavated in a series of mutually perpendicular trenches.

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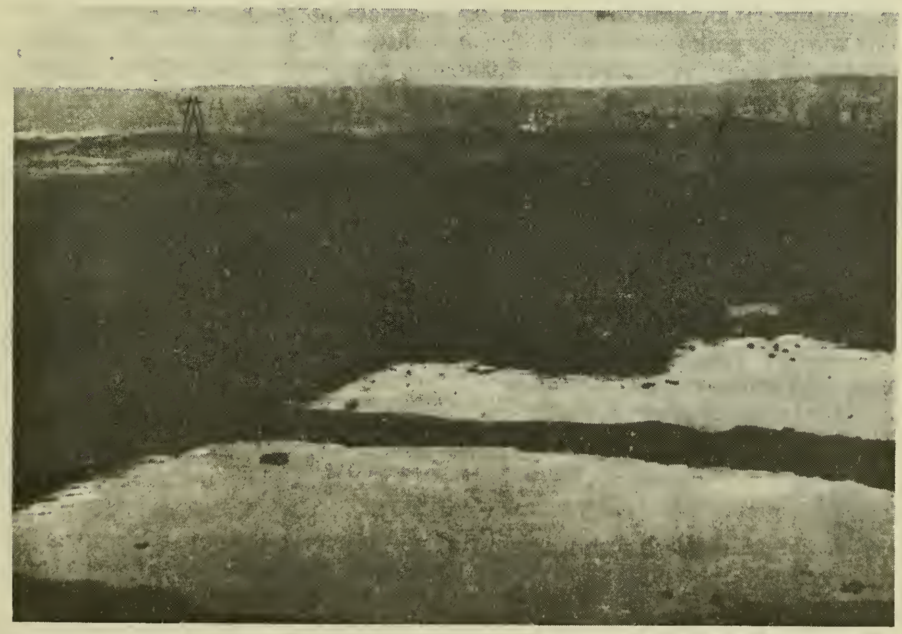

FIGURE 62. Binagady hollow remaining from bitumen-mining in area where rhinoceros bones were found

Photograph by author, 1941

The Binagady locality is on the crest of a hill 0.5 km southeast of the village of Binagady, and 7 km north of Baku. The coast at its closest is 10 km to the south and 25 km to the north.

132 The bone-bearing area comprises approximately $1\frac{1}{2}$ hectares and is located on a hilltop near the Kyrrar hill. The area is 54-57 m above present sea level, and 48 m above the level of Lake Beyuk-Shor. An ancient mud volcano (Kichik-Dag) lies north of the fossiliferous area; further to the north is the meridionally elongated, saline Lake Masazyrskoe (Mirdalyabi) and to the northeast, Lake Binagady. To the east is the saline depression Kariatakh-Shor, beyond which rises the Balakhany Plateau. Extending from the Binagady hill are oil-bearing salinas and the saline Lake Beyuk-Shor, which stretches far to the southeast (Figure 63).

According to the Volarovich-Lednev map (1913-1929) and Bogachev's description (1940b), the base of the Binagady hill is a broad, anticlinal fold made up of Maikop (Oligocene) and diatomaceous (Miocene) clays and of productive sandstones (Middle Pliocene). South of the hill is the Middle Quaternary Caspian terrace. An eroded cone of the mud volcano Beyuk-Dag, 105 m above sea level, is of Pleistocene age. The volcano probably formed on the northeastern part of the Miocene fold in two stages. The loessial sands at its base are dated Q_2^{ls} (Riss-Würm) and at its top Q_2^{b} (Early Würm).

The crest of the fold was eroded by waves of the transgressing sea. As a result of erosion the oil from the productive beds seeped into the
133 coquinas of the ancient Caspian terrace and into the later Quaternary beds. The pressure within the productive beds resulted in oil and asphalt seeps at the surface of the fold and subsequent cementation of the overlying sediments by asphalt. Consequently, a series of fossiliferous asphalt layers of varying ages appears in the syncline. The most recent asphalt seep occurs on the southeastern slope of the hill; it probably formed during oil formation in the last two centuries.

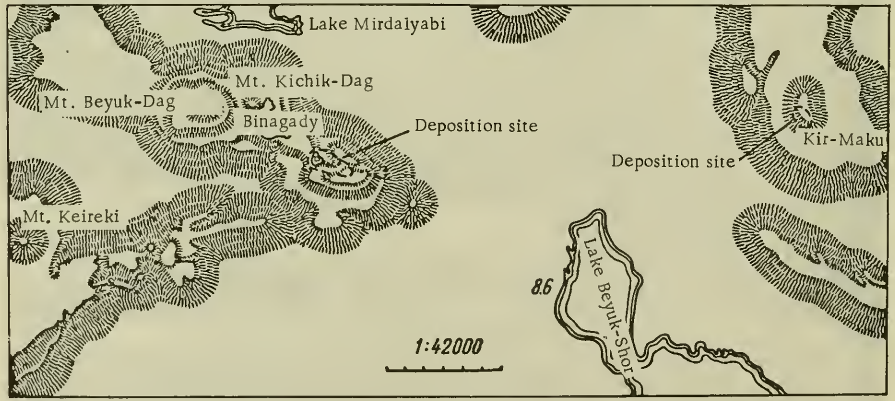

FIGURE 63. Present topography of the bone-bearing localities at Binagady and Kir-Maku

The bituminous area extends to the ancient Caspian "Khasar" terrace in the south. The following fossils are characteristic of this terrace: Dreissensia polymorpha Pall., Didacna surachanica Andr.,

D. kovalevskii V. Bog., Neritina pallasii Lindh. It is possible that the lower part of the bone-bearing beds correlates with the near-shore coquina of the Khazar terrace. The terrace slopes gently downward to the south, an indication of tectonic movements in post-Khazar time. It does not extend beyond the northern slope, which, in Khazar time, was probably dry land which was later subjected to strong erosion. If, as agreed upon by many geologists, the landscape of the area at the time when the bone-bearing beds were being formed was similar to the Recent landscape, it follows that during the marine transgressions the area became an archipelago of small islands and peninsulas.

The present-day relief of the Apsheron Peninsula was formed through the interaction of tectonic forces and eolian and subaqueous erosion (M. Mirchink, 1934). The incidence of shallow, elongated salt lakes in the area is a result of wind erosion. Even the deep Yasamal'skaya valley, extending from Binagady to the sea, was probably formed by wind erosion. The Apsheron limestones which cover the Tertiary loams in places were evidently not sufficient to protect the loams from erosion by northerly winds. The Upper Pleistocene and Holocene produced tectonic and epeirogenic movements which were responsible for much important change in the relief of the Apsheron Peninsula.

134 According to Shlepnev (1947), the epeirogenic movements in the Apsheron over a mere 16-year period (1912-1928) resulted in differences in elevation between various points as great as 114 cm. Thus the present-day relief in the Binagady area cannot be used as a starting point in the restoration of the relief at the time of bone deposition.

A generalized stratigraphic section from the center of the bone-bearing area is given in Figure 64. Surface layer A is diluvium, 0.2 to 1.0 m thick, underlain by bed B, which is 0.75 to 1.4 m thick and contains fine-grained sand with fairly coarse coquina of marine mollusks, impregnated with oil. The southern portion contains large trunks and branches of juniper and occasional bones of horses, deer and large birds. Bed C consists of dense, viscous, dark brown bitumen, 0.1 to 0.5 m thick, which seems to form a lens toward the margins of the bone-bearing area. Pockets near the top of the bitumen bed contain bones of birds (mainly ducks), beetles and grasses. Bones of large animals are embedded in the bitumen of bed C, and occasionally at the boundary of beds B and C.

Bed D is fine-grained sand with fine coquina and some small pebbles; it measures 0.3 to 0.6 m in thickness. Horizontal bedding, produced by streams, and films of narrow, swamp-plant leaves occur in this bed, which is the main bone-bearing bed. It contains bones of mammals, birds and reptiles, as well as insects, mollusks and plants.

The granulometric analysis of beds B and C shows that the fine-grained material amounts to 62.5 and 75.4%. This probably indicates the littoral eolian origin of the Binagady beds (Vereshchagin, 1951b).

Fossil animals and plants occur in pockets in the oil-impregnated sand which underlies the bitumen bed. These pockets are more heavily impregnated with bitumen than the surrounding rock.

The osseous strata 3 m from the surface gradually grades into the fine-grained sands of the productive beds, which are slightly impregnated with oil. A bitumen bed, 10-15 cm thick, can be seen in the holes dug at
135 the highest point of the hill. This bed, 0.8-0.1 [?0.8-1.0] m from the

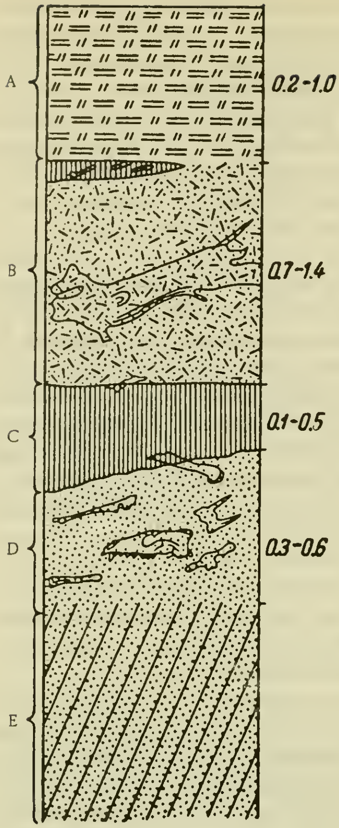

FIGURE 64. Section through the asphalt beds at Binagady

A — surface loams; B — bituminous sands with coquina, bones and wood; C — bed of "rich" asphalt; D — oil-impregnated sands with animal and plant remains; E — sands of productive beds. On the right — thickness in meters

surface in Holocene loams, was probably formed during a recent phase in the migration of oil. It is rich in bones of small birds.

The origin of deposition of the beds shown in the section is not entirely clear. Bed B was probably formed along the shore of a body of standing water, as indicated by the coarse coquina of marine shells composed of fragments 2-5 m in diameter. Bed C was probably formed as a result of migration of oil along a fault in the productive beds somewhat to the north of the Pleistocene bituminous lense.

Mastan-Zade (1939) has hypothesized that an oil flow occurred during the eruption of the Kichik-Dag volcano.

It is obvious that bituminization (oxidation and thickening of oil) occurred at the surface. This being the case, bed B must have been formed during a transgression in the basin which covered the bituminous lens, since the bituminization could not have occurred under water or else the oil floating to the surface would have been dispersed by wind.

Bed D was probably formed in a short-lived body of stagnant water. It is difficult to detect the boundary between the osseous bed and the productive sands, because it is not clearly defined. The negligible percentage (0.2-1 %) of shell fragments, 2.0-3.5 mm in diameter, indicates littoral marine or estuarine deposits, in addition to windblown, fine-grained sand.

The incidence of xerophilous grasses, small tree branches and detritus mixed with animal bones and fossil beetles indicates that the material was deposited in topographic depressions from small mud-oil flows. Individual bird bones, remains of insects and plants, skulls of animals filled with bituminous material — all these indicate poor sorting of the kind that occurs in a river flow. The likelihood is that the remains accumulated in a stagnant basin where the bones were only slightly moved over the substrate.

With the exception of individual skeletons of small birds (dove-size or smaller) all the skeletons at the site are disjointed. Remains of ligaments and feathers occur only on the bones of birds from the younger beds, e.g., the bituminous intercalation in bed B. No complete skeletons of large animals were found in the first excavation, possibly due to the scale of the excavation. Scattered bones of large and medium-sized animals occur in the asphalt beds mostly in horizontal positions. Burchak-Abramovich has found bones of a horse and of a deer scattered over an area of several square meters. In the bituminous bed complete skulls of medium-sized animals (wolf, hyena, badger) were found separately from the cervical vertebrae; even the atlas was separated from the skull. One find has been recorded which consisted of six joined cervical vertebrae of an ass and the mandible of a horse in two sections: the anterior part, which had been broken off, was deposited in a bed adjoining the horizontal layer where the posterior section lay. Broken bones of large animals and birds occur, as a rule, in the lower part of bed B.

The deposits in bed D are characterized by quite complete bones, 136 including some broken epiphyses and intact skeletal bones of large birds — all with asphalt-filled cavities as a result of the penetration of oil into the bone tissue pores.

One seldom finds bones that show tooth impressions of wolves, bears or hyenas, although gnawed humeri of bears, the pelvis of Equus hemionus and the femur of a rhinoceros have been described by Vereshchagin (1951b) and by Burchak-Abramovich (1953a). There are no signs on the rodent skulls of beak or claw puncture by birds of prey, which indicates that the bitumen-preserved skulls probably were not deposited in the excreta or stomachs of birds which fell into the asphalt. Puparia of flesh flies occur, although not frequently, in nasal and brain cavities, and in the depressions of a rhinoceros humerus. When the puparia were opened, it could be observed that the flies had hatched from the pupae. There were no bones found which displayed cuts or breaks made by prehistoric man. Paleopathological evidence of osteomyelitis, rachitis and helminthiosis is common (Vereshchagin, 1946b, 1951b; G. V. and D. V. Gadzhiev, 1952). Only two bones of a wolf and deer with polished distal epiphyses are known. Among the Binagady bones, there are only very few which have been rounded by streams, or which show sand-polished surfaces or other signs, such as brittleness or cracking, of origins in land surfaces or well-aerated soils.

The extent of permineralization of the bones is relatively slight. The diaphyses, when they are sawed, smell of damp bone, which is unusual for Middle Pleistocene material. Proteins were detected in the humerus of a wolf, and juniper wood from bed B contained 30.52% cellulose (Mamedaliev and Kaplan, 1948).

The dry bones and polished surfaces of diaphyses are dark brown and, in some places, bronze. In fresh fracture the bones show a grayish brown or chestnut color. Upon being boiled in alkali, the bones become brittle and light chestnut in color. The enamel and dentine of teeth are usually gray-brown to chestnut. However, the large molars of hyenas, saigas and bulls are bluish in color on the inner surface.

Because the extensive excavations of 1938-1942 at Binagady were poorly documented, very little is known about the nature of the deposition.

Almost all the investigators who worked with the Binagady material were concerned with the Apsheron landscape and the origins of the deposit: the reasons for death and the circumstances under which the remains accumulated.

Bogachev (1939c, 1940b, 1944) maintains that the present-day relief is very old and that the contemporary Lake Beyuk-Shor is a relict of an ancient and much larger lake. He thought that rhinoceroces, horses, Bos and deer attempting to reach clear water were trapped in the oil-surfaced lake, and that quadruped and feathered predators attracted to the floating bodies fought and died over their prey. According to Bogachev, the region

was also inhabited by migratory birds, and numerous streams presumably entered the lake carrying plant detritus, juniper trunks and pear fruit. He assumes the climate of the region to be somewhat colder
137 and more humid than that of today.

Considering all the evidence, Bogachev compares the locality with the asphalt deposits at Starina (Galicia) and at La Brea (Los Angeles, California). He points out that organic remains accumulated gradually without any of those catastrophic episodes which kill thousands of animals of morphologically and ecologically different species.

There are, however, a number of facts which do not fit into this elegant picture. If the relief in the past were similar to the present, then the Binagady hill would have been a small island when the level of the lake was higher and there would not have been room for all the animals nor for the accumulation of oil on such a small island.

The absence of freshwater mollusks and fish in the bone-bearing bed and the concomitant incidence of xerophilous plants do not support a picture of a large freshwater lake. And, indeed, if there had been numerous clear streams, there seems little reason for animals to have waded into oily mud. The idea of rhinoceroses and boars dying trapped in mud can practically be dismissed. There are no silt deposits in the Binagady beds, and the animals could not sink in the very thin layer of fine-grained sand and coquina.

From the plants identified in the asphalt, the botanist Petrov (1939) has inferred the existence of savannah and sparse arid forests in the Apsheron. He thought the site of deposit was in the delta region.

According to Argiropulo and Bogachev (1939), the occurrences of forest dormouse, red-tailed gerbil, migratory (gray) hamster and jerboa, and of mesophilous species of beetles indicate that the forests were of tugai type and the climate was more humid than now.

The ornithologist Serebrovskii (1948), in an analysis of the avifauna, included migratory birds in the species composition. He visualized the area of the locality as a shallow, reed-grown swamp surrounding a marine bay. Bird casualties were attributed by Serebrovskii to oil film on the water.

According to the geologist Sultanov (1947), the deposit site was located on the shores of a shallow marine bay beyond the main zone of wave action. His conclusions that rhinoceroses, Ellobius, mole voles and jerboas drowned in the sea and that flying birds died of fumarole gas poisoning do not require comment.

Efremov's statement (1950) in his excellent "Taphonomy" that bone-bearing bed D is alluvial in origin and was presumably protected by the asphalt from later erosion is in error.

Gromov (1952), who studied the rodents, adopted Efremov's taphonomical viewpoint and explained the accumulation of organic remains at Binagady by the agency of river sediments. He assumed the existence of treeless steppes on the Apsheron in the Upper Pleistocene.

All the authors mentioned above have failed to explain the occurrence in one and the same bed of plants, mollusks, insects, birds and small rodents, medium-sized carnivores and large, hoofed mammals. Even though the
138 data confirm the deltaic origin of the bed and the transport by river of animal remains, other questions, such as the causes and places of death and the distances traversed by the remains, have not been answered.

However, an analysis of the available geological and biological data can give a true picture of the Binagady site at the time of animal deposition and of the landscape of the Apsheron in the Pleistocene.

In addition to Binagady, we studied cases of mass death among insects, birds and animals on the Apsheron and in Kabristan and the conditions of continuous accumulation and burial of their remains.

A study of geological sections in both older and newer excavations showed that a lacustrine or river origin of bone-bearing bed D is doubtful. The osseous strata are always found beneath asphalt bed C, and when C wedges out, the organic remains disappear. This can only mean that the oil-asphalt provided the prerequisite condition for the accumulation of organic remains.

FIGURE 65. Upper part of the stem of *Phragmites communis* with closely spaced internodes from the bone-bearing bed at Binagady

Observations in Kabristan near Khurdalan, Kir-Kishlag and Beshbarmak show that incrustations and accumulations of asphalt occur on mountain slopes and in depressions, near peculiar fissures from which the oil is forced to the surface. Gas and salt water are ejected, in addition to the asphalt, by the mud-oil craters or wells. The margins of the latter are overgrown by sparse reeds (also found in Binagady, Figure 65), the green of which, in the spring, makes a remarkable contrast to the yellow background of semidesert, mountains and salinas. The wells attract the cattle, and at Beshbarmak cows and asses died after sinking into the thick mud of the well.

Rainwater often accumulates in the asphalt crusts. When the asphalt is hot and soft, the water forms lenses which are fatally attractive to animals in periods of drought. Asphaltic pools such as these annually trap many animals, and remains of various sizes, from that of mouse to that of goitered gazelle and ass, can be found in them. The decaying remains sink into the asphalt and the bones and mineral particles brought by winds and streams become incorporated in the silty beds underlying the asphalt.

It is not essential that the asphalt pools be located in large reservoirs, valleys or gulleys for animal remains to accumulate in the asphalt. On the contrary, asphalt located on gentle slopes or even on the crest of a ridge is guaranteed long and effective action, because on such terrain it is not buried under sediments (Vereshchagin, 1951b).

These Recent examples indicate that animal death in the Pleistocene might have occurred at or near the site of deposit, without necessarily involving any transport over long distances.

Over the centuries, the sticky surfaces and oily freshwater pools created by the heavy Binagady oil seeps on the shores of the marine bay probably
139 became poisonous traps and burials for a variety of animals (e.g., hares, jerboas, gerbils, voles, hamsters) and for many types of birds and insects. Heavier animals such as rhinoceroses, horses and bulls would have been supported by thicker layers of asphalt. This herbivore carrion undoubtedly

attracted carnivores and scavenger birds which accounts for the many bones of foxes, wolves and hyenas in this area as compared with their paucity on the river shoals. The author has described elsewhere the pursuit by foxes of birds which were trapped in the asphalt (Vereshchagin, 1946a).

Transport of bodies by water with decomposition occurring at the site of deposit could have taken place only on a small scale.

The absence at the site of mesophilous vegetation of forest and meadow animals and freshwater mollusks and fish would indicate that the streams which carried the bodies must have been small and ephemeral. They were probably short-lived torrents originating not more than a few kilometers or more likely, a few hundred meters distant from the site.

Bed (with coquina and juniper trunks) was probably formed during a marine transgression over a shallow estuary. It covered the bitumen and contributed to the consolidation of the bone-bearing bed. During the erosion of the southern part of the osseous lense, it would have been possible for bone fragments to be redeposited and incorporated into bed B. Tree trunks carried into the bay by waves were also preserved in bed B (Figure 64).

TABLE 16. Age groups of wolves at the Binadagy locality

Number of specimens		Age
absolute	percent	
1	0.8	Approximately 1 month
20	16.6	3.5-4 months
15	12.5	7-8 months
61	50.8	1-3 years
20	16.6	3-5 years, with slightly worn teeth
3	2.5	Over 5 years, with heavily worn teeth

Such biological data as the seasonal mortality pattern and the composition of animal populations can contribute greatly to an understanding of the nature of the Binagady locality. Clearly, the insects and pear fruits could only have been trapped in the asphalt in the warm seasons of the year. The incidence of migratory birds both from the south (spoonbill, purple heron, black stork) and from the north (snowy owl) indicates that bird deaths occurred during both the summer and winter seasons.

Death occurred at all ages, from infancy to senility, advanced age being indicated by some individuals with molars completely worn down to the base. Wolves are a particularly clear example. Because of the greater size and strength of the wolf bones, it is easier to extract them from their matrices than bones of other species, and thus to form estimates of the size of the wolf population.

The age groups of wolves based on their mandibles are given in Table 16.

The numbers clearly show that animals of all ages, not only the very young and very old, were buried in the Binagady beds. Data in Table 16 indicate that the main part (67.4 %) of the fossil wolves are adults (Figure 66). In other words, the dead assemblage represents not a selected

140

FIGURE 66. Mandibles of wolves of varying age groups from Binagady

(Illustrates Table 16)

age group, but a cross-section of the animal population which lived in the area throughout most of the year.

Analysis of other carnivore fossils also indicates that the animals perished throughout the warm season of the year (Vereshchagin, 1951b).

Taken together, these facts show that the Binagady locality itself provided the single cause of death at this site, rather than at some other locality.

From these preliminary assumptions it is possible to evaluate with greater certainty the faunal complex at Binagady, as well as the ecology of that period in eastern Transcaucasia.

According to calculations by Burchak-Abramovich and Dzhafarov (1953), nearly 8,213 bones of at least 412 individual ungulates were collected during the 1938-1942 excavations. Carnivores are represented by 2,043 bones of 11 species and at least 440 individuals, lagomorphs and rodents by approximately 2,300 bones of 15 species and at least 180 individuals, and insectivores by nearly 50 bones of three species.

Bird bones total at least 30,000. Hundreds of bones of turtles, lizards and snakes, many thousands of insect remains (mostly beetles), and hundreds of land mollusk shells have been found. Thirty-nine species of mammals have been identified (Bogachev, 1938b, 1940b; Argircpulo, 1941b; Vereshchagin, 1948, 1949c, 1951b; Burchak-Abramovich, 1951c, 1952d; Dzhafarov, 1950, 1955; Alekperova, 1952, 1955; I. Gromov, 1952, and others).

We estimated the number of common forms from individual mandibles and the number of rare species from all the bones. The statistics on ungulates were taken from Burchak-Abramovich and Dzhafarov (1953). The data in Table 17 is taken from collections which, in 1945, were in the
142 museums of Baku, Leningrad and Moscow. The quantities shown for bones and individuals reflect not only the actual number of animals, but also the method of extraction from the rock matrix. For small species, the quantities shown are less than the actual numbers.

(141)

TABLE 17. Mammalian species and number of individuals from the Binagady locality

Species	Number of individuals
Insectivora	
Crocidura aff. russula	3
Hemiechinus aff. auritus	3
Erinaceus aff. europaeus	1
Subtotal	7
Carnivora	
Canis lupus apscheronicus	120
Canis sp.	1
Vulpes corsac	85
V. vulpes aff. alpherakyi	125
Crocuta spelaea	20
Ursus arctos binagadensis	4
Vormela peregusna	13
Meles meles aff. minor	55
Panthera spelaea	11
Felis cf. lybica	2
Acinonyx jubatus	4
Subtotal	440
Lagomorpha	
Lepus europaeus gureevi	4
Subtotal	4
Rodentia	
Mus musculus	2
Apodemus sylvaticus	3
Cricetulus migratorius argiropuloi	8
Mesocricetus auratus planicola	3
Meriones erythrourus intermedius	12
Allactaga elater dzhafarovi	4
A. williamsi	10
A. jaculus bogatschevi	26
Dyromys nitedula	1
Microtus arvalis	70
M. socialis	
M. apsheronicus	2
Ellobius aff. lutescens	10
Arvicola cf. terrestris	1
Hystrix vinogradovi	25
Subtotal	177
Perissodactyla	
Equus aff. hidruntinus	73
E. caballus subsp.	154
Rhinoceros binagadensis	31
Subtotal	258
Artiodactyla	
Sus apscheronicus	11
Megaceros cf. euryceros	2
Cervus elaphus binagadensis	52
Saiga tatarica binagadensis	82
Ovis cf. ammon	1
Bos mastan-zadei	6
Subtotal	154
Total	1,040

TABLE 18. Avifauna, by orders, from the Binagady locality

Order	Number of species
Limicolae	22
Anseres	21
Accipitres	17
Gressores	9
Passeres	8
Palludicola	7
Coraciiformes	6
Steganopodes	2
Lariformes	2
Pterocletes	1
Columbus [?]	1
Podicipites	1

Characteristic bones are shown in Figures 67, 68, 70 and 71.

The total number of bird species, as given by Serebrovskii (1948) and Burchak-Abramovich (1951c), is 97 (Table 18).

Among the reptiles, bones of the grecian tortoise (Testudo graeca L.) and small unidentified lizards are known.

Insect remains are abundant, but only beetles are well preserved. A. Bogachev (1947) has described 107 species of beetles of the following families:

Cicindelidae
Carabidae
Dytiscidae
Cyprinidae
Staphylinidae
Silphidae
Histeridae
Buprestidae
Dermestidae
Hydrophilidae
Coccinellidae
Tenebrionidae
Cerambycidae
Chrysomelidae
Curculionidae
Scarabaeidae

Kirichenko has identified six species of bugs of the Thyreocoridae, Pentatomidae and Gerrididae families.

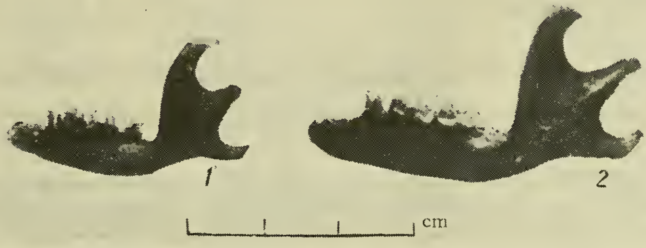

FIGURE 67. Binagady

Mandibles: 1—Hemiechinus auritus; 2—Erinaceus europaeus

Remains of flies, fly puparia, butterflies, dragonflies and grasshoppers are poorly preserved and difficult to identify. Shells of mollusks belong to local land species of Helix, Helicella and Pupilla.

Plants identified by Petrov (1939) and the author (Vereshchagin, 1949c) are represented by the following forms:

Pirus salicifolia
Pistacia cf. mutica
Vitis cf. silvestris
Zozimia sp.
Tragacanthum sp.
Juniperus polycarpos
Punica granatum
Allium sp.
Phragmites communis
Colchicus sp.
Scirpus sp.

Bogachev (1940b) has also reported Alhagi, Isatis, Artemisia, Salsola and Tamarix from the bone-bearing bed. However, these finds have not been confirmed.

Some of the tree remains listed above come from coquina bed B, and thus are younger than the main bone-bearing bed. This does not, however, 143 exclude the possibility of a stable xerophilous landscape in eastern Transcaucasia.

The paleontological material from Binagady is so complete that one can speak of entire Pleistocene complexes of different taxonomic groups and biocenoses of Transcaucasia.

An ecological analysis of mammal assemblages reveals specific features of the Apsheron landscape, climate and zoogeography. Changes which have occurred since the Pleistocene in faunal species composition should be projected to the level of orders (Tables 19, 20, 22, 24), taking into account the Recent zoogeography of the northeastern and southeastern periphery of the Bolshoi Range.

Insectivora

The absence of shrews and moles from the Pleistocene of Apsheron indicates a xerophilous landscape. At present, the long-tailed white-toothed shrew inhabits forests and semidesert, and the long-eared hedgehog the steppe and semidesert, sometimes frequenting sparse, arid forests. The European hedgehog lives in damp forests and in the dry bush of the semidesert.

TABLE 19. Comparison of Quaternary insectivore species in the piedmont of the eastern Caucasus

Species	Pleistocene	Historical time	
	Apsheron	Apsheron and Kabristan	Dagestan piedmont
Crocidura russula	+	+	+
C. leucodon	?	?	+
Suncus etruscus	?	+	-
Hemiechinus auritus	+	+	+
Erinaceus europaeus	+	+	+
Total	3+ 2?	4 + ?	4

Note. The query (?) in this and similar tables indicates species likely to occur within the given period of time.

Carnivora

The absence of forest species of carnivores (pine marten, European wildcat, lynx) excludes the possibility of extensive forests on the Apsheron. The lack of otter and mink indicates that there were no rivers or reed-grown lakes rich in fish. Since weasels and stone martens are rare on the Apsheron in present time, they may not have been preserved. The presence of European brown bear (at present found in the sparse, arid forests of Transcaucasia) suggests that the ancient Apsheron was a dry plateau with juniper and pistachio forests growing along the creek beds.

144 The presence of small fox and corsac fox is further evidence of the resemblance of the ancient landscape to the present. The incidence of cave bear is notable and can probably be attributed to the dry climate.

Fast-moving carnivores were also common: wolf, fox, corsac fox, cave hyena, badger, Panthera leo, cheetah, African wildcat. These animals are adapted to the steppe or to brush and wooded areas of semidesert. The climate of the region might have been colder than it is in the present. However, the snow cover must have been thin for the African wildcat, corsac fox and fox to have been able to hunt.

In order to clarify the nature of the deposit and the evolution of species assemblages from the Pleistocene to the Recent, the number of carnivores at Binagady was compared with estimates of Recent carnivores based on contemporary commercial game hunting in the Shemakha area near Baku. The study revealed some similarities and some differences in the ecology of the two assemblages, and changes in the proportions of five common forms: fox, wolf, corsac fox, badger and jackal (Table 21).

A comparative examination of carnivore species of both periods confirms the fact that the characteristically mesophilous Shemakha forest of the Recent, which is the habitat of martens and cats, is not at all similar to the Binagady trap and mountains.

Lagomorphs and rodents

The rodent species composition was almost twice as rich in the Pleistocene (Table 22) as in the Recent on the Apsheron. Their ecological grouping resembles that of the Recent Dagestan piedmont and indicates that, in Pleistocene time, Apsheron was a piedmont steppe marked by small, dry forests and some lakes which were overgrown by reeds and cattails.

Common hamsters live in an environment more mesophilous than the one that exists at present on the Apsheron (see Chapter III). The presence of the common and the Apsheron vole is another indication that the habitat was more mesophilous than now. In contemporary distribution patterns, the lower boundary of the common vole lies in the piedmont brush near Shemakha at an altitude of 700 m, whereas the pine vole does not descend below approximately 1,000 m.

Other species (hare, migratory hamster, steppe mouse, common vole, red-tailed gerbil, jerboa, mole vole and porcupine) form an assemblage characteristic of the present-day xerothermic valleys of northern Iran and Karabakh, which are covered with spiny astragali, willow-leaved pear, juniper and hawthorn.

Comparison of the Binagady rodents trapped in oil pools with those caught on the Apsheron in the Recent by eagle owls and by personnel of the Azerbaidzhan anti-plague station, indicates that in the Holocene the proportion of xerothermic forms gradually increased at the expense of mesophilous forms, which ultimately disappeared (Table 23).

Man is not responsible for the observed decrease of rodents from the Pleistocene to the Recent (see Chapter VII).

FIGURE 68. Binagady

1, 2 — skull of Vulpes corsac; 3, 4 — skull of V. vulpes aff. alpherakyi; 5, 6 — skull of Canis lupus apscheronicus; 7, 8 — canines of Ursus arctos binagadensis; 9-12 — skull, atlas and humerus of Crocuta spelaea; 13-17 — skull and humerus of Meles meles aff. minor; 18 — skull of Vormela peregusna; 19, 20 — jaws of young Acinonyx aff. jubalus; 21 — humerus of Felis aff. lybica; 22, 23 — jaws of young and 24 — jaw of adult Panthera spelaea.

(148)TABLE 20. Changes in the species composition of the Quaternary carnivores in the piedmont of the eastern Caucasus

Species	Pleistocene	Historical time	
	Apsheron	Apsheron and Kabristan	Dagestan piedmont
Canis aureus	-	+	+
Canis sp.	+	-	-
C. lupus	+	+	+
Vulpes corsac	+	-	+
V. vulpes	+	+	+
Hyaena striata	-	+	+
Crocuta spelaea	+	-	-
Ursus arctos	+	+	+
Vormela peregusna	+	+	+
Mustela nivalis	-	+	+
M. lutreola	-	-	+
M. eversmanni	-	-	+
Lutra lutra	-	-	+
Martes foina	-	+	+
Meles meles	+	+	+
Panthera spelaea	+	-	-
P. leo	-	?	?
P. pardus	-	+	+
Felis lynx	-	+	+
F. silvestris	-	?	+
F. lybica	+	?	?
F. chaus	-	+	+
Acinonyx jubatus	+	?	?
Total	11	12+ 4?	17 + 3?

TABLE 21. Relative proportions of carnivores in Apsheron (asphalt trap) and in Shemakha area (commercial game hunting data)

Apsheron in Pleistocene		Shemakha area, 1930-1940	
species	percentage of individuals	species	percentage of individuals
Fox	28.1	Fox	75.5
Wolf	27.5	Badger	16.4
Corsac fox	19.2	Jackal	3.5
Badger	13.0	Wolf	2.3
Cave hyena	4.5	European wildcat and jungle cat	0.8
Tiger polecat	2.9	Pine marten and stone marten	0.7
Lion	2.5	Bear	0.2
Bear	0.9	Lynx	0.2
Cheetah	0.6	Weasel	0.1
Spotted hyena	0.4	Otter	0.04
Wolf (small)	0.2	Tiger polecat	0.04
—	—	Striped hyena	0.001
—	—	Panther	0.0001
Number of species	11	Number of species	15
Number of individuals	440	Number of individuals	12,890

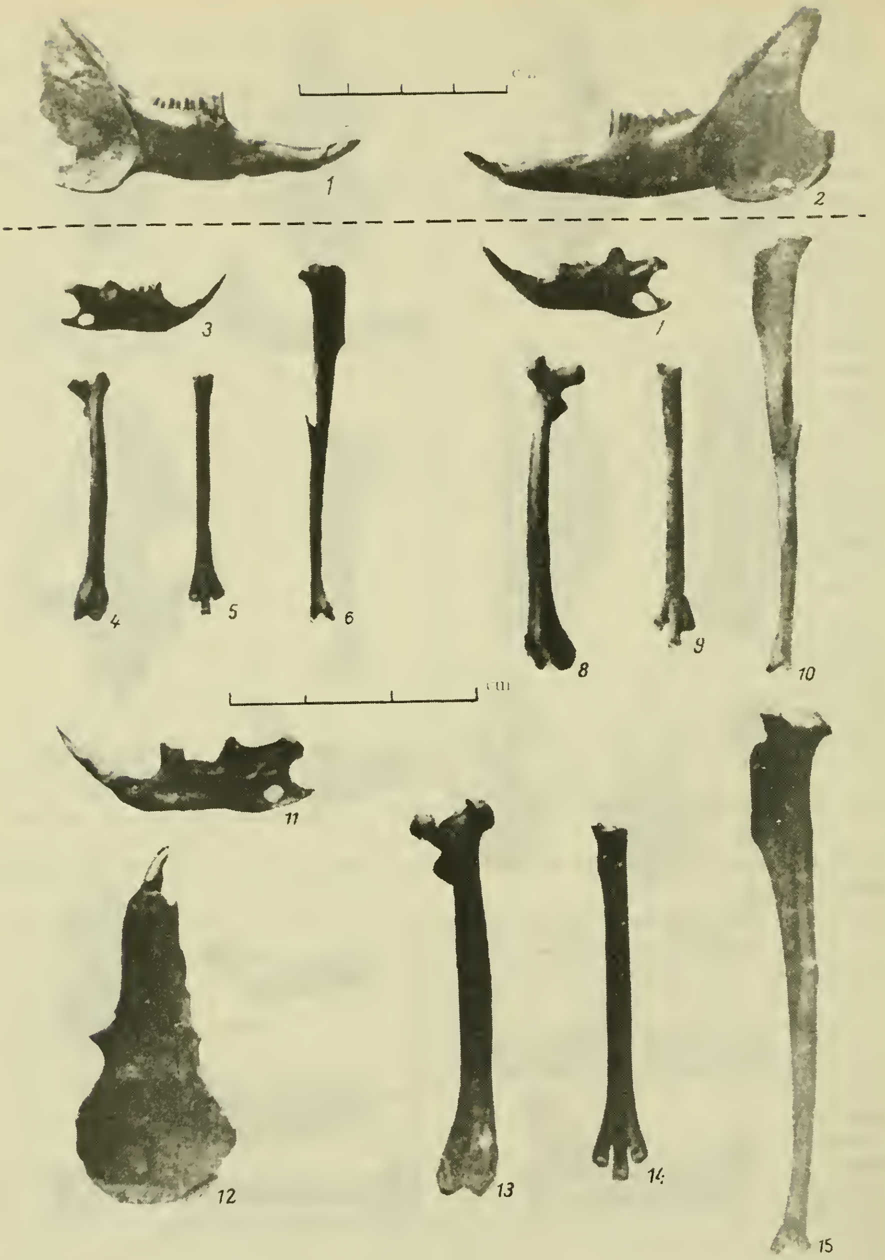

FIGURE 69. Binagady

1, 2 — jaws of Lepus europaeus aureevi; 3-6 — femur, metatarsal and tibia of Allactaga elater; 7-10 — jaw, femur, metatarsal and tibia of A. williamsi dzhafarovi; 11-15 — skull, femur, metatarsal and tibia of A. jaculus bogatschevi;

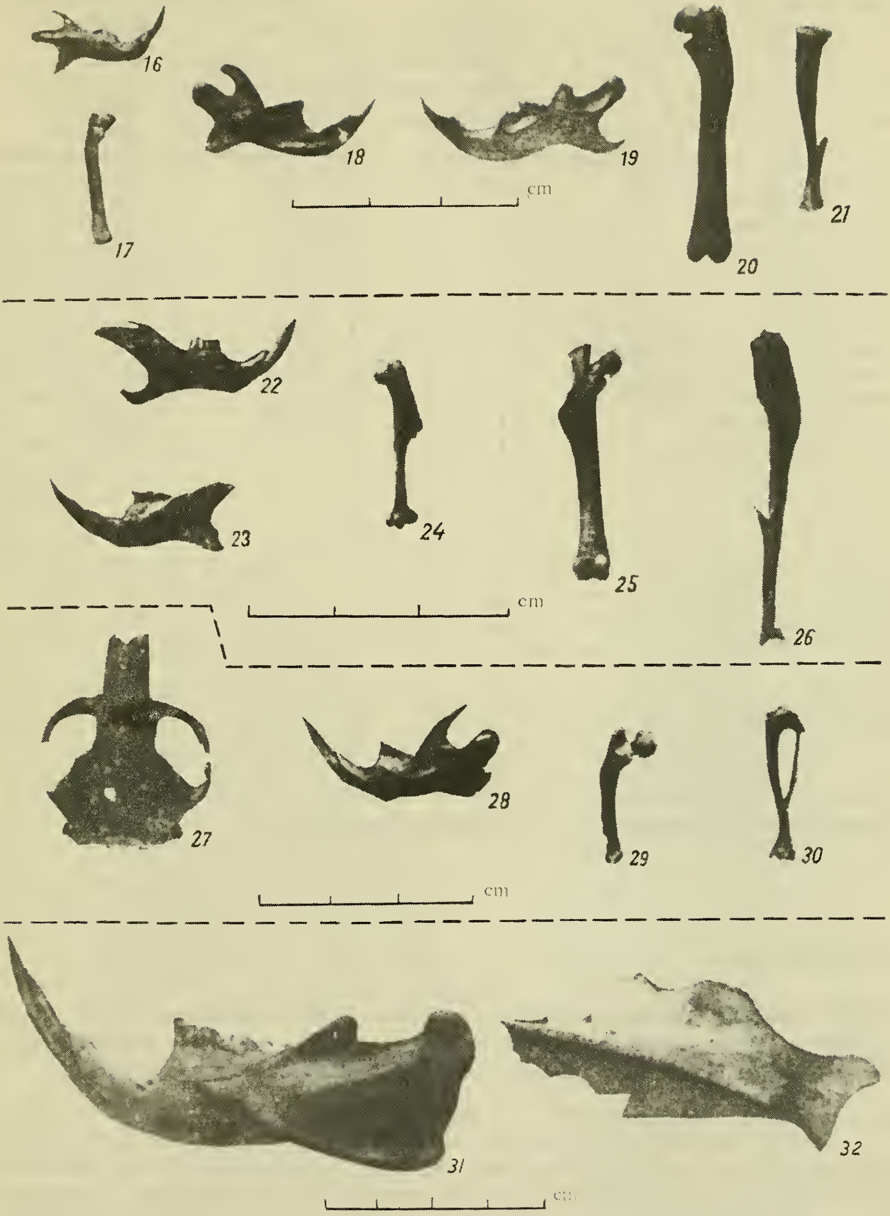

FIGURE 69 (continued)

16, 17 — maxilla and femur of Cricetulus migratorius argiropuloi; 18-21 — maxilla, femur and tibia of Mesocricetus auratus planicola; 22-26 — maxilla, humerus, femur and tibia of Meriones erythrourus intermedius; 27-30 — skull, femur and tibia of Ellobius aff. lutescens; 31-32 — maxilla and scapula of Hystrix vinogradovi

149 TABLE 22. Changes in the species composition of Quaternary lagomorphs and rodents in the piedmonts of the eastern Caucasus

Species	Pleistocene	Historical times	
	Apsheron	Apsheron and Kabristan	Dagestan piedmont
Lepus europaeus	+	+	+
Citellus pygmaeus	-	-	+
Micromys minutus	-	-	+
Mus musculus	+	+	+
Apodemus sylvaticus	+	+	+
A. flavicollis	-	-	+
A. agrarius	-	-	+
Cricetulus migratorius	+	+	+
Mesocricetus auratus planicola	+	-	-
M. auratus nigriculus*	-	-	+
Meriones erythrourus	+	+	-
Allactagulus acontion	-	-	+
Allactaga elater	+	+	+
A. williamsi	+	+	-
A. jaculus	+	-	+
Dyromys nitedula	+	+	+
Microtus arvalis	+	-	+
M. socialis	+	+	+
M. apscheronicus	+	-	-
Ellobius aff. lutescens	+	-	-
E. talpinus	-	-	+
Arvicola terrestris	+	-	+
Hystrix vinogradovi	+	-	-
Total	16	9	17

* Recent black hamster is a possible descendant of the Binagady species.

150 Perissodactyla

The presence of Equus hidruntinus, horse and rhinoceros (Table 24) indicates that the Apsheron in Pleistocene time was a grassy steppe with bush-grown gulleys. The grasses were probably burnt by midsummer.

Artiodactyla

The Pleistocene boar on the Apsheron could have lived in estuarine reeds and in the pistachio-juniper forests. Boars now live throughout the year in the thin, arid pistachio-juniper forests of Transcaucasia. The presence of saiga indicates wide-open areas with steppe vegetation. The Binagady Bos and deer might have entered the Apsheron during the spring growth of grasses. The decrease of artiodactyls on the Apsheron near the beginning of the historical epoch was caused by man.

(149) TABLE 23. Changes in the species composition and proportions (in %) of rodents and hares on the Apsheron from Pleistocene to Recent

Species	Pleistocene, caught in asphalt pools	17-20th centuries, caught by eagle owls	1939-1940, caught in traps	1947, caught in oil pools
Steppe vole	38.6	23.8	4.6	25.0
Common vole		Absent		
Great jerboa	14.4	Absent		
Binagady porcupine*	13.8	Extinct		
Red-tailed Libyan gerbil	7.1	18.1	85.4	29.2
William's jerboa	5.5	9.5	2.0	20.8
Transcaucasian mole vole	5.5	Absent		
Migratory hamster	4.4	42.4	2.9	12.5
Small five-toed jerboa	2.2	0.2	0.3	0.3
European hare	2.2	—	0.6	4.1
Asia Minor hamster	1.6	Absent		
Common field mouse	1.6	5.7	0.2	—
Steppe mouse	1.1		3.2	—
Apsheron vole	1.1	Absent		
Forest dormouse	0.5	—	0.1	—
Norway rat	—	—	0.1	—
Number of species	15	7	9	6
Number of individuals	181	347	2,473	24

* Recent Indian porcupine is a possible descendant of the Binagady species.

TABLE 24. Changes in composition of Quaternary Perissodactyla in the piedmonts of the eastern Caucasus

(150)

Species	Pleistocene	Historical time	
	Apsheron	Apsheron and Kabristan	Dagestan piedmont
Equus hidruntinus	+	-	-
E. hemionus	-	+	+
E. caballus gmelini	-	?	+
E. caballus subsp.	+	-	-
Rhinoceros binagadensis	+	-	-
Total	3	1+ 1?	2

152 In studying the Pleistocene landscapes of the Apsheron, birds contribute little to our knowledge because of their seasonal migrations. Beetles, however, are more reliable. The proportions of beetles found at Binagady in aquatic, amphibious and terrestrial habitats respectively is given in Table 26 (identification by A. V. Bogachev; author's figures).

Aquatic beetles, as such, are not indicative of the landscape, because of their capability of flying great distances; water-scavenger beetles and water beetles have even been known to cross great expanses of desert to reach water. According to Bogachev, land beetles in the Binagady bone-bearing bed comprise 8% (out of a total of 75.7%) of relatively mesophilous forms which are characteristic of the present piedmont brush near Shemakha and are absent from contemporary Apsheron. In other

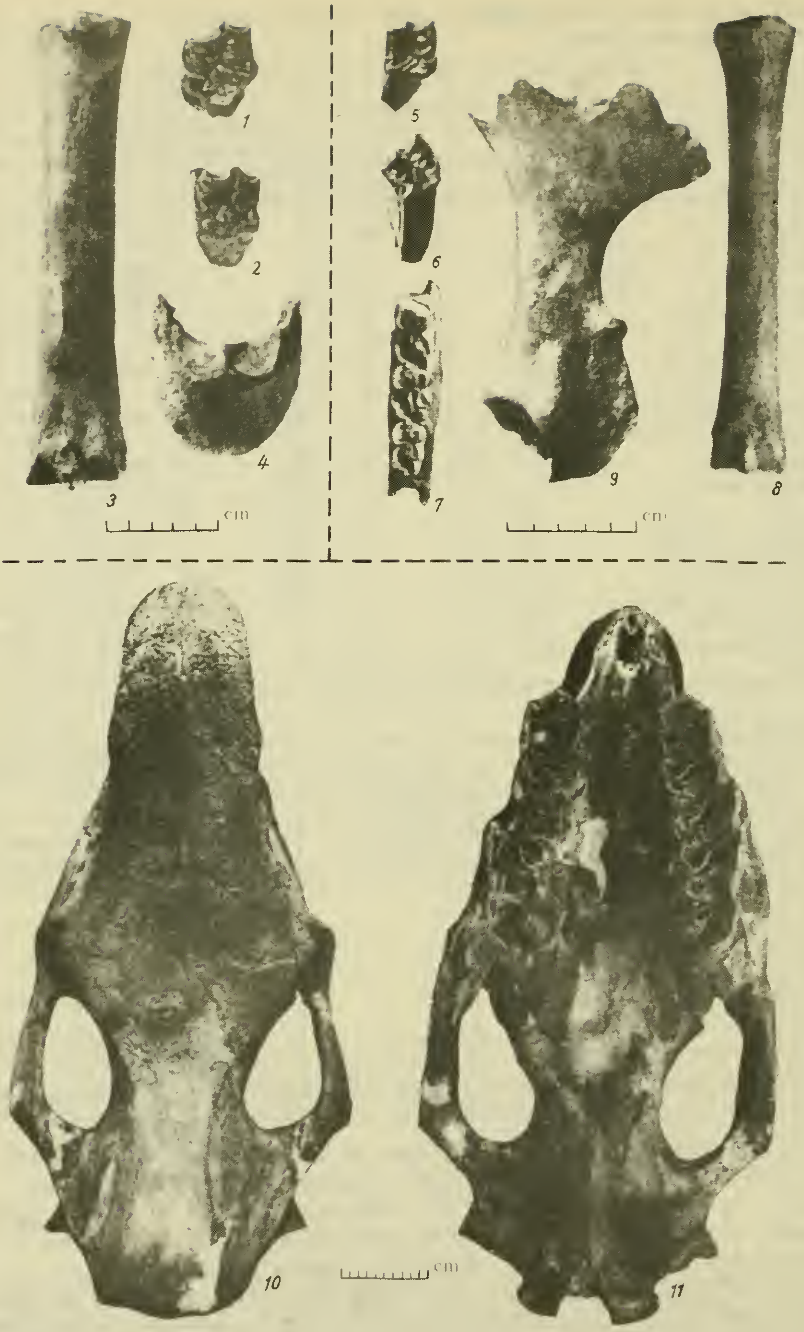

FIGURE 70. Binagady

1-4 — M^2, M^1, heel bone and hoof of Equus caballus subsp.; 5-9 — M^2, M^3, Pm_3-M_2, heel bone and pelvis of Equus hidruntinus; 10, 11 — skull of Rhinoceros binagadensis (top and bottom views)

(150) TABLE 25. Changes in composition of Quaternary Artiodactyla in the piedmonts of the eastern Caucasus

Species	Pleistocene	Historical time	
	Apsheron	Apsheron and Kabristan	Dagestan piedmont
Sus apscheronicus	+	-	-
S. scrofa*	-	+	+
Cervus elaphus	+	+	+
Megaceros euryceros	+	-	-
Saiga tatarica	+	-	+
Gazella subgutturosa	-	+	+
Ovis cf. ammon	+	-	-
Bos mastan-zadei	+	-	-
B. primigenius**	+	?	?
Bison bonasus	-	-	+
Total	7	3 + 1?	5 + 1?

* It is possible that the Apsheron boar is ancestral to the contemporary species.

** The primitive bull inhabited Apsheron later than the period of the Binagady trap.

words, the shift in the range areas of beetles confirms a progressive development of xerophilous landscapes in the Holocene.

Thus, both qualitative and quantitative data on the mammal and beetle fauna and on the flora show that the climate of the Pleistocene Apsheron was colder and moister than in the present. The ecological conditions were similar to those which now exist in the thinly forested, arid zone on the southern slopes of the Armenian Highland at elevations of 1,500-1,600 m, and in the Dagestan piedmont at elevations of 0-500 m.

153 The universality of the Binagady assemblage leads to other conclusions regarding the stratigraphy, paleoecology and history of the formation of the fauna.

The Binagady faunal complex contains a representative group of species widely distributed in the Pleistocene over steppes and forest-steppes, and known from Paleolithic and other localities of Europe. These include:

Erinaceus europaeus
Canis lupus
Vulpes corsac
V. vulpes
Crocuta spelaea
Ursus arctos
Meles meles
Panthera spelaea
Allactaga jaculus
Apodemus sylvaticus
Mus musculus
Microtus arvalis
Arvicola terrestris
Equus caballus
Megaceros euryceros
Cervus elaphus
Saiga tatarica

The origin of most of these species is not yet clear. Only the corsac fox, great jerboa and saiga migrated from the north into eastern Transcaucasia.

From the ecological point of view, the above assemblage is heterogeneous. It includes some species which, at present, are adapted to open habitats, and some species which live in the forests and moist river valleys of the same regions. There are no true xerophilous forms in the assemblage.

Some of the listed species (fox, wolf, bear, badger, great jerboa) are represented at Binagady by southern forms, an index of the antiquity of the conditions under which the Binagady faunal complex evolved.

(152)

FIGURE 71. Binagady

1, 2 — epistropheus and metatarsal of *Sus apscheronicus*; 3, 4 — metatarsal and humerus *Ovis* aff. *ammon*: 5-8 — horn, atlas, scapula and metatarsal of *Saiga tatarica binagadensis*; 9, 10 — skull of *Bos mastan-zadei*, from above and side (1/20 natural size) (from Bogachev, 1940)

TABLE 26. Ecological groups of beetle species and numbers of individuals from the Binagady asphalt

Ecological groups of beetles	Number of species		Number of individuals	
	absolute	percent	absolute	percent
Water	15	14.1	760	21.1
Land and water	11	10.2	74	2.0
Land	81	75.7	2,758	76.9
Total	107	100.0	3,592	100.0

The species which became extinct are: cave hyena, cave lion, horse, giant deer. The ranges of corsac fox, great jerboa and saiga have shifted considerably, but only localized changes took place in the distribution areas of the common and water voles.

154 There is a prominent group of Mediterranean species adapted to xeromorphic landscapes, such as the upland steppes of southwest Asia. These species are:

Crocidura russula
Hemiechinus auritus
Vormela peregusna
Felis lybica
Acinonyx jubatus
Lepus europaeus
Allactaga williamsi
Cricetulus migratorius
Mesocricetus auratus
Microtus socialis
Ellobius lutescens
Meriones erythrourus
Hystrix vinogradovi
Rhinoceros binagadensis
Equus hidruntinus
Sus apscheronicus
Ovis ammon
Bos mastan-zadei

The group includes species adapted to mixed biotopes (white-toothed shrew, long-eared hedgehog, tiger polecat, jungle cat, cheetah, William's jerboa, steppe vole and boar), to upland steppes (Radde's hamster, migratory hamster and Transcaucasian mole vole), and to hot valleys and lowlands (red-tailed gerbil and Binagady porcupine).

Most of these Mediterranean forms were represented in the Pleistocene by distinct subspecies, whose main areas of distribution at that time lay definitely to the south of the Caucasian Isthmus. The extinct Pleistocene ass (Equus hidruntinus), Binagady rhinoceros and Binagady goat were also of southern and southeastern origins. The extinct Apsheron vole, which has been identified from its molar classification as belonging to the European type of subgenus Pitymys, can be included among the endemic species. The range of the Dagestan hamster shifted into inner Dagestan, and that of the mole vole, to the mountain-steppe of Talysh.

Thus, the general evolutionary trend of the faunal complex on the eastern Transcaucasian plains was toward either extinction or shifts in distribution patterns of relatively mesophilous forms. The disappearance of these forms from the area was caused by the development of a drier climate and consequently of a more xerophilous landscape.

The general paleozoogeographical relationships within the Binagady complex can be understood when the complex is compared with the Pleistocene faunas of the southern part of the Russian Plain and of Southwest Asia.

Some common species of the Middle and Upper Pleistocene of Eastern Europe do not occur at Binagady (e.g., mammoth, woolly rhinoceros, Bison priscus, cave and other bears). Northern species were also absent from the Binagady complex: arctic fox, blue hare, lemming, reindeer, musk-ox.

The absence of these forms may be accounted for in part by the existence of a xeromorphic landscape in the eastern Caucasus, and in part by the geological age of the locality.

Tundra species probably did not extend as far south as the area of the Binagady trap, at the time it existed. Neither the harvest mouse, striped field mouse nor Siberian polecat reached the area from the north. And so it was that only some of the faunal elements of the southern Russian Plain and of the Iranian-Asia Minor uplands met in Apsheron and in Kabristan
155 during the Pleistocene. Certain southwest Asian species, listed below, which have been found in the Middle and Upper Pleistocene of Palestine, Syria and Lebanon, were also absent from the area under consideration:

Herpestes ichneumon L.
Felis chaus Güld.
Panthera pardus Schreb.
Rattus rattus L.
Spalax sp.
Phacochoerus garroda Bate
Hippopotamus amphibius L.
Dama mesopotamica L.
Gazella arabica L.
Gazella cf. subgutturosa Güld.
Capra primigenia Fraas
C. beden Schreb.
Bubalus sp.
Procavia cf. syriaca Schreb.

The distance between Apsheron and Syria and Palestine indicates that the differences in composition of the fauna have zoogeographical significance which persisted through geologic time.

A comparison of the Binagady complex with the Recent fauna of the eastern Transcaucasian plains shows the absence in the earlier period of a number of eurytopic species — species which probably penetrated the Apsheron at a later time, some still extant, such as Suncus etruscus, Canis aureus, Hyaena hyaena, Mustela nivalis, Felis chaus, F. lynx, Panthera pardus, Rattus norvegicus, Gazella subgutturosa and Martes foina, and some recently extinct, such as Panthera leo and Equus hemionus.

Thus an interesting feature becomes apparent: a number of southern thermophilous species migrated to eastern Transcaucasia, while a number of European steppe species retreated into eastern Ciscaucasia in the period following the time of the Binagady trap.

All of which emphasizes the specific features of the Binagady complex and the relatively short period of time during which the asphalt trap was operative in the Pleistocene.

Stratigraphic correlations and age of the Binagady complex

The age of the Binagady locality is significant in tracing the origin of Quaternary fauna and the morphogenesis of mammals.

Attempts at dating the bone-bearing bed and the faunal complex of Binagady have been based on the estimated age of the old Caspian terrace and of the orogenic compression of beds which was accompanied by an oil flow, and on paleozoogeographic correlations.

Assuming the age of the terrace underlying the bituminous beds to be Khazar, Bogachev (1939, pp. 47-51) has dated the Binagady locality Riss-Würm. He has also related the compression of the productive beds and the oil flow to the so-called "Kalinovka" phase of folding. According to Reingard (1937) this phase occurred at the beginning of the second Riss glaciation. According to Vardanyants (1948, table 3, pp. 104, 125), considerable compression occured in the pre-Khazar and pre-Khvalynsk orogenic phases, and later in the Neo-Pleistocene and Holocene, resulting in the formation of folds on the Apsheron and the development of mud volcanos. According to this scheme, the Binagady bed might have formed either in pre-Khazar or pre-Khvalynsk time.

Bogachev places the time of truncation of the Binagady fold at the Khazar transgression, and concludes from this that the oil which appeared during
156 the Kalinovka orogenic phase could not have been instrumental in trapping and preserving plants and animals, because the oil would have disappeared

prior to the Khazar transgression. Accordingly, Bogachev (1940b, p. 14) postulates the dislocation of Didacna surachanica beds and the existence of two Kalinovka compressive phases.

An assumption that the Binagady fold was truncated by the Baku sea would, in fact, lead to a correlation between the formation of the asphalt trap and the pre-Riss and the Kalinovka orogenic phases, and would affect an estimate of the age of the locality.

The peculiar features of the Binagady complex, as compared with the Quaternary complexes of the Russian Plain, complicate biostratigraphic correlations. Moreover, the difficulties are compounded by the lack of index fossils, such as elephant and bison, at Binagady.

Gromov (1948, p. 424) has dated the Binagady complex Upper pre-Glacial, correlating it with the Middle Quaternary "Khazar fauna of the Volga region," which Nikolaev (1937) dated Mindel-Riss.

The Burchak-Abramovich—Dzhafarov summary (1955) indicates that a majority of paleontologists accepted the Bogachev estimates without verifying them independently.

In a study of carnivores from the Binagady asphalt (Vereshchagin, 1951b), the author employed the same age estimate with a disclaimer that the dating can be improved through more complete excavations and further study of the relationships of the continental and marine beds at the Binagady mound.

A comparison of the Binagady species with lists of species from the Paleolithic caves of Palestine, Syria and Lebanon (Bate, 1937; Picard, 1937) shows that the greatest similarity between the faunas of the two regions existed during the Mousterian and Aurignacian, i.e., in the Upper Pleistocene.

We determined the residual organic content of the Binagady horse and saiga bones by calcination (as used by Pidoplichko, 1952). The results showed that upon oil extraction by hot alkali and benzine, the calcination index was in the 480-520 range, which is close to the index of the bones of the Khazar complex.

V. V. Cherdyntsev's attempt at a radioisotope determination of the age of the bones was unsuccessful.

On the basis of all the paleobiological and geological data, the Binagady complex must have existed and been buried at the beginning of the Khazar transgression, i.e., the end of the Middle Pleistocene. In Reingard's scheme, this corresponds to the lower part of the Middle Caspian beds and the second Riss glaciation ("R_{II}"); in Gromov's, it corresponds to the Riss, "Q_{II}^{I}".

How long the Binagady complex existed within the framework of the faunal composition described is not accurately known. Some species of the complex continued to live even in the Khvalynsk age, while others were replaced. An example of a later deposit where the Bos of the Asian type (Bos mastan-zadei) shows replacement by the European tur, while the saiga continued to exist, is another asphaltic locality, Kir-Maku.

157 Morphological development of eastern Transcaucasian animals during the Upper Quaternary is discussed in Chapter IV.

The results of the taphonomical and zoogeographical analysis of the Binagady burial may be summarized as follows.

1. The Binagady mammals lived in a dry steppe and in sparse, arid forests which grew in gulleys and in areas of placer rock. The climate of the region was somewhat cooler and more humid than in the present.

2. Animals of various ecological types perished in the liquid oil and viscous asphalt, as well as in mudflows.

3. The animals were buried in the asphalt sand and fine-grained coquina at or near the site of death. The asphalt beds were later covered by eolian sandy coquina and lacustrine-estuarine sediments.

4. On the basis of the occurrence of Khazar molluscan index-species in the Early Caspian terrace, the Binagady bone-bearing bed on the terrace margin can be dated post-Baku age.

By relating the profuse oil flow and the deposit of animal remains with the orogenic phases, the Binagady faunal complex can be dated as either Lower Khazar or Lower Khvalynsk.

5. A comparison of the Binagady faunal complex with the Quaternary complexes of the xerothermal zone of southwest Asia (the Paleolithic of Syria, Lebanon, Palestine) indicates that the Binagady complex correlates with the Mousterian culture. The coefficients of the residual organic matter of the Binagady bones are similar to those of the Khazar bones of the Volga region.

6. Of the 39 mammal species in the Binagady complex, 19 (48.7%) are Pleistocene species found widely distributed on the plains of Western and Eastern Europe. Another 19 (48.7%) are Pleistocene species of southwest Asian and Iranian origin. Only the one remaining species (2.6%) can possibly be endemic.

The faunal complex probably did not include arctic or mountain animals, or cave bears, elephants and bison. During the time of the complex, the ranges of several animal species of the steppes of the Russian Plain and of the upland steppes of southwest Asia met on the Apsheron. Fossiliferous localities of younger age on the Apsheron contain faunal assemblages which are not as universal as that of Binagady.

Kir-Maku

The locality is 1½ km south-southeast of the village of Dygya, in the center of the Apsheron Peninsula, on the slope of the Kir-Maku asphalt mound.

The Kir-Maku site was discovered in 1870 by Shtukenberg, who collected and gave to the Kazan University a skull of a female saiga and a wolf mandible in an asphalt matrix.

According to the map of Volarovich and Lednev (1913-1929), the site lies 100 m above sea level; the mound is nearly 1.5 km wide at the base and is 60-70 m high. The top of the hill is composed of Early Caspian deposits, underlain by almost vertical middle productive sands (Middle
158 Pliocene). Two buried or half-buried asphalt flows lie on the northern slope of the hill; one asphalt flow occurs on the southeastern slope. A bone-bearing kir layer occurs somewhat below the top of the hill, at a depth of 2-5 m and covers an area of 1.5-2 hectares. A generalized stratigraphic section through the bituminous beds of the Quaternary at Kir-Maku as given by Sultanov (1947) is shown in Figure 72.

The bitumen in this area often occurs in vertical veins, nearly 20 cm thick at the base and 1.5-2 m long. However, the main mass of the bitumen lies on a continuous layer, probably of flow origin. Bones occur in both the stratum and the veins. The oil which was forced to the surface by compression of the beds probably formed sticky crusts and pools which were later covered by sand and dust. Only fragmentary skeletons and skulls are found, as a rule, in the bitumen, probably remains of animals that died trapped in the asphalt crusts.

The Kir-Maku locality has something in common with the travertines of Mount Mashuk in the northern Caucasus. However, the asphalt crusts probably acted as a more efficient trap.

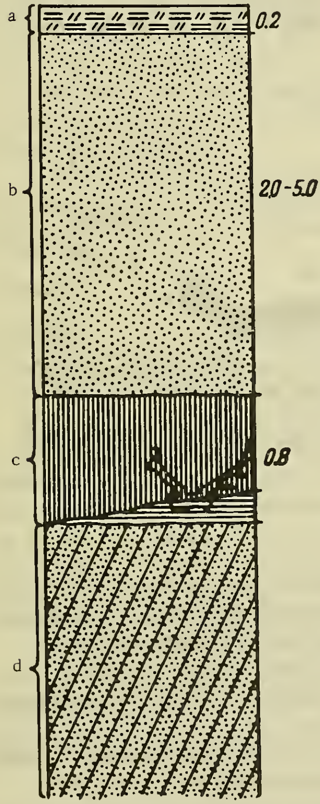

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FIGURE 72. Section through the asphalt-bearing beds at Kir-Maku

a — surface loams; b — sandy-clayey sequence; c — "rich" asphalt bed; d — productive sands. On the right — thickness in meters

Bogachev (1924, 1925b) reported a skull of Bos primigenius that was indistinguishable from a species which lived on the Russian Plain during the Pleistocene and Holocene. He dated the bituminous salina near the village of Dygya post-Baku and thought that the Bos died and was preserved during a period of increasing humidity and expansion of the steppe flora on the Apsheron Peninsula in Khvalynsk time.

In 1940-1941 a large number of bones of Bos primigenius, wolf, fox, cave hyena and vulture were found in the process of bitumen-mining. The miners buried the bones in a specially prepared trench (Bogachev, 1944; Sultanov, 1947).

The Kir-Maku beds are younger than the Binagady beds. The age of the relief at Kir-Maku can be readily determined, since the bituminous bed is concordant with the slope.

The Bos primigenius from Kir-Maku is a younger type which replaced the Binagady form in the Upper Pleistocene of eastern Transcaucasia. The Kir-Maku Pleistocene assemblage still included saiga and possibly hyena of the Binagady type.

Fossils found in the bitumens of the northeastern part of Artem Island belong to the Upper Pleistocene. These include two red deer skulls with broken antlers which were placed in the Museum of Natural History in Baku (Bogachev, 1938a). Other bones of red deer, and several bones of horse, wolf and large birds were collected at the same locality in 1944 from old caches (Burchak-Abramovich, 1951c).

The age of the bones from the island approaches those of Kir-Maku, as nearly as can be inferred from the state of preservation of the material.

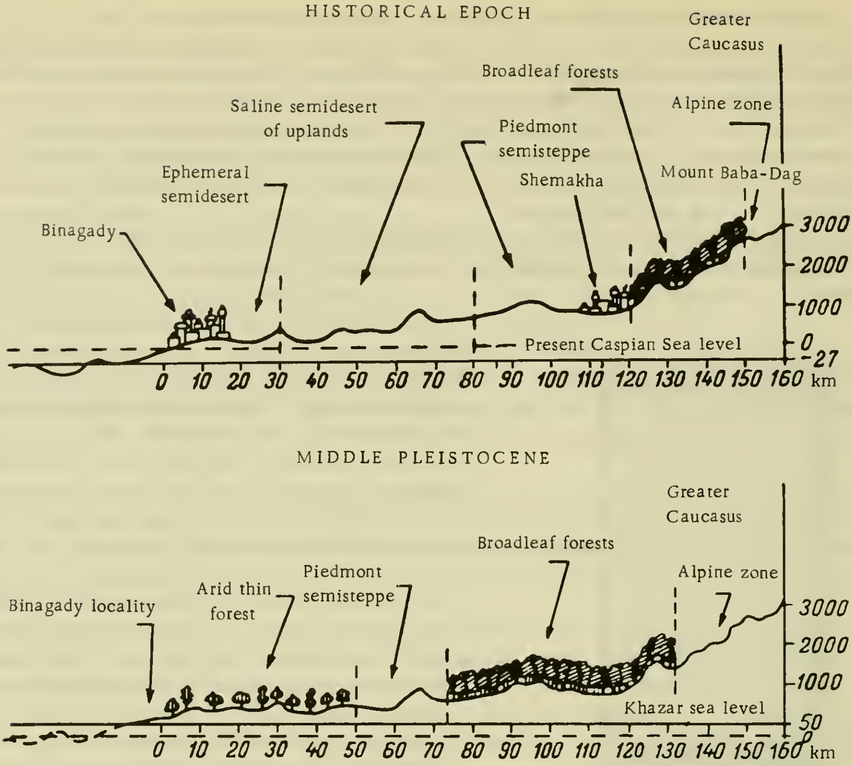

FIGURE 73. Changes and migration of landscape zones since the Middle Pleistocene on the Apsheron Peninsula, based on the study of the Binagady locality

Deer and horses probably lived on Artem Island during the relatively humid, cold period in the Top Pleistocene. At that time ungulates migrated freely over the Apsheron and to nearby islands, particularly during the spring growth of ephemeretum. Occurrences of animals on the islands, therefore, do not indicate a regression of the Caspian, since the animals could swim across the narrow straits.

The Pleistocene development of landscapes and faunal complexes on the eastern Transcaucasian plain can be described from data at hand, as follows.

The development of the xeromorphic landscapes which predominated in the Lower Pleistocene probably began in the Middle Pliocene (the time of the productive beds). During the Baku transgression the shores of Kura bay were inhabited by rhinoceroses, Elasmotherium, horses, camels, and, of the carnivores, hyenas which closely resembled the spotted or African brown hyena.

160 A distinct complex of mammals developed on the plains of eastern Transcaucasia toward the Middle Pleistocene, consisting of species widely distributed on the steppes of the temperate zone of Europe and on the upland steppes of southwest Asia.

By analogy with western Transcaucasia, it can be assumed that the mountains of the Bolshoi Range were inhabited by European brown bears and cave bears, martens, lynx and herds of mountain goats and chamois.

Glaciation over the eastern spurs of the Bolshoi Range, while probably not extensive, was sufficient to create a number of changes in the fauna of the plains. The general landscape was characterized by sparse forests and steppes.

The Bos of the Asian-Indian type was replaced by the European tur. Argali and giant deer probably disappeared. A number of Pleistocene species of the steppes and forest-steppes of Eastern Europe penetrated Transcaucasia, and possibly the Iranian Plateau, during a cool, humid climatic phase in the Upper Pleistocene. During this stage the altitudinal vegetation zones probably migrated down the mountain slopes (Figure 73). This, however, did not interrupt the continuity of the xerophilous fauna of southwest Asian origin.

The East European steppe animals (corsac fox, great jerboa, saiga) retreated to the north only at the very end of the Pleistocene during a new xeric climatic stage.

A new migration of southern species into Transcaucasia occurred at the beginning of the xeric Holocene epoch. Some of the species migrated as far north as the Ciscaucasian plains.

Lesser Caucasus upland (southern Transcaucasia)

The high plateaus of southern Georgia, Armenia and Karabakh were taphonomically in a special position in the Pleistocene. Frequent mudflows, landslides, rockfalls and volcanic eruptions, associated with the mountainous terrain, caused death among animals. However, their incidence as fossils is rare. The known Pleistocene localities are situated on the margins of broad river valleys and in sink holes of high plateau lakes. The bones were deposited in river and mudflow fanglomerates, in diluvial sediments near mountain slopes and in lacustrine sediments.

Although Paleolithic material is plentiful on the Armenian Highland, the instrumentality of man in the accumulation of animal bones was negligible (Zamyatnin, 1947; Panichkina, 1948, 1950a, 1950b; Sardaryan, 1954), probably because of the erosion of most of the Middle Paleolithic caves and open sites.

A site containing bones of Lower Pleistocene mammals in ancient lacustrine deposits near Akhalkalaki is particularly interesting. The locality was discovered by Vekua in 1958 and from it he has identified the following species: Canis sp., Crocuta spelaea, Meles cf. meles, Marmota sp. (small form), Elephas cf. trogontherii, Equus sp., Rhinoceros etruscus, Hippopotamus sp. (large form), Megaceros sp., Bos cf. primigenius. The presence of the hippopotamus and of an unusual marmot in the assemblage emphasizes its southern aspects. The incidence of both forms indicates that the landscape
161 of the area at the dawn of the Anthropogene was comprised of low plateaus with a well-developed river network and warm climate.*

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* The age of this assemblage may be older, possibly Upper Pliocene.

FIGURE 74. Skull of Bos primigenius from Bayandur on Armenian Highland

A large accumulation of bones was discovered in 1928 in the sand-gravel quarries near the Kazachii post on the southern outskirts of Leninakan, of which up to 300 kg were removed to the Yerevan Museum (Bogachev, 1938c, 1938d; Avakyan, 1948). Bogachev has identified the following species in the material collected: Bison priscus, Megaceros sp. (hibernicus?), Cervus elephas maral, Equus caballus. Bones of an elephant (Elephas cf. armeniacus) were taken from a lower bed which has been assigned to the Upper Pliocene (Apsheron age or equivalent). The rest of the bones were dated Pleistocene. Avakyan and Burchak-Abramovich (1945) have identified the camel Camelus knoblochi in the material and the following species occurring with it: Equus stenonis, Rhinoceros cf. mercki, Elephas meridionalis, E. trogontherii (?), Cervus sp., Bos sp.

Elephant teeth from near Leninakan, described by Sardaryan (1954), indicate that the predominant species in the collection is Elephas trogontherii, which closely resembles the Tiraspol E. wusti and, to a lesser extent, the elephants from the Taman Peninsula conglomerates. A fragment of skull of Bos primigenius from this locality (collections of the Museum of Georgia) has been described by Burchak-Abramovich (1951d).

Another fragment of Bos primigenius skull (Figure 74), taken from near the village of Bayandur in the Leninakan area, has been described by Gromova (1931). Even this brief review of the material clearly shows that fossils in the alluvial deposit near Leninakan are of varying ages. The deposit strongly resembles the gravels of the inclined Ciscaucasian plains.

A Lower Quaternary faunal complex, with such indicative forms as Elephas trogontherii, Equus stenonis and Rhinoceros mercki, is distinguishable in the material collected and shows a correlation of the Leninakan freshwater deposit with the upper part of the Psekups gravels and the lower beds of the Girei quarry on the middle Kuban.

The Lower and Middle Quaternary bones from the sands and gravels near the village of Eilas, 12 km southwest of Yerevan, are close in age to the material described. In the Adzhi-Eilas site the gray, fine-grained river sands containing mammalian bones underlie the 3—3.5-m-thick gravels and loessial loams. The bone-bearing lenses are up to 1-1.5 m thick. Some of the bones had been redeposited, being apparently derived from older lacustrine sediments. The beds were dated as Riss age by Avakyan (1946). The fragments have lost most of their organic matter. The surrounding matrix of the horn fragments is "chalky" and "marly." The enamel of the deer teeth is grayish brown from staining of the dentine. The material which

162 we studied includes teeth of Elephas trogonthetii, a fragment of the skull of "diluvial-type" Bos, Bos trochoceros, fragments of deer horns and teeth, Cervus ex. gr. elaphus and Dama cf. mesopotamica (Figure 75).

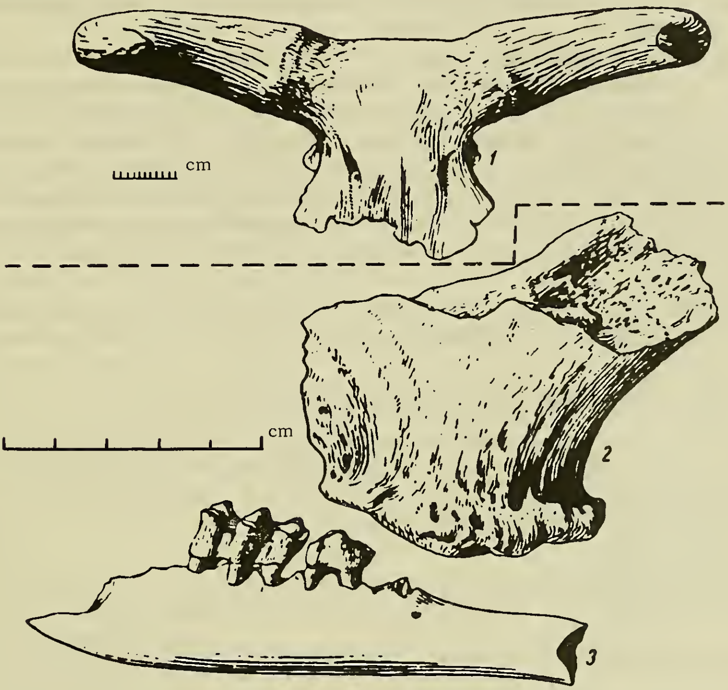

FIGURE 75. Adzhi-Eilas

1 — skull of Bos trochoceros; 2, 3 — fragment of horn and jaw of Dama cf. mesopotamica

Younger, Upper Pleistocene bone deposits, partly created by primitive hunters, are so far known only in the northern sections of the Lesser Caucasus upland. There is a record of rodent bones, a fragment of a deer horn, fragments of tusks and skeletal bones of Elephas primigenius and a tooth of Equus caballus taken from a depth of 10 m at a site on the left bank of the Chichkhana rivulet near Nalband, 30 km north of Leninakan (Karakash, 1898).

Zurtaketi site. This Paleolithic site discovered by Maruashvili (1946) on the Tsalka Plateau in southern Georgia was ascribed particular stratigraphic significance. The site is located at an elevation of nearly 1,320 m on the right slope of the Karabulakh River valley (the right tributary of the Khram River), 15 km north of Bashkicheti. Fractured bones and tools of flint, obsidian and bone reflect human activity at the site. The obsidian tools are ten times as abundant as the flint implements. The bone and stone tools must have been attached to handles, because they resemble darts and arrowheads. From the stone material the site has been dated as Solutrean.

Because he assumed that the primitive tribe was driven off the site by a lava flow which burned and covered the cultural layer, Maruashvili thought that the uplands relief and the volcanic activity dated from a period later
163 than that of the site. His age estimates were disproved by Paffengol'ts (1951) who established that the site is located in a collapsed recess of a doleritic lava wall.

The mammalian material collected by Maruashvili in 1945 and 1948 consisted of molars, incisors and metatarsal epiphysis of a horse, molars of an ass, vertebrae of a proto-bison and a fragment of a ram radius.

Most of the bones are weathered and have slightly dendritic surfaces. Their state of preservation indicates a very late stage of the Pleistocene.

The material from the Zurtateki site, as identified by Burchak-Abramovich (1951a), is given in Table 27. In addition, partridge bones which resemble rock partridge have also been identified in the locality material.

The species composition of the game of the Zurtaketi people reflects a Khram Basin landscape of rolling plateaus covered with meadow-steppe, and underdeveloped forest-steppe vegetation in the Upper Pleistocene.

TABLE 27. Mammalian species and number of bones from Zurtaketi site

Species	Number of bones	Number of individuals
Equus caballus subsp.	14	3
E. (Asinus) sp.	3	1
Bison priscus	6	1
Ovis cf. gmelini	1	1
Total	24	6

The asses (kulans) and small rams were quite common until recently in the woodless territories farther south.

Prehistoric hunters were also active along the upper Khram River, where a Mesolithic cave site, approximately 8 m above the riverbed, was discovered by Kuftin (1941) near the village of Barmaksyz.

At this site, a cultural layer of no more than 40 cm in depth yielded 9,900 broken obsidian tools and 600 flint tools in a 70 m^2 area of eroded slope with surface soil up to 80 cm thick.

The bone material consists of fragments of diaphyses and ungulate teeth, stained with humus.

According to Burchak-Abramovich (1951b), the collections include six molars of a small horse and a lower molar of a Bos.

During the artificial lowering of Lake Sevan, Dal' (1950b) collected material along the shores which is the same geologic age as the collections mentioned above.

The extensive collections are mostly fragments of bones of domestic animals of post-Paleolithic age which are discussed in more detail below.

As far as the state of preservation shows, the oldest bones belong to a Bos cf. minutus and a dromedary (Camelus dromedarius),
164 tentatively identified by Khaveson (1954b) as a wild form.

The fauna of the Pleistocene beds of southern Transcaucasia is relatively poor in species. Nevertheless, there is a regularity in the replacement of the faunal complexes one by another, similar to the process which operated in Ciscaucasia.

It is interesting to note that a number of index species characteristic of the "cold steppes" of Europe occur in the Pleistocene deposits of the Lesser Caucasus plateau. The following species are known: Elephas trogontherii, Rhinoceros mercki, horse, Camelus knoblochi, Megaceros, Cervus elaphus, Bos primigenius. Of the species peculiar to southwest Asia, only fallow deer and mouflon-like sheep are known. The southern east Mediterranean aspects of this faunal complex were probably better developed among the smaller forms in the Pleistocene.

The species under study have not yet been classified stratigraphically, nor have morphological characteristics been established for the index forms which take into account their environmental adaptations.

As opposed to the Greater Caucasus, the Upper Pleistocene faunal complex of the highland region under discussion has not yet been recorded. This is partly accounted for by the poor development of the karst, and by the fact that the karst itself has been inadequately studied. In the face of the scarcity of Paleolithic material, it is impossible to form a judgment of the effects of Pleistocene cooling and glaciation of the plateaus on the development of the fauna. There is no doubt, however, that the increase in water and in mesophilous vegetation on the plateau did not preclude the existence of camels in the hot intermontane valleys. The vertical shifts of vegetation zones and faunal complexes which occurred during the period of cooling in the Pleistocene were probably less extensive than in the Greater Caucasus.

The period of transition to the Holocene on the Armenian Highland is not very well known; it is probable, however, that it was similar to that in eastern Transcaucasia.

The stratigraphic and geographic distribution of Pleistocene mammals in the Caucasus is given in Figure 2 (see Introduction).

ECOLOGY AND LANDSCAPES OF THE CAUCASIAN ISTHMUS ACCORDING TO PALEONTOLOGICAL DATA

A review of the geological data and of Pleistocene fossiliferous localities by regions provides a basis for a summary of the specific features of the development of Caucasian fauna.

From the excavations at Kudaro I, the faunal complex which existed in the mountains that were uplifted in the Lower Pleistocene can be recognized as the direct ancestors of Recent Caucasian species of insectivores, rodents and ungulates which are characteristic of the Mediterranean region of the Alpine folded belt. From the zoological point of view, the strong peneplanation of the Caucasus in the Lower Pleistocene which is assumed by some geologists (see, for example, Vardanyants, 1948) is an impossibility. The evolution of the Caucasian mountain fauna with such
165 highly specialized forms as Prometheomys, Microtus nivalis, Caucasian goat and chamois took place at the same time as the evolution of similar forms in the Alps, the Carpathians and Asia Minor. It is difficult

to support a case for the origin and development of these mountain species only in the Pleistocene, since, by the end of the Middle Pleistocene, they had already assumed characteristics which are identified with the Recent.

The main sections of the Greater Caucasus which had been uplifted during the Miocene probably retained their elevation into the Pleistocene, even though they might have been somewhat eroded.

The better-known death assemblages of Middle and Upper Pleistocene mammals in the Caucasus reflect a continuing cooling of climate and modernization of fauna.

Elasmotherium and Cervus pliotarandoides disappeared in Ciscaucasia and Transcaucasia toward the Middle Pleistocene. Steppes and forest-steppes replaced the semideserts and savannahs on the piedmont plains and the evolution of landforms promoted further isolation of faunal complexes in different landscape zones. At that time, the forest-steppes of Ciscaucasia were inhabited by Elephas trogontherii, Rhinoceros mercki, red deer and long-horned bison. In eastern and southern Transcaucasia the bison were replaced by Bos primigenius.

A widespread invasion of eastern Ciscaucasia by some xerophilous species of the Aral-Caspian fauna (e.g., little suslik, Central Asian gerbil and jerboa) might have occurred very early, perhaps even at the close of the Apsheron. It is possible that the ancestors of these species survived the Caspian transgressions on lands bordering the east Ciscaucasian bay, or that, having disappeared from the area, they returned in new migrations during the regressions of the sea.

A mountain-forest faunal complex, consisting of bear, boar, deer, Caucasian goat and bison, existed in western Transcaucasia on the steep, southern, seaward slope of the Bolshoi Range.

The faunal migrants from the Russian Plain were represented by the common hamster which appeared as far south as Tsebel'da.

The low plateaus of Imeretia formed the northwestern boundary of the distribution zone of Upper Pleistocene xerophilous species of the southwest Asian uplands: Radde's hamster, porcupine, ass, argali-like sheep. Apes also survived in the area from the time of the Pliocene. The presence of horses and asses indicates a steppe development along the middle section of the Rion.

Similar steppes, covered in places by very extensive lava flows, also developed in the Lesser Caucasus uplands and in central Transcaucasia.

At the end of the Lower Pleistocene, the large mammalian fauna first showed noticeable effects of Paleolithic man's presence in the environment. These effects were more pronounced in the western part of the Isthmus.

Commencing in Upper Pliocene time, the eastern Transcaucasian landscape, composed of dry foothills, juniper-pistachio forests and steppe grasses dry in summer, persisted throughout the Middle Pleistocene. The faunal complex of this region had a mixed composition of animals from the Pleistocene steppes of the Russian Plain (corsac fox, saiga, etc.), from
166 the southwest Asian uplands (jungle cat, cheetah, mole vole, etc.),
and from deserts of the Turan type (small five-toed jerboa). It also included endemic Caucasian species (Apsheron vole).

As a general rule, cave bear, elephant and bison were not to be found. The only northern steppe species from the Pleistocene Russian Plain to occur in eastern Transcaucasia during the Middle Pleistocene were corsac fox, great jerboa and saiga (Figure 76).

▨ Caucasian mountain-forest and mountain-meadow complex

▥ Southwest Asian mountain-steppe complex

□ South Russian steppe complex

▤ Central Asian semidesert complex

FIGURE 76

The ranges of the "northern" and "southern" steppe species expanded along the margins of the Isthmus toward each other, probably moving closer together in irregular waves—irregular, that is, in the sense of both space and time. It seems possible that the extension over the Caucasus of the ranges of some other northern steppe species (e.g., common vole, Bos primigenius) also proceeded unevenly even in the Middle Pleistocene. The process was controlled by the alternation of arid and humid climatic phases.

The proportion of faunal elements from the Russian Plain steadily grew throughout the Pleistocene. The effects of this incursion of Russian Plain species was more pronounced in the fauna of the Ciscaucasian plains than in that of the Transcaucasian.

True mammoths and bison, but of somewhat diminished size, lived in the western Ciscaucasian foothills at the beginning of the Upper Pleistocene, at a later time than that of the Binagady complex.

167 The extensive development of steppes on the Trans-Kuban Plain at the beginning of the Upper Pleistocene can be seen in the occurrences of grass beetle, horse, ass and saiga remains at the Il'skaya site. Mammals from the Upper Pleistocene localities of the Ciscaucasian plains also indicate the degree of development of the steppes. The mammals of this region include horse, boar, red deer, saiga, bison and Bos primigenius. Such an assemblage may be characteristic of either a steppe or a forest-steppe, but not of extensive forests nor of mesophilous meadows, and certainly not of moss swamps and tundra.

From available paleofaunal data, it appears that glaciations in Eastern Europe and on the Caucasian mountains did not noticeably affect the composition of the faunal complexes on the piedmont plains. Moreover, development of desert and semidesert landscapes, rather than mesophytic landscapes, is indicated by the large collections of bones from the shoals of the lower Don. The occurrence of Upper Pleistocene and Holocene bones of blue hare and reindeer along the lower Don must be regarded as evidence of a late extension of their ranges southward along the valleys of the larger rivers of the Russian Plain, and not as a direct shift in the distribution areas caused by the cooling and glaciation of northern Europe. Mountain forms, such as snow vole, Caucasian goat and chamois, are completely unknown in the Pleistocene of the Caucasian foothills and plains. This might be taken as a contrary indication to the assumptions of continental glaciations and major shifts in the phytolandscape (such as displacement of alpine groupings to the plains) held by earlier zoologists and contemporary geomorphologists.

If, during the glaciations of the Caucasian mountains, the glaciers descended to the piedmont plains, then the highland fauna (mountain goat, chamois, Prometheomys) must have either been completely displaced to the piedmont plains, or migrated to some adjacent mountain refuge, or become extinct.

The cooling and the concomitant down-slope movement of the altitudinal zones can be traced through paleontological material which reflects the wider distribution of mesophilous animals and animals of the mountain-forest zone from the time of the Middle Pleistocene in western and eastern Transcaucasia.

It should be noted that the Caucasian Isthmus, because of its more southerly location and more varied relief, had a more variegated species population during the Pleistocene than the southern part of the Russian Plain. Evidently, during the Pleistocene a number of subtropical and hydrophilous species of mammals found refuge in Transcaucasia. A number of such forms, such as macaca, black rat and porcupine, survived through the Pleistocene in Colchis and Asterabad because of proximity to the Black Sea and Caspian basins.

All of this is fairly well in agreement with the results of paleontological studies in Palestine, Syria and Lebanon which are discussed in more detail below. Comparison of the Upper Pleistocene Caucasian faunal complexes with those of Syria-Lebanon indicates that the southward migration to the Caucasus of European forest forms (such as pine marten) followed the Aegean route (over the Balkans and the marginal ridges of Asia Minor) more frequently than the route over the plains of southern Russia and Ciscaucasia.

168 During the Pleistocene the Caucasian Isthmus was an ecological barrier to the dispersion routes of the Russian Plain and southwest Asian species. The barrier prevented the southward migration to Transcaucasia of a number of steppe mammals of the Russian Plain, such as Siberian polecat and suslik. The barrier also blocked the migration of animals of the upland steppes of southwest Asia (southern-type gerbils, mole vole and other species) to Ciscaucasia.

The Recent fauna does not reflect a series of xerothermic phases in the Pleistocene.

At present one can speak of only one phase of development of the steppes in the Middle Pleistocene, the postglacial dry climatic phase.

The warm (interglacial?) phases during the Pleistocene did not bring a return of the subtropical fauna or flora from south and southwest Asia and Africa, even to Transcaucasia. The fauna of the foothills and low plateaus remained xerophilous and relatively thermophilous in character. Some species of the Asia Minor and Iranian uplands moved north by way of Transcaucasia, and animals of the Turan deserts migrated south and west through Ciscaucasia mostly through the Manych area, but there were no new immigrations of southern species into Transcaucasia.

The patterns and stages in the development of the Pleistocene Caucasian fauna are better understood when the fauna is compared with the Pleistocene faunas of the adjacent areas: the Russian Plain, the Crimea and southwest Asia. Comparative studies can be done on the Middle and Upper Pleistocene faunas; the data for the Lower Pleistocene and for the Pliocene-Pleistocene transitional period are insufficient.

The total number of known species of mammals in the Middle and Upper Pleistocene of the Russian Plain is 74. (The number is based on the identifications of Gromov (1948), Pidoplichko (1954) and our unpublished data for the Volga and Don areas). The faunas of the Russian Plain and of the Caucasus have 36 species in common, which amounts to nearly 50%. The quantitative faunal resemblance might be even higher if the alluvium in the river valleys of the Ciscaucasian plains were to be successfully searched for fossils.

The previously noted absence of boreal species (arctic fox, blue hare, lemming, reindeer and musk-ox) and the presence of mountain species (goat, chamois, sheep and a number of southwest Asian upland rodents) in the Caucasian fauna of the Pleistocene are the main features that distinguish it from the fauna of the Russian Plain of the same period.

Of the 58 species of Pleistocene mammals known in the Crimea (Birulya, 1930a, b; Vinogradov, 1937b; Gromova, 1935a; Gromova and Gromov, 1937; Gromov, 1948), 35 species (approximately 50%) also occur in the Caucasus. Among the species in common are the following representatives of plain and steppe assemblages: long-eared hedgehog, wolf, fox, corsac fox, cave hyena, badger, Panthera leo, great jerboa, small five-toed jerboa and mammoth.

The main difference between the faunas of the two areas is the absence in the Caucasus of steppe species (small pika, large-toothed suslik, Eversmann's hamster and yellow steppe lemming) and of northern species (arctic fox, blue hare and reindeer) which are highly characteristic of the Upper Paleolithic of the Crimea. The pronounced resemblance in other respects of the large-mammal faunas of the Crimea and the Caucasus may indicate
169 that the Pliocene-Pleistocene faunas in both regions evolved from a common

stock, and even that the regions were connected in the Lower Pleistocene by a landmass in the area presently covered by the Sea of Azov. It was the fauna of the southern part of the Russian Plain which primarily contributed to the faunas of the Crimea and the Caucasus.

Any discussion of the faunal relationships in the Pleistocene between the Caucasus and the areas to the south and southwest must be based on a sound paleontological record of the southern Black Sea coast and inner Anatolia. However, there are no data on the Pleistocene faunas of those regions, although the activity of Acheulean man has been traced in the interior of the country by Pittard (1929), Pfannenstiel (1941) and Sauter (1948).

According to Sauter, the interior of Asia Minor (Lake Tuz-Golii and other regions) was inhabited by prehistoric man from the early stages (Chellean-Clactonian-Acheulean) to the Mesolithic. This indication of natural conditions favoring the maintenance of human life means that large mammals were abundant in the Quaternary in regions bordering the Caucasus which are today deserts and salinas.

Furon (1955) has noted that inner Turkey was less of a desert in the Pleistocene than it is in the Recent. Lakes Tuz-Gölü and Budur-Gölü were 100 m deeper than their present depth. Of the Pleistocene cold phases, only the Würm phase is recognizable.

The Pleistocene fauna of the southern parts of southwest Asia and northeastern Africa is known mostly from the studies of Blanckenhorn (1901, 1910, 1921-1922), Vaufrey (1931), Bate (1937), and Picard (1937). Of the 69 species reliably identified by these authors, 22 (approximately 31%) also occur in the Caucasus. If species which are in doubt (Panthera leo, Bos and woolly rhinoceros) are included, the resemblance is even greater. As Picard correctly noted, there is no evidence that elk and reindeer lived in Syria or Palestine in the Pleistocene. Nor did they live in Egypt, contrary to Berg's uncritical quotation (1947, p. 82) of Blanckenhorn's statement on the occurrence of these northern forms. In the study of the development of the Caucasian fauna, it is important to take into account the occurrences of pine marten, European wildcat, Asia Minor hamster, tiger polecat, roe deer and other forms in the Pleistocene of Palestine. The late, postglacial stage of infiltration of southern Asian species into the Caucasus is represented by occurrences of jackal, striped hyena, jungle cat, kulan and goitered gazelle in the Upper Pleistocene. The core of the Pleistocene fauna of Syria-Palestine are the southwest Asian and north African (Mediterranean) forms, such as civet cat, lion, true ass, warthog, hippopotamus and Sinai ibex. The distribution ranges of these species in the Pleistocene probably did not include areas near the Caucasus. The confirmed absence of mammoth and the presence of the Acheulean Elephas trogontherii are important indicators in tracing the extinction of some "northern" species and the southern range extension of others (via the Aegean landmass and the Caucasian Isthmus) in the Pleistocene.

The paleontological material of Palestine has been studied in more detail with reference to evolution of climates and landscapes than has the material of the Caucasus. Bate (1937) attempted to represent the climatic changes graphically. Taking the bone-count as an index, he used several gazelle
170 species as representative of a xeromorphic landscape, and the fallow deer

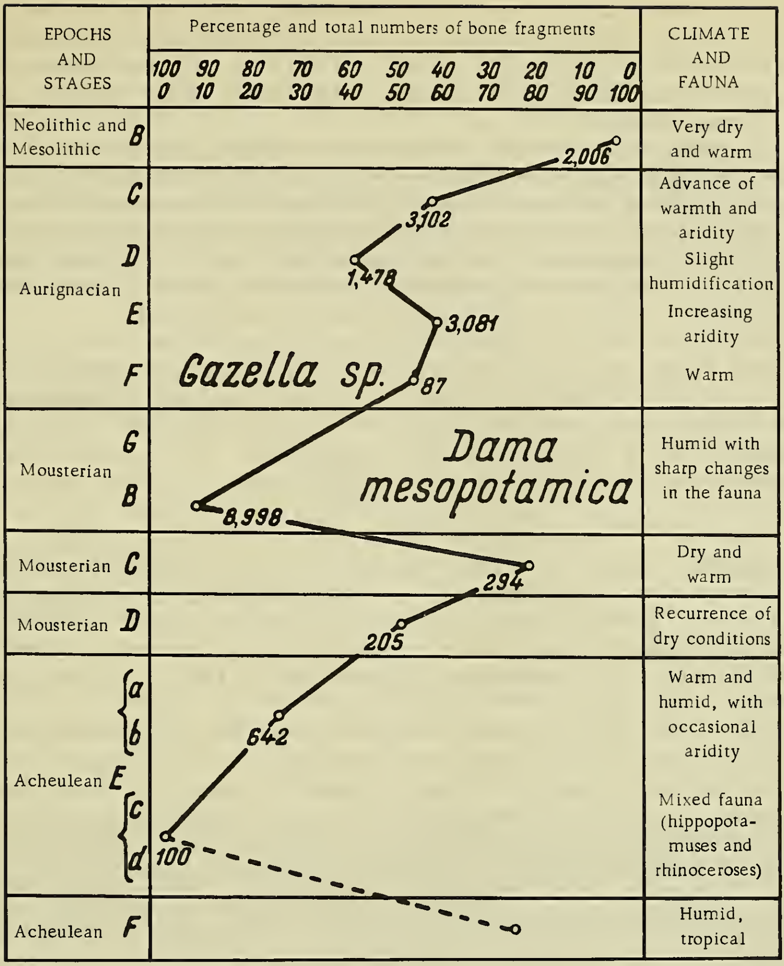

FIGURE 77. Variation in number of bones of Gazella and Dama during the Anthropogene based on food remains in caves of Mount Carmel, Palestine (excavations of Garrod and Bate, 1937)

(Dama mesopotamica) as representative of broadleaf forests and of a more mesophytic landscape. Gazelle and fallow deer were the main food of the ancient Carmelites inhabiting the Wadi el Mügharah and other caves.

Bate's study showed that Dama bones predominate over gazelle bones mainly in the Lower Acheulean, in the Upper Mousterian and in the Upper Aurignacian. According to Bate, hippopotamus and rhinoceros lived in Palestine at the time of the Lower Acheulean when the climate was dry and warm, as it was in the Middle Mousterian. The Upper Mousterian brought a humid, pluvial climate, with an abrupt change in fauna, and the Upper Aurignacian marked the last weak advance of humid conditions (Figure 77).

The pluvial stages in Palestine probably corresponded to mountain glaciations of the Lesser and Greater Caucasus. Picard (1937) concluded

that statements of Blanckenhorn's (1910, 1921) and others that the Pleistocene climate of Palestine was similar to the present climate of
171 Germany are erroneous. The paleontological data indicate that the climate of Palestine was of the Mediterranean type, fairly stable and dry, from the time of the Pliocene.

Cooler and pluvial periods, according to Picard, are represented by gravels possibly corresponding to the major glaciations in the north. The main pluvial stage in Palestine correlates with the maximum, Riss, glaciation of Europe. In addition, two poorly developed pluvials occurred between the Acheulean and the Mesolithic. As a whole, the landscape of Palestine was dry desert with islands of broadleaf forests in the more humid valleys, that is, a landscape similar to the Recent.

Three localities with Pleistocene mammals are known from the region south and southwest of the Caucasus (northwestern Iran). The mammals occur in diluvial sediments of marly hills near the town of Marāgheh and in the Bīsotūn and Tamtama caves. A. Gebel's collection from the Marāgheh vicinity (deposited in ZIN; see Brandt, 1870) contains fragmentary bones showing the Pleistocene type of preservation: Canis lupus, Crocuta spelaea, Rhinoceros cf. tichorhinus, Equus caballus, E. cf. hemionus, Bos sp., Ovis cf. ammon.

Paleolithic beds of the Tamtama cave, west of Lake Urmia near Rezaiyeh, which was excavated by Coon (1951), yielded fifteen identified mammal species, e.g., gerbil (Meriones), porcupine (Hystrix), deer (Cervus elaphus), goitered gazelle (Gazella subgutturosa).* Bones of deer constitute nearly 66%, and bones of horse nearly 12% of all the collected material.

Sixteen species of mammals are known from the Upper Paleolithic and latest beds of the Bīsotūn cave, near Behistun (a rock landmark) on the Baghdad-Hamadan road. The finds of jackal (Canis aureus), panther (Panthera pardus), pika (Ochotona sp.), goitered gazelle and other forms are of considerable interest. The most abundant are deer (nearly 50% of the collected material); these are followed by horse (23%) and goitered gazelle (12%). A seal tooth reported from this site was probably introduced from the Caspian coast; beaver remains were erroneously recorded.

This extremely interesting material indicates the northern range limits of some southern species not found at the Binagady locality. The fauna indicates a late Pleistocene climate and landscape in the northern part of the Iranian plateau quite similar to the Recent. However, the abundance of deer indicates well-developed tugai forests, which were later destroyed by man.

The stratigraphic and geographic distribution of Pleistocene species in the Caucasus and adjoining areas is given in Table 62.

The figures in Table 28 reflect the extent and detail of present knowledge of the Pleistocene "faunas" of the Caucasus and adjacent regions. From them it is possible to estimate the degree of faunal resemblance and the age of faunal connections between regions. They also confirm what has already been said of the predominantly northern and northwestern (southwestern [sic]) influence on the fauna of the plains and foothills of the
172 Isthmus in the Middle and Upper Pleistocene. At that time the areas of

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* Following Fraser's identification, Coon mentions the occurrence of a European beaver (Castor fiber), which is evidently a misidentification of porcupine bones.

distribution of the southern (southwest Asian) and local (Caucasian) species either had already moved to the south, or had been reduced to isolated relicts.

A survey of the stages and paths of development of Caucasian fauna by zoogeographic subdivisions can be made at this point only for the Upper Pleistocene, for which the following categories are recognizable:

1. Ciscaucasian steppes and forest-steppes, including the Ciscaucasian plains, the Stavropol Plateau and the Taman Peninsula, from the Manych in the north to the foot of the Bolshoi Range in the south, and to the Apsheron Peninsula in the southeast. The fauna is characterized by mammoth, bison, horse, cave bear, giant deer and saiga.

TABLE 28. Degree of similarity between Middle and Upper Pleistocene mammalian "faunas" of the Caucasus and adjacent territories*

	Caucasian Isthmus	Russian Plain	Crimea	Southwest Asia
Number of species known from Middle and Upper Pleistocene	83	74	58	69
Percentage of species in common between Middle and Upper Pleistocene	100	54	53	33

* These estimates rapidly become obsolete as new localities are discovered and new collections made available.

2. Caucasian mountain region, including the mountain system of the Greater Caucasus. In this region mesophilous mountain-forest types of mammals predominate: European brown and cave bear, mole vole, goat, chamois. Also present in the eastern part of the region are a few xerophilous species: Radde's hamster, wild goat and little suslik. These species originated in the Lower Pleistocene and have survived to the present in Dagestan and Kabarda.

3. Transcaucasian foothills region, which includes the foothills and the plains of western and eastern Transcaucasia. The eastern section of the region is characterized by southwest Asian rodent, southern-type rhinoceros, and horse and tur; the western is characterized by bison.

4. The region of the Lesser Caucasian plateau, characterized by an abundance of horse, mouflon and Bos primigenius. The hot valleys of the southern part of the region were probably inhabited by the camel and the northwestern slopes by mountain-forest species: mole vole, goat, chamois.

Conditions under which animals died and formation of deposits in the Holocene

The conditions under which animals died and their remains accumulated were generally constant from the Pleistocene into the Holocene but for some important changes in the later period. As the dry warm period advanced, there was a reduction of slope erosion by running water and consequently the deposition of diluvium and alluvium decreased, and fewer bones and animal remains were transported to river deltas, lakes and marine bays.

Man began to affect the landscape markedly by cutting and burning trees and changing the flow pattern of streams and, as the result of his direct and indirect influence on the landscape, the large mammals of the plains began to decrease rapidly in the Holocene. As another consequence, natural deposits of animal remains became very rare.

Some cases of mass death of Recent animals from natural causes and the modes of their deposition are described for the plains of the Caucasian Isthmus by Kolesnikov (1950) and Vereshchagin (1951d).

Mesolithic, Neolithic, Copper-, Bronze- and Iron-Age sites with bone-bearing beds have been discovered (Piotrovskii, 1949) and these remains of human cultures of the postglacial epoch in the Caucasus have been thoroughly studied. The map of Paleolithic localities, shown in Figure 78, is after Krupnov.

174 The scale and the location of human settlements changed radically in the Neolithic. Settlements were located on the shores of lakes and on riverbanks, and cave dwellings remained only as relicts of the Paleolithic until they reached a new stage of development during the feudal wars of the Middle Ages.

Because there was little tectonic activity in the Holocene, marine, deltaic and lacustrine deposits remained undisturbed, as they had during the Tertiary and the Pleistocene, and consequently they lie unexposed today. The possibilities of finding bones in relatively young deposits in diluvium, small niches and caves are considerably greater. Such accumulations of bones resulted from temporary settlements and predator activities, particularly those of owls and eagle owls.

Bone fragments similar to the Paleolithic constitute the food remains in the deposits of Holocene settlements. However, many more bone and horn implements were found from the Holocene than from the Paleolithic.

Occurrences of bones gnawed by domestic dogs are highly characteristic of the Holocene, but phalanges and metapodials from which bone marrow was extracted were no longer as thoroughly broken as in the Paleolithic.

Beginning with the Eneolithic, certain bone accumulations in the Caucasus which contain complete skulls and skeletons of both wild and domestic mammals give evidence of being ritual burials. The religious-cultural customs of several Caucasian mountain tribes account for peculiar ceremonial accumulations of domestic and wild animal skulls in the last few centuries of our era.

The discussion which follows, organized into geomorphological regions, treats all these types of deposits, some of which have been studied to a greater and some to a lesser extent.

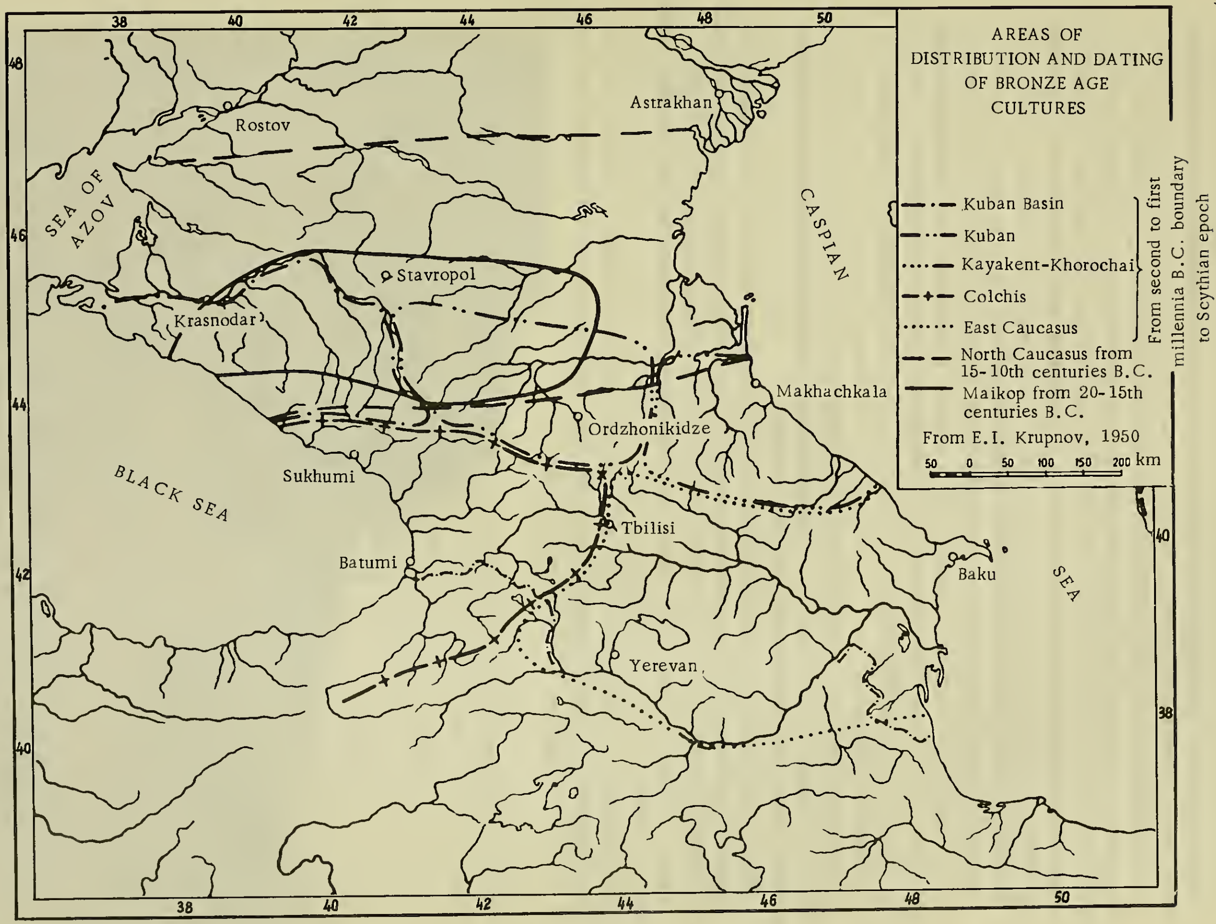
AREAS OF DISTRIBUTION AND DATING OF BRONZE AGE CULTURES
Kuban Basin
Kuban
Kayakent-Khorochai
Colchis
East Caucasus
From second to first millennia B.C. boundary to Scythian epoch
North Caucasus from 15-10th centuries B.C.
Maikop from 20-15th centuries B.C.
From E.I. Krupnov, 1950
50 0 50 100 150 200 km
Rostov
Astrakhan
SEA OF AZOV
CASPIAN SEA
Stavropol
Krasnodar
Makhachkala
Ordzhonikidze
Sukhumi
BLACK SEA
Tbilisi
Batumi
Baku
Yerevan
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FIGURE 78

Western Ciscaucasia and the south Russian Plain

The establishment in the Holocene of firm land connections between the Ciscaucasian and south Russian plains enabled mammals to migrate freely from one region to another.

Investigators studying Pleistocene fauna in the lower Don region uncovered abundant mammal remains from the Holocene. These bones were washed out of floodplain sediments and redeposited on sandy-gravelly spits. Archaeological excavations of settlements and mounds in this same area which were carried out by the Institute of Material Culture, AN S.S.S.R., also yielded large collections of bones.

Particularly valuable bone material was collected by Gol'msten during the excavation of mud-hut settlements on the Tsaritsa River dating from the fifteenth to tenth centuries B.C., and during the excavations of the Khazar fortress of Belaya Vezha (Sarkel) near the village of Tsimlyanskaya (Artamonov, 1952).

Eleven species of domestic and 23 species of wild animals have been identified from the more than 30,000 bones collected in these excavations on the lower Don, mainly at Belaya Vezha.*

The faunal complex of the steppes and plain forests is still pronounced in the wild mammal fauna of this period. The assemblage of game animals includes 16 species, ranging from corsac fox, steppe polecat and beaver to bear, elk and bison. The materials indicate that even in the Middle Ages
175 (700 to 1300, A.D.) the ranges of forest animals (taiga and forest-steppe zones) extended along the river valleys to the Ciscaucasian plains, where in the thickets of the floodplains of the Yeya and Kuban rivers they joined the Caucasian ranges of the same animals.

TABLE 29. Mammalian species and number of bones from Early Bronze Age mud huts near Gelendzhik**

Species	Number of bones	Species	Number of bones
Domestic		Wild	
Horse	2	Felix lynx	2
Pig	55	Lepus europaeus	1
Large cattle	396	Delphinus delphis	282
Small cattle, primarily sheep	106	Sus scrofa	2
Subtotal	559	Cervus elaphus	6
		Subtotal	293
		Total	852

The main archaeological monuments within Ciscaucasia proper are Neolithic settlements, Scythian mounds and cultural layers many meters thick of ancient Greek colonies and of the so-called Bosphorus kingdom (Rostovtsev, 1918; Kallistov, 1949) on the Taman Peninsula and on the

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* This material is being published separately.

** This and other similar tables were compiled from the author's unpublished data.

Kuban and Trans-Kuban plains. The Gelendzhik settlement is among the oldest settlements of the region.

In 1952 Akhanov collected many bones from pits in the Upper Neolithic-Lower Bronze Age mud-hut settlement on the shore of the Gelendzhik bay. The material consists of mottled and yellowed diaphysal and vertebral fragments which, when tapped, emit a light, ringing sound like calcined bones. Most of the bones are those of large cattle and dolphins; those left by man were later gnawed by some small predators.

The wild animals are represented by deer, bear, lynx and hare (Table 29). Individual bones of fish, shells of marine mollusks and edible snails were also collected at the site.

The wild species at the Gelendzhik settlement indicate that sea game was important to the ancient Tamanians, or at least that they consumed the bodies of dolphins washed ashore by the sea. Forest game species (lynx, boar, deer) were also abundant in the vicinity.

Thick bone-bearing beds, usually no more than 2-3 m and occasionally as much as 10 m thick, occur on the shores of the Taman Bay, at the sites of the ancient towns of Cepi, Phanagoria and Taman. The beds are being
176 eroded by the sea because of the subsidence of the coast in historical times. Bones of domestic animals, sturgeon-like fishes and characteristic layers of purple Mytilus shells comprise the food remains which are plentiful at these sites. Bones of wild animals rarely occur in these beds, which confirms the accepted concept of a high degree of cultural development in this region at that time (Figure 79).

FIGURE 79. Exposures of cultural layers of Phanagoria on south shore of Taman Bay

Photograph by author, 1952

TABLE 30. Species and number of bones of domestic mammals from Taman towns

Species	Cepi	Phanagoria	Taman
Dog	4	10	5
Cat	2	—	3
Horse	11	18	13
Pig	5	6	2
Large cattle	9	68	27
Sheep	15	34	32
Goat	3	6	—
Small cattle (no closer identification)	—	4	10
Total	49	146	92

Table 30 lists bone fragments collected from several hundred meters of cultural layers from the three towns.

177 From the incidence of identified domestic species it appears that the landscape of the Taman Peninsula in the second half of the first millennium B.C., on the whole, was similar to the Recent. The nomadic herds of the Scythians and the local animal husbandry of the Greeks must have strongly depleted the vegetation cover of the peninsula at that time. Large species decreased and the remainder of the animal assemblage probably consisted, as it does in the present, of European hedgehog, fox, hare, field mouse, house mouse, common vole and mole rat.

More complete and interesting data are available for the ancient site of Semibratnoe near the Cossack village of Varenikovskaya, east of the Kuban River mouth. Anfimov's excavations in 1938-1939 and in 1951-1952 showed that a small settlement occupied the site as early as the fifth century B.C. A town of considerable size developed in the third to second centuries B.C., which was later destroyed and abandoned. A small settlement of hunter-fishermen occupied the site in the first century A.D. The bone material, collected in stratigraphic sequence, completely confirms the conclusions drawn from study of the material culture. Particularly significant are the large numbers of bones of wild species occurring in the fifth century B.C. and again in the first century A.D. (Table 31).

178 Some bird bones were also collected in the beds of this town: domestic chicken, wild duck and stork. The collections also include numerous bones of sturgeon, stellate sturgeon and cyprinid (mostly wild carp).

Ancient animal husbandry was evidently not highly developed in the Bosphorus. Dogs were uniformly small, about the size of a spitz, and were probably used only as watchdogs. The bones of goats, sheep and swine are light, which indicates poor feeding. Cows were of the European short-horned type, somewhat larger than northern "peat" cattle. The occurrence of bones of otter, boar and deer may indicate that reed-grown swamps covered the area, in which there were probably no large forests.

Bones from excavated Scythian mounds in the Maikop area, dating from the middle of the first millennium B.C., are known only from Vselovskii's drawings (1901). He depicted many tens and hundreds of skeletons of horses which had been killed during funeral ceremonies for tribal chieftains.

TABLE 31. Mammalian species and number of bones from the ancient town of Semibratnoe

(177)

Species	Present Era	Before Present Era					Total individuals
	I	I	II	III	IV	V	
Domestic							
Dog	2/2	1	46/32	26/17	25/16	48/31	99
Horse	7/5	10/6	102/52	33/18	74/32	142/75	188
Pig	15/8	5/4	64/44	36/16	101/42	103/70	184
Large cattle	39/14	13/5	153/67	87/37	215/53	303/183	309
Sheep	9/6	13/12	72/43	27/11	98/37	152/72	181
Goat	—	—	17/8	4/3	32/17	63/28	56
Small cattle (no closer identification)	—	3/2	—	3/2	—	—	4
Subtotal							1,021
Wild							
Canis lupus	—	—	—	—	—	4/4	4
Meles meles	—	—	1	—	—	2/2	3
Lutra lutra	—	—	—	1	—	—	1
Lepus europaeus	—	—	1	—	2/2	4/4	7
Sus scrofa	25/7	2/1	4/2	3/3	2/2	16/3	28
Cervus elaphus	24/7	12/8	6/6	4/3	6/6	6/5	35
Capreolus capreolus	—	—	1	—	1	—	2
Subtotal							80
Total							1,101

Note. Slash separates number of bones from number of individuals.

TABLE 32. Mammalian species and number of bones from mounds near Ust-Labinskaya

Species	Present Era	Before Present Era						Total individuals
	I-II	I	II	III	IV	V	VI	
Dog	1/1	3/1	17/1	—	—	—	—	3
Horse	1/1	19/3	5/5	90/3	1/1	—	8/1	14
Pig	—	—	49/5	20/6	10/1	—	1/1	13
Large cattle	32/5	18/4	1/1	55/6	3/1	1/1	—	18
Sheep	—	6/2	31/2	6/1	—	—	—	5
Goat	—	—	—	33/3	—	—	—	3
Small cattle (no closer identification) . .	—	2/1	11/3	13/6	—	—	—	10
Total								66

Note. Slash separates number of bones from number of individuals.

Excavations on a limited scale carried out by Petrovskii and Anfimov (1937) in the towns and burial grounds of the Kuban area east of Krasnodar uncovered bones of horses and large and small cattle from layers of the fourth century B.C. to the third century A.D.

Pieces and amulets carved from large deer antlers and bear tusks which were collected from these burial grounds are housed in the Krasnodar Museum.

We identified only eight species of domestic animals among the 337 bones from the burial grounds excavated by Anfimov near the Cossack village of Ust-Labinskaya. The animals were sacrificed during funerals and buried with the dead as food supply (Table 32).

The dogs in this region were about the size of a small husky. Swine, cows, sheep and goats were also quite small.

The ancient site of Elizavetovskoe and mounds on the left bank of the Kuban, 13 km west of Krasnodar, were excavated by Gorodtsov (1935, 1936) in
179 1934-1935. From layers of the early centuries of the present era, Gorodtsov recorded "many bones of cows of two varieties, small pig, sheep, goat (?) and three varieties of dog. Bones of wild animals are very rare; only antlers of red deer, placed in the grave with the dead, were found."

Artamonov (1937) collected remains of the following animals from Late Bronze Age mounds on the steppes of the northern bank of the Manych (near the Manych canal and the village of Spornyi):

Domestic	Wild
Horse	Lepus europaeus
Pig	Marmota bobac
Large cattle	
Sheep	

TABLE 33. Mammalian species and number of bones from hills on the south bank of the Manych

Species	Number of bones	Number of individuals
Domestic		
Dog	16	1
Horse	12	2
Large cattle	4	2
Sheep	71	5
Subtotal	103	10
Wild		
Vulpes vulpes	38	3
Canis lupus	1	1
Meles meles	1	1
Lepus europaeus	2	1
Subtotal	42	6
Total	145	16

Other species are known from the southern bank of the Manych, near the village of Veselyi; they occur in mounds of the middle of the first millennium B.C. (Table 33). Had marmot bones been found at this site, it would be of great paleogeographic interest, since marmots have not been documented on the Ciscaucasian plains by twentieth-century zoologists.

Domestic animals were probably sacrificed in rituals. The bones of fox, wolf, badger and even hare, however, which were collected from the talus of the mound, are the remains of animals which died in their holes.

The foothill regions and river canyons of northwestern Ciscaucasia are
180 paleontologically unknown. Interesting data can probably be obtained from a study of the bones in the ancient Alani settlements, which are preserved in ruins in the Laba, Belaya and Zelenchuk river gorges and in the old pits in asphalt crusts near Khadyzhensk (Vinda, 1910).

The only bones known from this region are the skeleton of Microtus (Chionomys) roberti — from a 14th-century burial chamber in the gorge of the Malaya Laba River, near the village of Andryukovskaya — and a horn of a Caucasian elk (Alces alces caucasicus), collected in 1949 in the gravels of the Urup River near the village of Otradnaya.

Central Ciscaucasia

At present the Stavropol Plateau and Pyatigor'e are peculiar meadow-forest "mesophytic islands" in the steppe plains. As such, they have retained to the present a number of mesophilous species of mammals which migrated to this region during the cold phases of the Pleistocene. The migrations came from the north, from the south and from the Greater Caucasus.

Deer and lynx which have completely disappeared from the relict forests of the Stavropol area are known from published records (Dinnik, 1914a) and from material in the Stavropol Museum to have inhabited the region until recently.

Small mammals are among the species which have disappeared, or are about to. The length of time that the little suslik was isolated in the inner valleys on the northern slopes of the Greater Caucasus is a particularly interesting paleontological problem.

Toward its solution, bone material from the layers of the ancient towns has been studied and special reconnaissance excavations have been carried out in caves and under overhangs on the margins of the Stavropol Plateau, in laccoliths of Pyatigor'e and in cliffs of the river canyons cutting the Kabarda Plain.

The region of the Kabarda Plain was well populated by man in the Lower Holocene, as shown by occurrences of Neolithic tools, numerous mounds and remains of ancient settlements. The Eneolithic burials at Nal'chik, excavated by Miller in 1929, contained ornamentations made of teeth of domestic and wild animals: cat, fox, boar, red deer, goat, sheep and a very large Bos, either domestic or wild.

Similar ornamentations from excavations by Kruglov, Piotrovskii and Podgaetskii (1941) were found in the Neolithic burials of the Nal'chik mound, near the ancient site of Agubekovskoe. The ornamentations consisted of teeth of boar, deer, fox, bear, and Bos.

The Degen-Kovalevskii (1935) excavations of the 6th—8th-century settlement near the village of **Zeyukovo** (53 km from Nal'chik) found the Alani food remains to consist mostly of bones of domestic animals (Table 34).

The bull from this locality was small, as shown by its bones, and undoubtedly belonged to a domesticated variety. Characteristic of the locality is the first occurrence of domestic pig and of a very primitive variety of goat, with horns curved similarly to the horns of Capra prisca.

Kistyakovskii (1935) recorded remains of 15 species of extant rodents in the pellets of predatory birds of the steppes to the north and east of the Stavropol Plateau, and reported their occurrence in the same area of distribution as at present.

Some bones of rodents and insectivores were collected by Lyutyi (1940)
181 from eagle owl pellets on the western slopes of the plateau, near Stavropol. His data did not contain any new zoogeographical information.

TABLE 34. Species and number of bones of mammals from Alani settlement near Zeyukovo

Species	Number of bones	Number of individuals
Domestic		
Dog	2	1
Horse	8	2
Pig	15	3
Large cattle	29	3
Small cattle	10	2
Subtotal	64	11
Wild		
Cervus elaphus	1	1
Total	65	12

In the fall of 1950 we made a paleontological reconnaissance survey of the western part of the limestone cliff of **Mount Strizhament** on the southern margin of the Stavropol Plateau. The presence of forest, springs and "a sea of rocks" indicated a likelihood of finding bones of forest and steppe animals, left by ancient hunters and cave predators, in this area.

In four small caves only individual bones of sheep and cows, brought by shepherds and wolves, were collected. The unstable ceilings and big blocks of limestone on the floors prevented a more detailed survey.

A considerable number of small-mammal bones brought by eagle owls during the last century were collected in one of the caves on the cliff. The results of the identification of the bones are given in Table 35.

The most interesting find was the remains of a pine vole, which is not recorded in the literature as occurring in this region, although the species commonly occurs nowadays on the meadows of the plateau. This occurrence of the species, separated from its main area of distribution in the Caucasus, is biogeographical evidence that the climate in the past was more humid than in the present.

Pyatigor'e. Studies were done on isolated elevations in the steppes of Pyatigor'e and compared with the Stavropol Plateau. Particular attention was devoted to the permafrost of Mount Razvalka, 5 km north of Zheleznovodsk, and to the gorge of the Berezovka rivulet south of Kislovodsk.

Reconnaissance excavations were carried out on the eastern slope of Mount Razvalka near the Selitryanaya cave. At the site, dense broadleaf forest surrounds two picturesque trachytic rocks, weathered by wind erosion. A small dry cave, formed at the junction of three vertical joints,
182 is located under the southern rock. Over the last millennia, deposits accumulated to a depth of 8-9 m under the entrance to the cave through erosion of the upper cliff platforms and the rock face, and as the ancient dwellers cleared the cave of rock fragments. The site of the debris was probably used as a resting place for cattle, since the bones of small and large mammals and fragments of pottery occur in layers at the foot of the cliff and in the cone of the cave debris.

TABLE 35. Mammalian species and number of bones from pellets of eagle owls on Mount Strizhament

Species	Number of bones	Number of individuals
Hemiechinus auritus	13	2
Erinaceus europaeus	25	4
Talpa caucasica	7	1
Mustela nivalis caucasica	8	2
M. nivalis dinniki	5	1
Lepus europaeus	3	2
Cricetus cricetus	19	3
Mesocricetus auratus	290	34
Cricetulus migratorius	211	29
Microtus arvalis	215	32
M. majori		
Spalax microphthalmus	17	3
Apodemus sylvaticus	30	7
Micromys minutus	5	3
Mus musculus	1	1
Rattus norvegicus	5	1
Total	854	125

Our trial trench, 1 m wide and 3 m long, was dug 1.5-1.9 m deep into the talus in front of the cave entrance. The collections consisted mostly of simple black pottery, made with broken shells, of ancient Alani type. The pottery from the deeper layers is ornamented with pitted and striated markings, characteristic of the Bronze Age. An obsidian fragment, a fragment of a stone hammer and a small whetstone made of black slate were found in the upper 60-cm-thick layer.

(183) TABLE 36. Mammalian species and number of bones at the Selitryanaya cave in Pyatigor'e

Species	Depth (cm)			Total bones
	0-60	60-120	120-200	
Domestic				
Dog	1	1	—	2
Horse	9	8	2	19
Pig	34	17	7	58
Large cattle	103	74	39	216
Sheep	103	72	—	175
Goat	29	5	—	34
Small cattle (no closer identification)	32	77	67	176
Subtotal	311	254	115	680
Wild				
Hemiechinus auritus	2	—	—	2
Erinaceus europaeus	—	2	—	2
Talpa caucasica	1	1	1	3
Vulpes vulpes	—	—	1	1
Ursus arctos	1	—	—	1
Mustela nivalis	2	1	—	3
Meles meles	4	—	—	4
Putorius eversmanni	2	—	—	2
Vormela sarmatica	1	—	—	1
Felis silvestris	1	—	—	1
Lepus europaeus	17	1	1	19
Glis glis	10	4	1	15
Cricetus cricetus	173	23	1	197
Mesocricetus auratus	159	22	2	183
Cricetulus migratorius	13	4	—	17
Arvicola terrestris	31	10	—	41
Microtus arvalis	18	—	—	18
M. majori	1	1	—	2
Rattus norvegicus	2	—	—	2
Apodemus sylvaticus	2	2	—	4
Mus musculus	1	—	—	1
Spalax microphthalmus	1	—	—	1
Sus scrofa	4	8	—	12
Cervus elaphus	1	5	—	5
Capreolus capreolus	3	1	1	6
Subtotal	450	85	8	543
Total	761	339	123	1,223

Fragments of large-mammal bones are typically found as food remains. The burial also contains rare fragmentary implements made of deer antlers. Remains of small animals are represented by bones from the pellets of birds of prey, mostly eagle owls which habitually rested on the rocks above the cave. The locality is a rare and valuable example of a deposit formed by the three processes of bone accumulation: remains of food transported by birds, remains of game transported by hunters who used the cave for shelter, and remains of food left from ritual tribal feasts or transported by ancient shepherds.

Nearly 1,500 fragments of domestic and game animal bones were collected in stratigraphic sequence, all showing an approximately uniform mode of preservation. In small fracture, they are yellow or white in color, and very few show any signs of fossilization.

184 It can be estimated that the layer accumulated over the last 2,000-2,500 years.

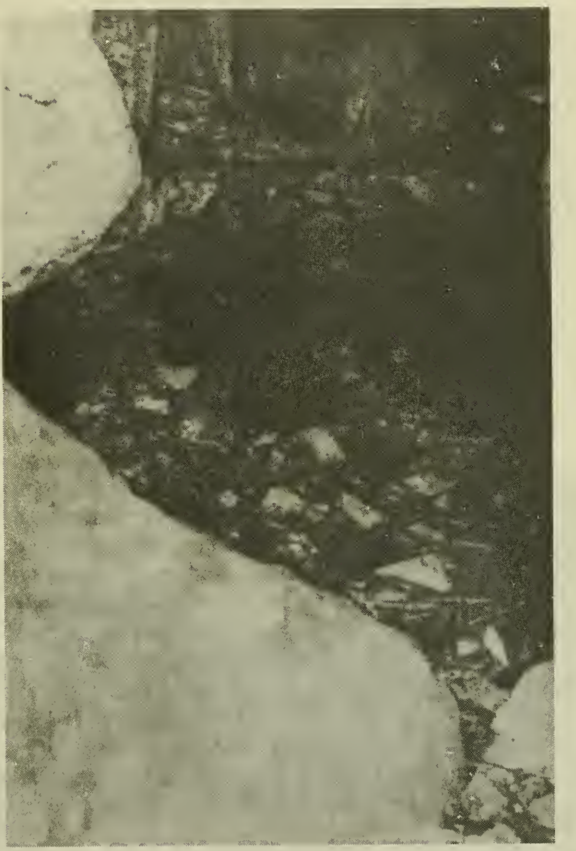

FIGURE 80. Cave inhabited by eagle owl on Mount Lysaya. On top are bodies of seven hedgehogs and one corncrake

Photograph by author, 1952

Six species of domestic and 26 species of wild animals have been identified in the collection of bone material (Table 36).

Remains of birds, toads, frogs and shells of Clausilia and Helix were collected at the same locality.

At the time of the ancient Alani settlement most of the Razvalka slope was probably deforested and man's occupation of the site probably drove away the eagle owls and other predators. As a consequence of their disappearance from the area at that time, the deeper layers of the deposit show a sharp decrease in the number of rodent bones. In the main, the deeper layers reflect man's activities, and it is only in the last quarter of our era, when Pyatigor'e and Razvalka again became covered with forests, that most of the wild-animal bones, particularly those transported by eagle owls, were accumulated. Large forest game inhabited the area at this later period: bear, boar, deer and roe deer. Old records show that deer disappeared from the region at the beginning of this century. Bears, roe deer and boars occasionally enter the forests of Pyatigor'e in our times, although they do not live there permanently. During the same late period, the last four to five centuries, the food of the eagle owl consisted of small species characteristic of the laccolith region in the present: three hamster species and water, pine and common voles. Bones of snow voles (Chionomys gud), hamsters and water rats were collected in rock crevices over the stone-covered permafrost area.

A few specimens of snow vole were collected in the rocks of the "century-old freezer" of Mount Razvalka, at altitudes of 400-500 m above sea level. The nearest that the species has been found elsewhere is a site 3 km south of Kislovodsk in the gorge of the Berezovka rivulet, which is 50-55 km away from Mount Razvalka. Thus the occurrence of the snow vole at Mount
185 Razvalka indicates that during a cold period in the past, probably at the time of maximum glaciation, the mountain animals migrated to these minor elevations in Pyatigor'e.

FIGURE 81. Crevice in limestones on western wall of Berezovka rivulet gorge near Kislovodsk — day resting site of eagle owl

Photograph by author, 1954

TABLE 37. Mammalian species and number of bones from pellets of eagle owls near Kislovodsk

Species	Number of individuals*	Species	Number of individuals*
Sorex araneus	1	Arvicola terrestris	51
Talpa coeca	3	Microtus arvalis	2
Mustela nivalis...........	3	M. gud	4
Putorius eversmanni.......	3	Apodemus sylvaticus	1
Lepus europaeus	1	Mus musculus.............	2
Dyromys nitedula	1	Rattus norvegicus	3
Cricetus cricetus	45	Spalax microphthalmus	2
Mesocricetus auratus	23		
Cricetulus migratorius.....	3	Total	148

* Number of individuals given is based on number of mandibles.

Plentiful remains of insectivores and small carnivores in the pellets of eagle owls were collected in the laccolith farther northeast under the rocky overhangs of Mount Lysaya (Figure 80) and in the gorge of the Berezovka rivulet, south of Kislovodsk (Figure 81).

186 At the latter locality the material is older and more abundant. It was obtained from a half-meter-thick layer of Holocene dust deposit under a vertical joint in the Lower Cretaceous limestone cliff. This resting place must have been abandoned by the eagle owl not less than a century ago, since it is located only 1 km from the southern outskirts of Kislovodsk. The bones accumulated during several centuries of the second half of our era.

A total of 1,582 bones was collected. Their preservation is not uniform. The bones from the lower layer are coffee-colored with dendrites; bones from the upper layer are yellow.

The species composition of the collected fauna indicates that the landscape at the time of accumulation of the bones was very similar to the present (Table 37 and Figure 82).

Nineteen specimens of amphibians and 305 bones of birds were collected at the same site. The assemblage of relatively xerophilous steppe species is quite prominent, as at Mount Razvalka: hamster, polecat, mole rat.
187 This assemblage never occurs in complete composition this far into the mountains. The moist meadows and rock-covered areas of the Berezovka gorge account for the large numbers of water rat and the occurrence of snow vole.

The hamsters and mole rats in this region were the precursors of the relatively xerophilous assemblage which migrated in postglacial time from the dry Ciscaucasian plains to the north. This advance overlapped by tens of kilometers the northernmost occurrences of the forest and alpine species (pine and snow voles, forest dormouse, fat dormouse) which remained in mesophytic sections of the laccoliths and in the river gorges after the recession of the colder, more humid period. The uppermost limits of distribution of this assemblage are the moist meadows of the Pastbishchnoi ridge and the lower reaches of narrow gorges cut by rivers through the ridge (Vereshchagin, 1953a).

(186)

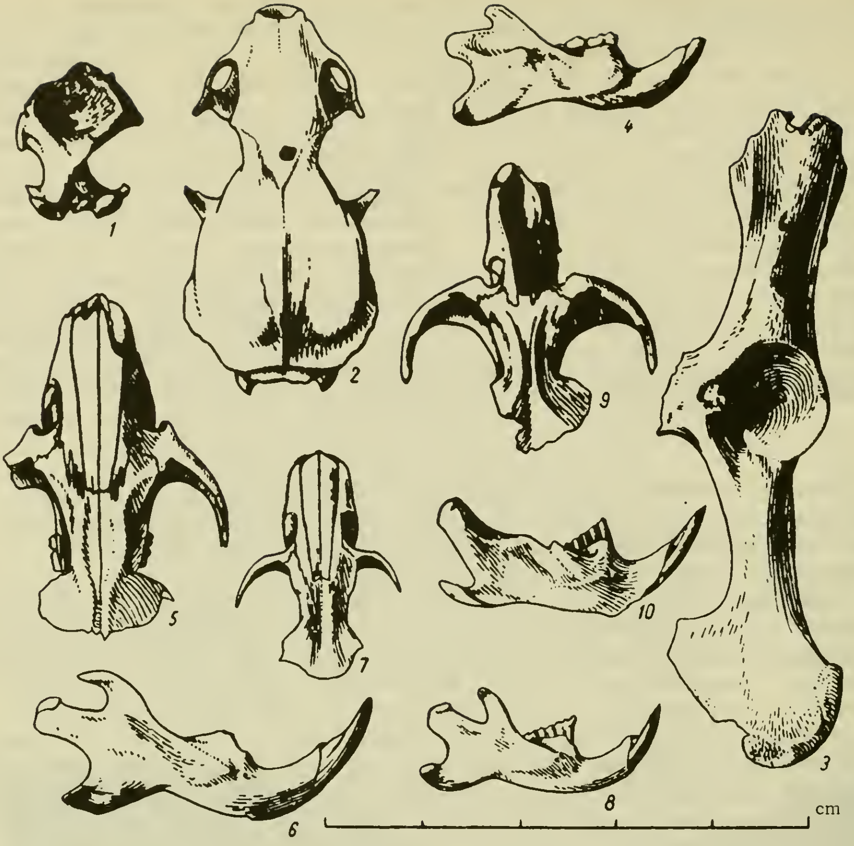

FIGURE 82. Mammalian bones from pellets of eagle owls in the Berezovka gorge

1 — humerus of Talpa caucasica; 2 — skull of Mustela nivalis; 3 — pelvis of Lepus europaeus; 4 — jaw of Rattus norvegicus; 5, 6 — skull of Cricetus cricetus; 7, 8 — skull of Mesocricetus auratus nigriculus; 9, 10 — skull of Arvicola terrestris

In the western part of the region, a similar picture exists, although at a lower altitude, on the right bank of the meridional section of the Kuban River.

The following conclusions can be drawn from the study of Holocene animal remains in the foothills of central Ciscaucasia:

1. The intensive exploitation of the region by man from the Neolithic to the present resulted in a diminution of the wooded area and the disappearance of large animals (bison, deer and, later, roe deer and boar).

2. The presence of mesophilous relicts of the cold (glacial) epoch has been established. The relicts survived in the steppe on the Pyatigor'e laccoliths and on the Stavropol Plateau. This fauna includes the snow and pine voles.

3. A dominant assemblage of relatively xerophilous species of rodents (hamster, mole vole, mole rat), characteristic of open areas, existed in the foothills of the Kislovodsk area and further south during the last millennium, and possibly during the entire present era. During this period the little suslik did not live in the Pyatigor'e area. The migration of this species in the Holocene to the longitudinal valleys of the range can be established only after its remains have been found in layers deeper than those excavated. Such an occurrence might prove the existence of a postglacial climatic phase drier and warmer than the present climate.

Eastern Ciscaucasia

The steppes of the eastern Manych area are of interest to the paleozoologist because of the occurrence of a microlithic culture, usually identified as Late Neolithic. Tribal sites containing microlithic material occur in the southern Ukrainian and Crimean steppes, along the northern coast of the Caspian and in the border scarps of the Ust'-Urt, and deep into Soviet Central Asia. The most permanent settlements of these tribes were located in the Berovskie hills, surrounded by elms and rich in fish and boar.

In this region, remains of material culture and fragments of animal bones occur in wind-blown depressions, on wind-eroded mounds and in sandy hills. Fragmentary bones of giant mole rat (Spalax giganteus), saiga and sheep occur at sites such as these in the steppes of the Kuma area; the great gerbil (Rhombomys opimus) occurs in blackland sands. Between the lower reaches of the Kuma and the Volga, the archaeqlogist Sinitsyn discovered numerous bones of animals of many varieties around the remains of ancient campfires. He also discovered many settlements and burial grounds of the Bronze and Middle Ages.

188 Remains of a large bull with horns similar to those of Bos primigenius from the pre-Scythian Tri Brata mounds near Stepnoi were photographed by Sinitsyn (1948, p. 151).

He dated the burials end of the second to beginning of the first millennium B.C. The culture, i.e., Transcaucasia, is similar to that at Trialet (Kuftin, 1941).

Similar and younger monuments of the pre-Scythian and Scythian epochs have been traced by Krupnov (1947) in the steppes between the Terek and the Kuma. Osteological material from this region would greatly clarify the notion proposed by Krupnov that there were considerable changes in the landscape during the last millennium B.C., and would probably also improve our concepts of the history of the ranges of central Asian desert animals.

Farther south, on the northeastern slopes of the Dagestan foothills, bone material is known from settlements and mounds of the Bronze Age. Primitive archaeological excavations were carried out by Russov (1879) and Tsilossani (1879) in the region of Derbent, Kayakent and Deshlagar. Their excavation log indicates "bones of rodents," "bones of animals," "bones of large and small domestic animals," etc., occurring in caves, mausoleums and burial mounds. The ZIN collections contain bone materials, obtained by Kruglov (1946a) in excavations in 1941 from layers of a settlement of the second half of the second millennium B.C. near the villages of Kayakent and Dzhemikent. The bone fragments from these layers are light brown in color and they clink slightly. Bones of boars tend to absorb water as do Upper Pleistocene bones. Identifications and counts are given for these fragments in Table 38.

TABLE 38. Mammalian species and number of bones from Bronze Age settlement near Dzhemikent village

Species	Number of bones	Number of individuals
Domestic		
Dog	82	1
Large cattle	129	6
Goat	11	4
Sheep	46	5
Small cattle (no closer identification)	401	15
Subtotal	669	31
Wild		
Phoca caspica	1	1
Ursus arctos	1	1
Vulpes vulpes	1	1
Equus hemionus	6	1
Sus scrofa	3	1
Gazella subgutturosa	6	1
Subtotal	18	6
Total	687	37

189 The occurrences of seal, goitered gazelle and kulan in the region are noteworthy (Figure 83).

The reconnaissance excavations of 1954 carried out under the picturesque cliffs of Kapchugai west of Makhachkala by the archaeologists of the Dagestan Branch of the AN SSSR revealed layers which have been dated late second to early first millennium B.C. The following bones have been identified by us from these layers: horses (3), large cattle (12), sheep (14) and red deer (Cervus elaphus) (12). These numbers indicate both the abundance of deer and the importance of game hunting in the economy of the ancient shepherd tribe. The cliffs of Chokrak sandstones at the site are covered with line drawings of animals, made only a few centuries ago. Panther, horse, deer and saiga can be recognized in some drawings.

Remains of Iron Age animals are known from excavations of ancient settlements in the valleys of the Sunzha River and its tributaries.

Krupnov (1948) has published the results of excavations of a settlement of Scythian time (second half of the first millennium B.C.), near the village of Alkhaste on the left bank of the Assa River (Table 39).

He also reports (1949) a similar ratio of domestic species distribution for the Assa River valley settlements of Nesterovo and Lugovoe (sixth to fifth centuries B.C.; identifications by Tsalkin). At the Lugovoe locality a horn stem of a saiga and individual bones of a roe deer have been identified among the numerous bones of domestic animals.

FIGURE 83. Mammalian bones from the Bronze Age settlement near Dzhemikent

1 — jaw of Vulpes vulpes; 2 — tarsus of Ursus arctos; 3-5 — first phalanx, hoof and astragalus of first phalanx and tibia of Equus hemionus; 6-9 — horn, head of femur, first phalanx and tibia of Gazella subgutturosa

(190)

TABLE 39. Mammalian species and number of bones from Scythian epoch settlement near Alkhaste village

Species*	Number of bones	Number of individuals
Domestic		
Dog	6	3
Horse	21	6
Pig	175	15
Large cattle	101	10
Small cattle (no closer identification)	54	8
Subtotal	357	42
Wild		
Vulpes vulpes	1	1
Cricetus cricetus	5	1
Cervus elaphus	2	1
Capreolus capreolus	6	3
Subtotal	14	6
Total	371	48

* N.A. Sugrobov's identifications. Bones of bear were probably included with domestic pig.

TABLE 40. Mammalian species and number of bones from settlements and burial grounds in the Sunzha valley

Species	Number of bones	Number of individuals
Domestic		
Dog	75	4
Cat	5	1
Horse	55	3
Pig	32	10
Large cattle	64	7
Sheep	145	12
Goat	6	3
Subtotal	382	40
Wild		
Equus hemionus	1	1
Cervus elaphus	1	1
Subtotal	2	2
Total	384	42

In the eastern part of the Sunzha valley, excavations of settlements and burials of the second to third centuries A. D. were carried out in 1938 by Kruglov near the villages of **Isti-Su, Alkhan-Kala and Khoro-Chai.** The bones from these excavations, identified by the author (Table 40) are heavy and stained in places with humus. There are only a few remains of wild 191 animals. However, the new evidence of past occurrences of steppe species of large mammals in the foothills of the eastern Caucasus is of considerable interest.

In 1952 we made a reconnaissance search for species of smaller mammals in the cavities and talus of the Sarmatian limestones above Makhachkala and in the sandstone cavities near Kapchugai. Large numbers of bones were collected: long-eared hedgehog (Hemiechinus auritus), hare (Lepus europaeus), little suslik (Citellus pygmaeus), hamster (Mesocricetus auratus nigriculus) and steppe vole (Microtus socialis). All the bones were collected in the pellets of eagle owls and flying predators which settled to rest on the cliffs.

Further paleontological studies of Holocene burials, which take into account the earlier archaeological data (Komarov, 1879; Shtein, 1879; Iessen, 1935), will undoubtedly fill in the detail of the general picture we have of postglacial steppe species of ungulate mammals in the region. They will also add to an understanding of the decrease in numbers and deterioration of composition of the fauna toward the present.

Longitudinal valleys of the northern slope of the Greater Caucasian and inner Dagestan

The longitudinal tectonic valleys, bounded in the north by the Pastbishchnoi and Skalistyi ridges, are well developed east of Elburz. Like woodless inner Dagestan, the valleys attracted post-Paleolithic tribes as inhabitants because of their natural shelters and dry, relatively warm climate. Mesolithic sites have recently been discovered in the valleys and in inner Dagestan. Some Bronze Age tribes left behind them remarkable burial monuments: mounds, underground burial sites and catacombs for mass burials. The sites of their settlements are represented by fairly thick layers of the "Kobanian culture" (Uvarova, 1900, 1902).

The medieval Alanis built numerous fortresses and war towers, fortified caves and individual trenches in the vertical, rocky cliffs. Their descendants, the Ossetians, built peculiar collections of hoofed-mammal skulls in ritual places called "dzuars."

Many bones of rodents from the pellets of eagle owls accumulated in natural niches and ruins of the fortresses.

We studied all these types of deposits, with the exception of the Kobanian burial grounds and settlements.

Mesolithic sites in the Baksan and Avar Koisu gorges

In 1955, Zamyatnin discovered and studied diluvial sediments, many meters thick, containing Mesolithic flint tools, on the right slope of the Baksan ravine at the head of the first gorge near the village of Byllym (Figure 84). Excavations to a depth of 6.85 m at the Sosruko overhang revealed a sequence of Middle Ages, Early Iron Age and five Mesolithic layers with characteristic flint tools of the transitional epoch.

Most of the bones taken from every layer were broken into small fragments. The loss of organic matter in the bones is in its initial stage. Identifications of the collected bone fragments are given in Table 41 and Figure 85.

193 In addition to the species listed, about ten bones of partridge, short-eared owl, griffon, vulture and small Passeriformes were collected from the Mesolithic layers.

The list of animal species, although variegated, presents no zoogeographic novelties. Most of the species are characteristic of the region in the last century, prior to the extermination of deer, chamois and goat on the Skalistyi ridge. The find of suslik bones in the Mesolithic beds is particularly interesting as related to the question of the age of the populations of this species in the mountains of Caucasus. However, these bones may have originated in the steppe plains of the Manych area and been introduced into the layers from pellets of eagle owls and predators flying south.

The Mesolithic site of Chokh in inner Dagestan was discovered in 1955 by Kotovich 2 km north of the village of Chokh in the Gunib area.
194 The site is located under a steep limestone rock (Figure 86) on the right bank of a small stream, which cuts deeply into a mountain ravine covered

FIGURE 84. Sosruko grotto in Baksan gorge

Photograph by S.N. Zamyatnin, 1956

by an alpine meadow. The thickness of the Mesolithic layer in the excavated area exceeds 0.5 m. The cultural layers contain flint tools in all stages of finishing and finely-fractured bones. Among the flint implements are tools with blunt backs, points, knifelike blades [or flakes] and various microliths.

(193) TABLE 41. Mammalian species and number of bones in Mesolithic beds of the Sosruko grotto in Baksan gorge

Species	Middle Ages	Early Iron Age	Mesolithic beds				
			1	2	3	4	5
Domestic							
Pig	7	4	—	—	—	—	—
Large cattle	20	15	7	—	—	—	—
Small cattle	23	28	44	—	—	—	—
Subtotal	50	47	51	—	—	—	—
Wild							
Vulpes vulpes	1	—	—	—	—	1	—
Martes sp.	1	—	—	—	—	—	—
Meles meles	—	—	1	—	—	—	1
Panthera pardus	—	—	—	—	—	—	1
Lepus europaeus	—	1	—	3	2	—	—
Citellus pygmaeus	—	—	1	—	—	1	1
Apodemus sylvaticus	—	—	—	1	—	—	—
Ellobius talpinus	—	—	1	1	1	—	—
Microtus gud	—	—	—	—	1	—	—
Sus scrofa	—	—	6	7	3	1	—
Capreolus capreolus	—	4	—	—	—	—	1
Cervus elaphus	1	1	1	2	12	—	—
Rupicapra rupicapra	—	—	—	—	—	7	1
Capra cf. caucasica	—	—	4	1	11	—	—
Artiodactyla (no closer identification)	7	3	73	125	526	198	45
Subtotal	10	9	87	140	556	208	50
Total	60	56	138	140	556	208	50

The state of preservation of the fragmented bone material is similar to that of fragments from beds of the third and second millennia B.C. in the foothills of Dagestan. Identifications of the bone material in the 1955-1957 collections are given in Table 42 and Figure 87; most of the fragments are unidentifiable. The rodents are represented by species which are characteristic of the region in the present. They were introduced into the site from the pellets of predatory birds. Among the ungulate bones, the most interesting are those of a bison and a small ram, probably a successor to the rams of the Lower Paleolithic Kudaro site.

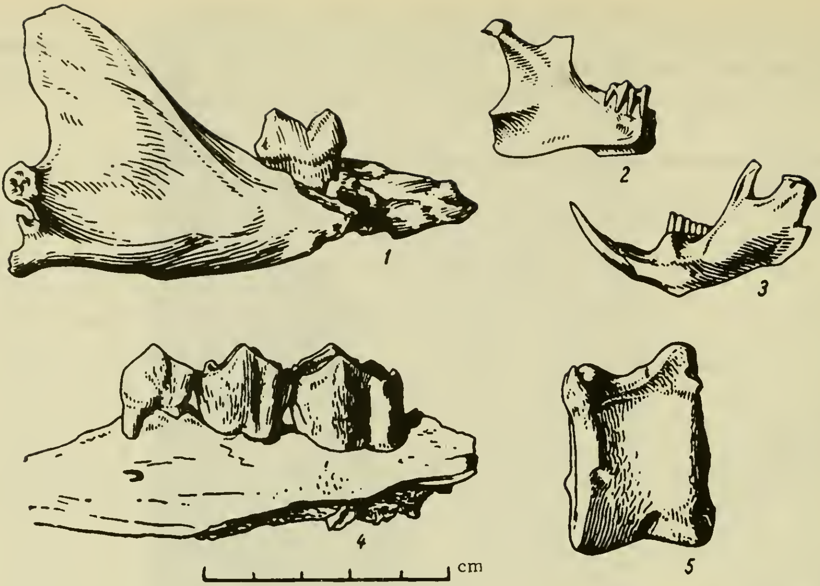

FIGURE 85. Mammalian bones from the Mesolithic layers of Sosruko grotto

1 — jaw of Panthera pardus; 2 — jaw (× 2) of Citellus pygmaeus; 3 — jaw (× 2) of Ellobius talpinus; 4 — jaw of Cervus elaphus; 5 — astragalus of Capra caucasica

From the Koban burial grounds of the Bronze Age in Ossetia, archaeologists long ago collected sculptures of local domestic animals. These sculptures were made of bronze or, more rarely, of gold and silver.

Pendants, fibulae, metal plates, buckles and heads of staves were often made by Koban craftsmen in the forms of heads of Caucasian goats, deer, elks, wild and domestic rams, bulls, goats, horses and bears (Uvarova, 1900).

The past occurrence in the Caucasus of some of these species was confirmed by our studies of Ossetian burials. The materials from those sites indicate a late stage of existence of a rich assemblage of mammals on the northern slope of the Greater Caucasus.

195 Dzuars of North Ossetia

Collections of skulls of domestic and wild ungulates from ritual sites in the Caucasus have long been known. These collections were mentioned by 17th century European travellers in Circassia (Jean de Luc, 1879). Reference is made to them in the notes of Güldenstaedt at the end of the 18th century (Pallas, 1831), and in papers by Dinnik (1890a) and Satunin (1914). The period of accumulation of skulls in the dzuars extends over the last five centuries.

TABLE 42. Mammalian species and number of bones from the Mesolithic site at Chokh in Dagestan

Species	Number of bones	Species	Number of bones
Domestic (?)		Capra sp. (cf. aegagrus or C. cylindricornis)	8
Horse	1	Ovis or Capra wild	94
Wild		Caprovinae (no closer identification)	7,202
Felis lynx	1	Bison bonasus (caucasicus?)	20
Lepus europaeus	1	Small fragments of skeletal bones, mainly Artiodactyla	712
Mesocricetus auratus	5		
Arvicola terrestis	5		
Sus scrofa	1	Total	8,400
Cervus elaphus	48		
Ovis sp. (cf. gmelini)	302		

In 1947 and 1948 we studied 18 dzuars in the ravines of Urukh, Ardon, Fiagdon and Gizel'don (Figure 88).

Skulls from dzuars located on the piedmont plains, e.g., the sacred Khetag grove, were taken in the thirties to bone-calcination plants. Up to 30% of the dzuars in the mountain zone were also emptied of their bones (Vereshchagin and Semenov-Tyan-Shanskii, 1948; Vereshchagin and Naniev, 1949).

The Adygeians, Digorians and Ossetians built their ritual sites in picturesque groves on the spurs of ridges, under rocky overhangs and in caves. Special buildings were also constructed: churches, chapels or large enclosed sheds made of stone or of large logs.

Dzuars were dedicated to different deities and each one belonged to a particular village; the villagers assembled there for feasts on special annual holidays of spring, summer or fall.

The custom of killing animals in the dzuars during feasts survived from pagan times in Abkhazia. According to Abkhazian legend (Veidenbaum, 1879), a white bull used to emerge from the Oggin cave and was sacrificed.

196 In addition to ritualistic killing of domestic hoofed mammals, the Digorians and Ossetians used to bring skulls of wild, hoofed animals to the sites. This custom of bringing skulls into the dzuars was connected with the belief in the god Avsati, protector of hunters and game, to whom the skulls were dedicated. The occurrence of bison leg bones, with hoofs intact, in the deep skull-bearing beds of the Digorized cave suggests that special hunting expeditions set out before the holidays to bring an intact deer, elk or bison into the dzuar. Skulls of wild, hoofed animals, boiled by hunters, were also brought into the dzuars without relation to holidays. They were either carefully laid in one common pile or on special shelves and supports, or they were hung on cut branches of trees and placed against the walls of the dzuar. It is difficult to estimate the age of the collections from the number of wild animal skulls.

The state of preservation was not uniform among the skulls of wild hoofed animals from different dzuars, because of differences in treatment

197 and preparation. No skulls had intact lower jaws; of the bison skulls, only the hardest frontal and occipital bones with horn stems attached, were preserved. This mode of preservation is identical to that of the skulls of primitive bison from the shoals of the Don, the Volga and the Ural.

FIGURE 86. Chokh site on the Gunib

Photograph by V.G. Kotovich

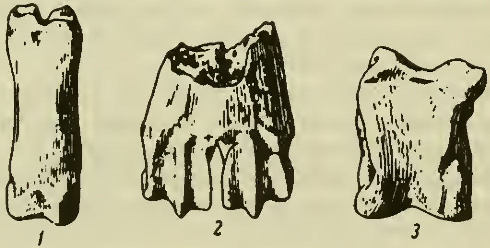

FIGURE 87. Mammalian bones from Mesolithic beds of the Chokh site

1-3 — First phalanx, metatarsal epiphysis and astragalus of Ovis cf. gmelini

Only a few skulls were preserved in their entirety with basal part, intermaxillaries and horns intact. The horns were fastened to the stems with iron arrowheads inserted into holes prepared for this purpose. Horns were also removed from their stems and used as wine goblets. Boiled skulls of turs, chamois and roe deer were usually brought in after the basal

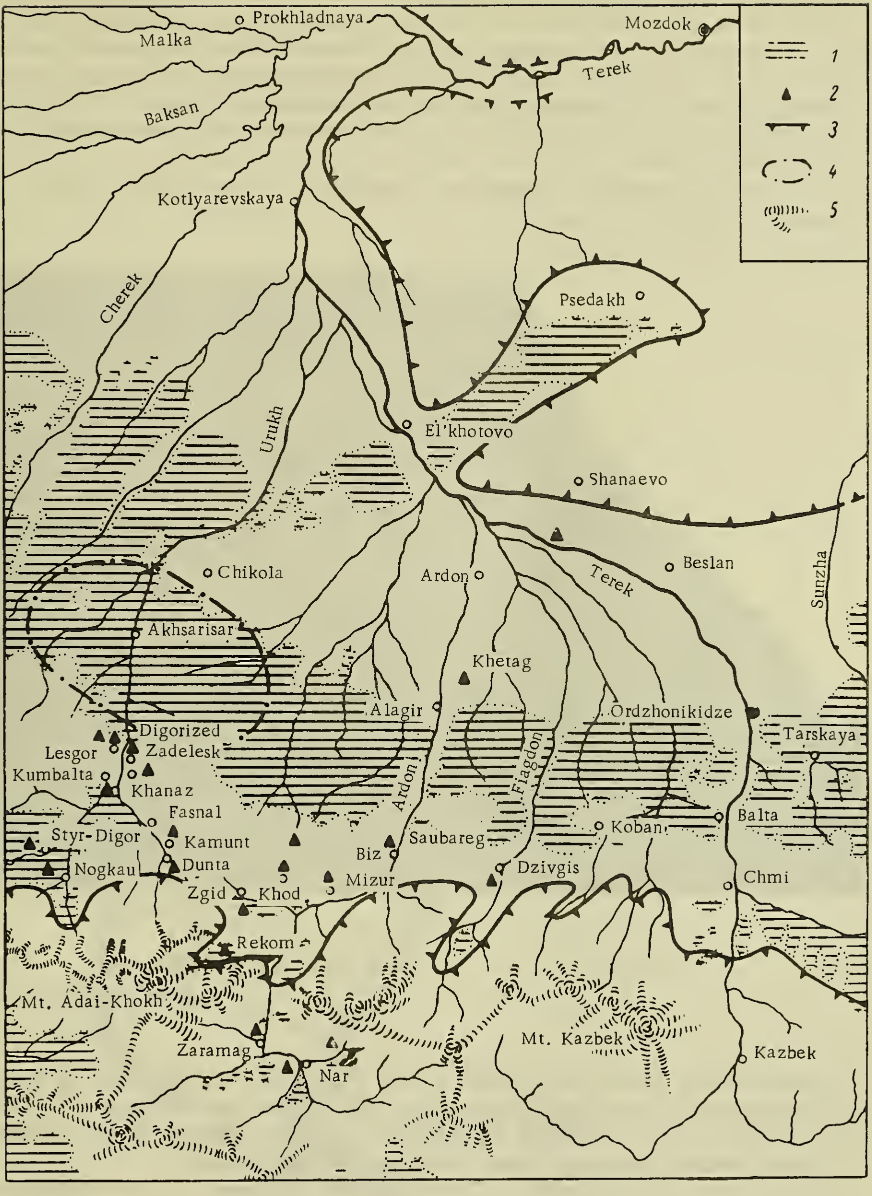

FIGURE 88. Map of some dzuars in North Ossetia

1 — remaining forests; 2 — ritual sites studied; 3 — limits of distribution of deer in the 19th century; 4 — area inhabited by relict bison and elk at the end of the 18th century; 5 — Recent glaciers

part had been removed with an oblique cut. The horns were removed, together with skin and parts of frontal bone, from the fresh skulls of male deer and elks killed in the fall. The brain was then removed through the
198 skull opening. The skulls were boiled, cleaned of flesh and small bones and placed in the dzuar. All the skulls of female deer and elks are without occipital bones which were excised to the dorsal mid-height. Most of the deer skulls did not have nasal parts, as they separated from the skull in the boiling process.

The most remarkable dzuars are Digorized (Olisai-Don), Lesgor I and Lesgor II and Rekom.

FIGURE 89. Digorized cave in Jurassic slate cliff in Urukh gorge

Photograph by author, 1947

Digorized cave is located on the right bank of the Urukh gorge in the southern cliff of the Skalistyi ridge. The cave was formed in the process of the weathering of Jurassic limestones. Ledges, picturesquely covered by pines, juniper and dog rose, occur on the giant cliff.

The cave is approximately 1,200 m above sea level. It lies within the village limits of Zadelesk, located 1.5 km to the south.

The mouth of the cave is triangular in shape, approximately 12 m high and 5.5 m at the base. The entrance is covered by a strong wall, 2.5 m high, made of limestone fragments (Figures 89 and 90).

The feasting hall is approximately 7 m wide and 12 m long and contains a primitive fireplace, narrow benches and tables made of split pine logs,

an iron cup for donations, two knotty-wood trunks placed against the wall,
carved wood fetishes hanging on the trunks and some utensils, consisting
of two large meat bowls, a wooden spoon and about fifteen horns of bison,
used as goblets. A pile of skulls and horns in the far left corner is heaped
199 between two fallen limestone blocks. A support, 2.7 m high, built of logs
and boards, stands in the forepart of the hall. Some 140-150 pairs of
antlers are piled on the support (Figure 134). The walls of the hall are
covered with resinous soot from the fireplace. The entrance to the narrow
right branch of the cave is blocked by an upright wooden log with a tin icon
of St. Nicholas. At the entrance, the height of the branching chamber is
about the height of a man; the height decreases and the chamber ends eight
meters from its entrance. The floor is covered by a meter-thick layer of
skulls and horns of artiodactyls (Figure 91).

The annual feasts in the Digorized cave took place in June during the mowing season.

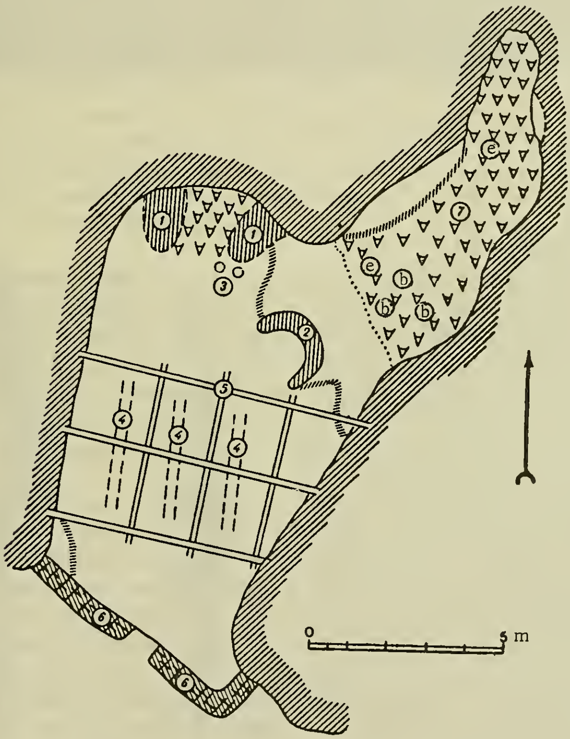

FIGURE 90. Map of Digorized cave

1 — fallen blocks; 2 — fireplace; 3 — ceremonial pottery; 4 — benches; 5 — support with deer antlers; 6 — stone wall; 7 — skulls of domestic goats, roe deer; e — elk skulls; b — bison skulls

On our first visit to the cave in August 1947, three elk skulls and 15 bison skulls were found in the front rows of skulls on the floor of the branch. These were probably the skulls noted by Güldenstaedt and Dinnik. Dinnik mentioned three camel skulls which were not in the cave; he probably misidentified the elk skulls. The pile of skulls in the left corner of the feasting hall was covered by centuries-old dust layers, whereas the skulls in the right branch of the cave had evidently been recently disturbed by archaeologists or tourists. As the layer of skulls was being sorted, bent or looped twigs (symbolic yoke), planed, half-burned sticks (shashlik spits), iron arrowheads (Figure 92) and small silver coins were found.

The greatest number of bones found at Digorized were skulls of sheep, and, in descending order, skulls of deer, large cattle, domestic goats, bison, roe deer, chamois, elks, Caucasian turs, wild boars and buffalo. The ratio was established by the value placed on the hunters' sacrifices and by the availability of various game species in the hunting area around the village of Zadelesk. The bison and elk skulls are the best-preserved bone material because they remained on the floor of the dry parts of the cave, between the entrance and the side branch. In many cases, ligaments on the anterior and posterior sections were preserved because of the absence of hide beetles. On the frontal bone of one of the bison skulls the figure "1833" had been engraved with a knife. The elk skulls were in the same state of preservation. Remains of tree twigs and bushes were well
200 preserved in the crevices of the animals' teeth. No elk horns were found in the cave. The horns had been removed from the frontal and occipital parts of one of the elk skulls in the front row. In another skull, found in a far corner, the horns had either fallen or been broken off the crown. It is possible that the horns were stolen from the cave or retained by the hunter as a particularly valuable trophy.

Deer antlers, found mixed with skulls in places protected from rain and snow, retained their natural brown color. Traces of molting were preserved on only a few antlers of deer which had been killed in August. Most of the bones left on the support, however, became uniformly whitened on the upper surface by rain, snow and sun, and blackened underneath by soot. Skulls of chamois and roe deer occur mainly in the middle and far section of the bone layer. Their state of preservation was much the same as that of the bison and elk skulls.

The Dagestan goat is represented by four skulls with preserved horns; their condition indicates that they were middle-aged. The three skulls of wild boar found in the upper layers piled to the side can probably be accounted for by the fact that the Digorians in later times abandoned their earlier religious prejudices against this animal, and also by the fact that the supply of more valuable animals dwindled. Fresh-boiled skulls and limb bones, fractured by an ax, and ribs were only those of large cattle, goats and sheep. It was clearly observed that large skulls of ancient, mature bulls had been replaced in recent time by skulls of small, immature specimens, which had been broken longitudinally.

201 The skulls indicate that the large cattle of the region belonged to only one variety during the entire period of accumulation of the bone bed. These were large animals, with a concave area between the horns, which extended forward, sideward and upward. The cattle belonged to the secondarily enlarged European Bos brachyceros. Skulls of goats and sheep

FIGURE 91. Interior of Digorized cave

Photograph by author, 1947

represent relatively small varieties with poorly developed horn stems and horns. If it is assumed that, from the beginning of the annual ritual, one bull and two to three sheep were sacrificed each year, it follows that the collection accumulated over not less than 500 years.

The skulls in the right branch of the cave were deposited over a thin layer of limestone debris and old dust, underlain by a solid plate. A reconnaissance trench dug in the left corner of the feasting hall down to the limestone floor (a depth of 60 cm) showed that there are no bones in the layer of old dust.

Because skulls of bison and elks were particularly valued by the Digorians as ritualistic offerings to Avsati, it would seem likely that most of the skulls of animals killed by the Zadelesk hunters were deposited in the cave.

It is clear that the incidence of deer and, particularly, of elk was very low even as early as the 15th to 16th centuries. In all probability, the period of accumulation of the skulls could not have begun before the

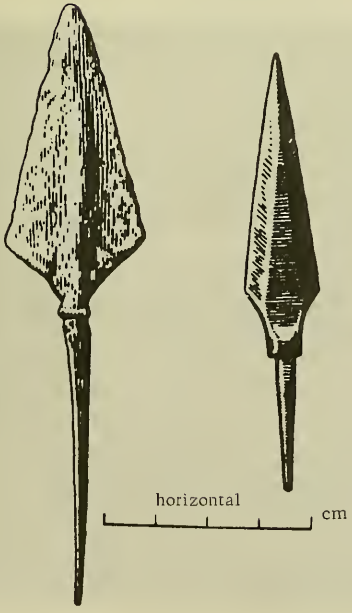

FIGURE 92. Iron arrowheads from Digorized cave

14th or 15th century and must have ended in the 18th or early 19th century. The accumulation in the cave of deer skulls and horns, as indicated by their state of preservation, ended only a little later than that of the skulls and horns of elk and bison. However, the deer survived until the time when the Ossetians obtained rifles. The Zadelesk hunters killed on an average up to ten deer each year.

The Digorized bone material is particularly interesting for analysis of the age and sex groups of the game, as well as the seasonal hunting yields. These data are given in Table 43.*

TABLE 43. Sex and age groups of wild ungulates from Digorized cave

Species	Females			Males			
	immature	mature	total	young	immature	mature	total
Sus scrofa	—	—	—	—	—	3	3
Capra cylindricornis	—	1	1	—	—	3	3
Rupicapra rupicapra caucasica	—	15	15	—	—	10	10
Bison bonasus caucasicus	9	26	35	1	8	21	30
Capreolus capreolus	10	10	20	—	2	32	34
Cervus elaphus maral	10	265	275	—	55	384	439
Alces alces caucasicus	—	4	4	—	—	2	2

The main game animal, deer, was hunted mostly in the fall, during the rut.

Dzuar Lesgor I (lower) was built on a small ledge of the same Skalistyi cuesta and at the same altitude as the Digorized cave, but on the left wall of the Urukh gorge. It belonged to the village of Lesgor, which was abandoned at the beginning of this century. The skulls were arranged in two layers behind a stone fence on an open wall. The lower layer rests directly on the ground, the upper on a big pine log inserted into a crevice in the rock, and on a "hanger" made of a knotty-pine trunk. The upper pile
202 of skulls is colored by the smoke of the ritual fire, which was regularly lit under the rock. Most of the skulls and antlers of deer in the lower layer decayed because of moisture. The following kinds of skulls (given in descending order of occurrence) were found: sheep, cow, goat, deer, east Caucasian goat, roe deer, bison and elk. Among them was a completely "fresh" skull of a young bison and a completely smoked skull of a she-bison with right horn intact.

Lesgor II (upper) is located 250 m higher on the cliff on the side of a very steep path in a picturesque crevice. The collection of skulls is under a small rock overhang and is poorly protected from weather. Deer antlers rest on a horizontal, elevated support made of pine logs. Some of the skulls on the ground have "grown" into the soil and become covered with sod. Skulls of wild, hoofed mammals are more numerous than at Lesgor I, probably because the dzuar is located closer to the hunting grounds

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* Only the skulls whose age and sex were identified with certainty were counted.

and farther away from the village. The descending order of occurrence is as follows: sheep, east Caucasian goat, deer, cow, goat, bison, chamois, elk and roe deer.

As at Lesgor I, the horns are missing on most of the goat skulls; they were broken off and probably taken to the village (Figure 93).

This group of the Urukh dzuars is very important in the study of the past ranges of deer and elk and their gradual shrinkage. Since it was difficult to carry the skulls and horns by mountain paths to the dzuars, hunters chose the most venerated dzuars and those which were closest to their hunting grounds. From the location of the ancient mountain paths through the passes of the Skalistyi ridge, which connected the villages Zadelesk and Lesgor with the piedmont plain, and from local legend, it can be established that most of the skulls of deer, elk and bison originated below the dzuars in the forests of the Chernye gorge and on the sloping Terek plain, particularly in the vicinity of the village of Akhsarisar. Even in the 'twenties, deer still appeared during the mating season in the upper Urukh gorge, near the villages of Styr-Digor, Nogkau, Kamunt and Dunta. The last of the bison and elk, however, mainly inhabited the foothill forests of Ossetia toward the end of the 18th century. This is confirmed by the absence of skulls of these forms in the upper dzuars. In the longitudinal 203 valley proper, between the Skalistyi and Bokovoi ridges, deer, elk and bison were probably either exterminated or driven out before the time of the Digorians by dense settlement and destruction of forests by earlier inhabitants. There are reasons to believe that elk and bison still frequented the forests of Ossetia at the time of Güldenstaedt's travels, although only sporadically.

FIGURE 93. Skulls of east Caucasian goats in Lesgor II dzuar

Photograph by author, 1947

Rekom Dzuar is the best known dzuar in the literature. It is located in the gorge of the Tseya (a tributary of the Ardon) in the pine-forest zone of the Bokovoi ridge and is greatly venerated by the Ossetians (Vyazigin, 1929). The dzuar belongs to the village of Tsei, but is visited by villagers from other places as well.

The dzuar is a massive structure dating from the end of the 17th century. It is constructed of pine and yew logs with one door and no windows and is situated in a pleasant meadow surrounded by old pine forest and rocks, with an outlook to snow-covered peaks (Figure 94). The site was inhabited as early as the Bronze Age.

Those skulls which remain after they were plundered by tourists for souvenirs rest on specially constructed wall ledges and shelving of raised earth. The material consists of skulls and horns of Caucasian goats, domestic sheep, cows, goats and deer. (Satunin (1914b) reported bison skulls from the Rekom dzuar.) Most of the remains of Caucasian goat consist of horns and soft horn stems weathered and split by moisture and sun. Six fresh-boiled skulls were also found, brought probably from the margins of the nearest glaciers during the last 20-30 years. Chamois still live in the rocks above the dzuar. Because of the deep winter snow deer and roe deer probably did not inhabit the region even in the past. Most of the deer skulls and horns of Rekom were brought there from the lower areas of the Ardon basin.

204

FIGURE 94. Rekom dzuar

Photograph by author, 1947

TABLE 44. Species and number of skulls of hoofed mammals from sacramental site in North Ossetia

Species	Fiagdon basin	Ardon basin						Urukh basin											Subtotal
	Dzivgis	Tabakhu	Nar	Zaramag (lower)	Biz	Mizur (upper)	Rekom	Sadon (upper)	Zgid	Khod	Dunta	Nogkau	Styr-Digor	Kumbulta	Khanaz	Digorized	Lesgor I (lower)	Lesgor II (upper)	
Domestic																			
Buffalo	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	1
Large cattle	4	118	155	166	42	68	39	53	81	73	79	39	3	6	500	492	118	50	2,086
Sheep	3	305	223	134	123	108	72	39	76	80	62	156	10	11	1,000	1,396	138	125	4,061
Goat	2	60	73	27	41	17	6	27	56	53	18	53	5	6	200	244	73	30	991
Subtotal																			7,139
Wild																			
Sus scrofa	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	3	—	—	3
Capreolus capreolus	9	—	—	—	2	—	—	—	—	—	—	—	—	—	—	51	3	1	66
Cervus elaphus maral	12	3	1	—	1	—	17	—	—	76	1	1	—	2	67	661	54	49	945
Alces alces caucasicus	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	6	1	1	9
Capra cylindricornis	1	10	—	5	—	5	292	11	5	10	11	21	—	8	—	4	40	86	509
C. caucasica	—	—	—	—	—	—	6	—	—	—	—	—	—	—	—	—	—	—	6
Rupricapra rupicapra caucasica	—	—	—	7	3	3	—	—	—	10	—	1	—	—	4	25	2	3	58
Bison bonasus caucasicus	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	73	2	3	79
Subtotal																			1,675
Total																			8.814

The horns and skulls of Caucasian goats belonged to mature or even aged individuals of 6-17 years; the most common age is 10-11 years (Figures 95-96).

From the 18 dzuars we collected up to 10,000 items: skulls, horns and fragments of skulls and horns of 8,815 individuals. They belong to 11 species of hoofed mammals: domestic species of bull, buffalo, sheep and goat; wild species of boar, bison, east Caucasian goat, chamois, elk, deer and roe deer (Table 44).

Our studies of the skulls in the Ossetian dzuars compared with data drawn from the literature and with other verified data lead to the following conclusions:

1. One and a half centuries ago the Terek-Sunzha inclined plain and the canyons on the northern slope of the Greater Caucasus were inhabited by eight species of artiodactyls: boar, bison, east Caucasian and west Caucasian goats, chamois, red deer, elk and roe deer.
2. Bison and elk were on the verge of extinction by the end of the 18th century, at which time deer were still abundant.
3. The final extermination of deer in that section of the Greater Caucasus under study occurred in the second decade of the 20th century.
4. The number of goats, chamois, roe deer and boars greatly decreased during the last century and the beginning of the present one.
5. It was chiefly human activity that brought about the extinction of some species and the population decrease of others, directly through unrestricted use of firearms and indirectly through the cutting down of forests on the inclined piedmont plain.

Ritual sites similar to those described earlier, containing bone material mostly consisting of skulls and horns of east Caucasian and wild goats and deer, are also known from Khevsuretia, Tushetia and Dagestan (Dinnik, 1914a; Makalatiya, 1935; Maruashvili, 1955).

206 Bones of small mammals in pellets of eagle owls and little owls have been collected by the author at two localities in the inner valleys. These bones occurred at the bottom of small caverns in limestone rock near the
207 village of Dzivgis in the Fiagdon gorge. They are not more than 150-200 years old, completely white and in a good state of preservation.

The present landscape of this area is composed of turfy dry slopes covered with tragacanth, astragali and rocks. Vegetable gardens, hay meadows and pastures are located near the river. The height above sea level is approximately 1,400 m. The list of the fauna is given in Table 45.

Approximately 40 fragments of lizards and toads were collected at the same locality.

All the species mentioned live in the present in the dry part of the Fiagdon valley. However, it should be mentioned that the occurrence of Norway rats, domestic mice and, possibly, migratory hamsters are related to the deforestation of the valley.

Bones of other species were found in the pellets of little owls in the ruins of a medieval fortress on the upper reaches of the Doniserdon, the right tributary of the Urukh.

The upper parts of the longitudinal valley are covered with mesophytic meadows and birch groves. The altitude is nearly 1,600 m above sea level. The fossil species correspond to the fauna of the Recent landscape (Table 46).

A comparison of Tables 45 and 46 which takes into account the evolution of landscapes in the inner valleys indicates that the composition of the mice fauna and their distribution in the dry inner valleys changed considerably over the last few centuries.

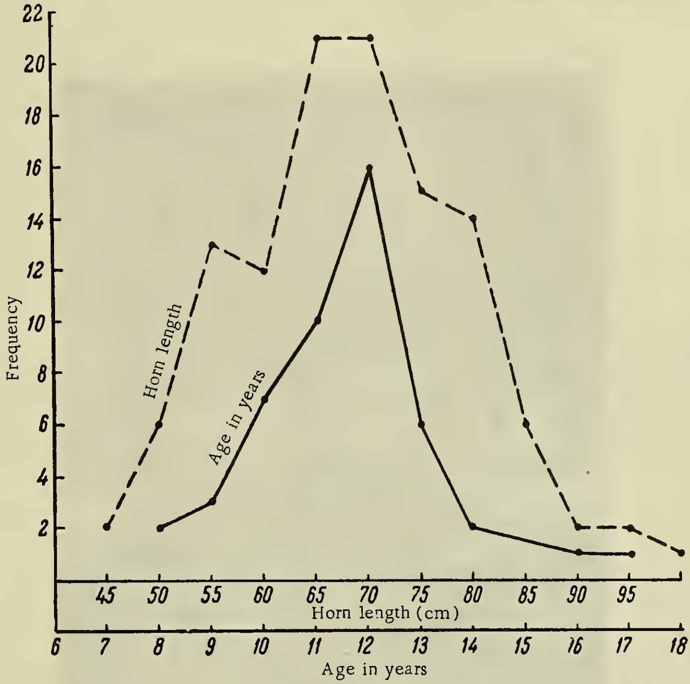

FIGURE 95. Relationships between age groups and size of horns of east Caucasian goats in Rekom dzuar (length of horns measured along the maximum curvature)

(206) TABLE 45. Species and number of bones of mammals from pellets of eagle owls and little owls near Dzivgis village

Species	Number of bones	Number of individuals
Vulpes vulpes	6	1
Mustela nivalis	2	1
Lepus europaeus	3	1
Cricetulus migratorius	139	22
Microtus arvalis	22	4
Mus musculus	8	3
Apodemus sylvaticus	15	6
Rattus norvegicus	93	7
Total	288	45

The increasing aridity in the valleys, caused by cutting the groves on the slopes and grazing of cattle, resulted in the replacement of the mesophilous ecological assemblage of rodents (Microtus arvalis, M. majori, Chionomys gud) by a xerophilous assemblage (Cricetulus migratorius, Mus musculus hortulanus, Lepus europaeus) and by the introduction of synanthropic forms (Rattus norvegicus, Mus musculus musculus).

FIGURE 96. Horn covers of goats and deer antlers along the walls of Rekom cave

There are no data on the recent extinction of small mammals in the areas under study. Also no remains were found of those ancient species of little suslik (Citellus pygmaeus musicus) and Radde's hamster (Mesocricetus auratus raddei) which are characteristic of the inner valleys of Kabarda in the west and Dagestan in the east.

208 Western Transcaucasia

In the Holocene human settlements clustered around the terraces of the Black Sea coast, mountain river gorges and the shores of water bodies in swampy Colchis.

TABLE 46. Species and number of mammal bones in pellets of little owls from the upper Doniserdon

Species	Number of bones	Number of individuals
Sorex araneus	5	1
Mustela nivalis	16	1
Microtus gud	37	6
Microtinae	727	80
Including the number identified with certainty:		
M. arvalis	—	(77)
M. majori	—	(3)
Mus musculus.	45	14
Apodemus sylvaticus	14	8
Total	844	110

TABLE 47. Species and number of bones of mammals from post-Paleolithic beds of the Akhshtyrskaya cave

Species	Number of bones	Number of individuals	Species	Number of bones	Number of individuals
Domestic			Wild		
Dog	3	1	Ursus arctos	4	2
Horse	1	1	Canis lupus	4	1
Pig	8	4	Meles meles	2	1
Large cattle	7	2	Lepus europaeus	3	1
Goat	17	6	Rattus rattus.	1	1
Small	25	4	Sus scrofa	27	4
			Cervus elaphus	5	1
Subtotal. . . .	61	18	Capreolus capreolus	25	5
			Subtotal	71	16
			Total	132	34

The fauna of the Neolithic and younger beds of the **Akhshtyrskaya cave** near Adler are of particular interest. These beds overlie the Paleolithic, but it is difficult to subdivide the material from the upper layers of the cave (Zamyatnin collections) into the various post-Paleolithic 209 cultures. The bones are light in weight, mostly light yellow in color with some dark stains. Some of the fragments have partially lost organic matter; in general, they resemble Upper Paleolithic bones. The identifiable material consists mostly of epiphyses. The species identified and their number are given in Table 47* (Figure 97).

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* The material from the Neolithic and Iron Age layers was combined, because the state of preservation of the bones definitely indicates that they were mixed in the layers and during the excavations.

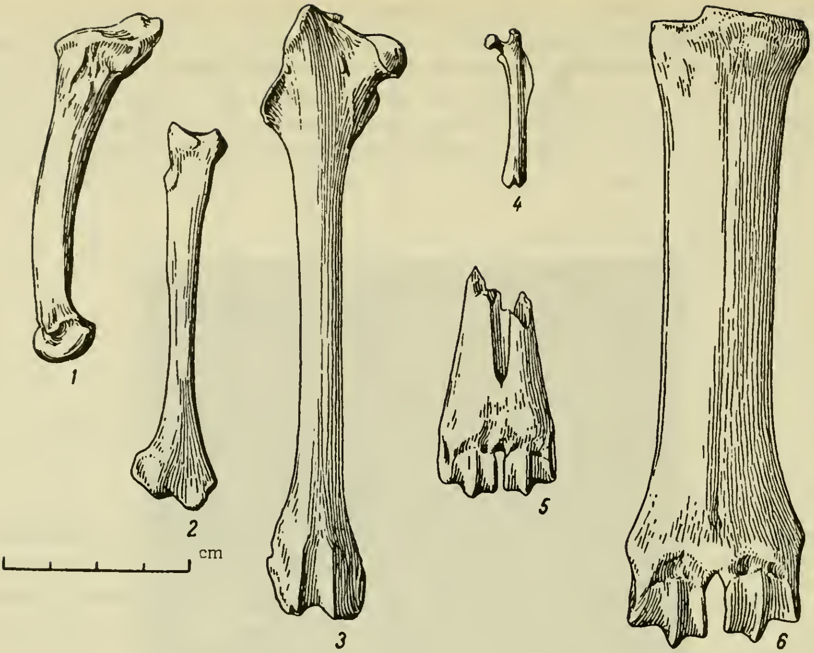

FIGURE 97. Mammalian bones from post-Paleolithic layers of the Akhshtyrskaya cave

1 — metacarpal of Ursus arctos; 2 — radius of Meles meles; 3 — femur of Lepus europaeus; 4 — femur of Rattus rattus; 5 — metatarsal of Capreolus capreolus; 6 — metacarpal of Capra caucasica

The composition of food remains at this site is more variegated in wild fauna than at other post-Paleolithic localities in the Caucasus, since the cave was probably used by hunters and shepherds.

The absence at the site of mountain ungulates (cave bear, elk, giant deer and bison) which were probably driven farther into the mountains is quite apparent, as is the appearance of black rat in the Iron Age beds.

In swampy Colchis the oldest cultural beds containing animal remains are known from the excavations of an Eneolithic site. The settlement was on a mound, at present submerged in a swamp, near the village of Ochamchiri, on the left bank of the Dzhikumur creek (Solov'ev, 1939). In the bone collections Gromov has identified a small cow, domestic pig, goats and sheep. Wild species include deer, roe deer and fish, particularly flounder. It is characteristic that horse is not found among the remains.

210 One of the Early Bronze Age settlements which is located near Anaklia, close to the mouth of the Ingur River, has been excavated by archaeologists of the Zugdinskii Museum. The cultural layer is overlain by Recent silty alluvium. According to Kuftin, the very primitive black ceramics place this bed in the second millennium B.C. The bones from this site are shiny, chestnut in color and slightly fractured. The latter characteristic indicates that the ancient settlers of the coast had an adequate supply of

animals for food. The species identified (Table 48) show that primitive animal husbandry and more developed hunting were carried on by the ancient settlers.

TABLE 48. Species and number of bones of mammals from the Bronze Age settlement near Anaklia

Species	Number of bones	Number of individuals
Domestic		
Pig	103	17
Large cattle	258	17
Goat	47	5
Subtotal	408	39
Wild		
Canis aureus	1	1
Delphinus sp.	4	3
Sus scrofa	15	3
Cervus elaphus	4	1
Capreolus capreolus	36	4
Subtotal	60	12
Total	468	51

Individual bones of fish and birds are also known from this locality.

At present deer do not inhabit the area near the site, but jackals are abundant, and boars and roe deer occur occasionally.

The absence of horses and the small number of dolphin bones, as compared with the Gelendzhik locality, is characteristic of the Anaklia site.

Rich bone material, which has probably been lost, was obtained from excavations of the numerous mounds and settlements of ancient Greek and later times on the Colchis plains, along the midde and lower sections of the Rion. The author has identified remains of a domestic goat, wild boar, deer and roe deer, found at the Naokhvamy site, from photographs by the archaeologist Kuftin.

A number of fragmentary antlers of red deer, obtained in the peat areas of Colchis during the construction of drainage canals, were deposited in the museum of the town of Poti.

A very important deposit of food remains was exposed in the excavations of Holocene (Neolithic and latest) beds at the Sagvardzhile site, on the eastern margin of the Colchis plain (Kiladze, 1953).

211 The collections from these beds which have been studied by the author contain the following wild species in order of decreasing abundance: *

Sus scrofa
Cervus elaphus
Capreolus capreolus
Bison bonasus
Capra caucasica
Rupicapra rupicapra
Ursus arctos
Equus caballus
Felis silvestris
Panthera pardus
Castor fiber

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* Judging by the state of preservation, this material, which is under study by Burchak-Abramovich, undoubtedly also includes Paleolithic bones.

The occurrence of the beaver bones confirms that it was in Colchis that this species survived the Pleistocene in the Caucasus.

Of the many western Transcaucasian monuments of ancient architecture and sculpture ornamented with animal design, the Bagrat temple (1003 A.D.) in Kutaisi is particularly noteworthy. A scene showing cheetahs and panthers attacking a horse or a kulan and a goat is depicted on the heads of the temple columns. Taking into account the broad base of medieval Georgian culture it is obviously difficult to maintain on the basis of these ornaments that kulans and wild horses existed in Imeretia in the 10th century (Figure 98).

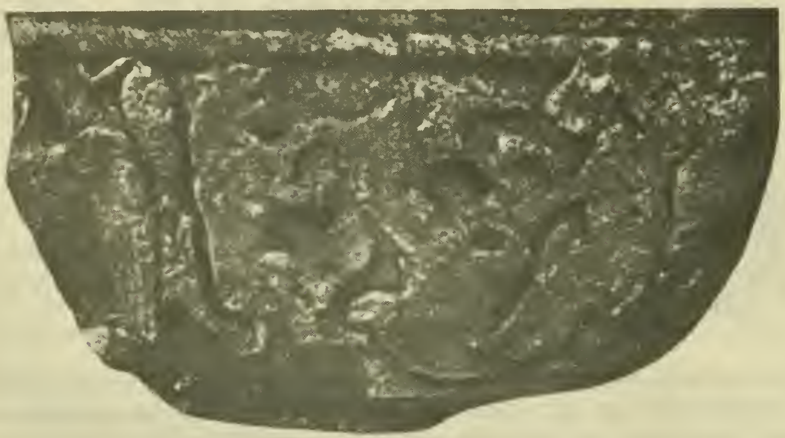

FIGURE 98. Scene on the head of Bagrat temple column — panthers attacking a goat

Photograph by author, 1956

The latest developmental stages of the ecological assemblages of small mammals in Imeretia can be traced through bones brought by eagle owls into small caverns in the walls of the canyons which cut through the Imeretian Plateau. In 1952 we collected material (identified in Table 49) from close by the **Sakazhia cave** in the Tskhali-Tsiteli gorge which shows the interesting, simultaneous occurrence of jackal, hare, Norway rat and fat dormouse, species not known from the Paleolithic beds of Imeretian caves.

As opposed to eastern Caucasia, no collections of game animal skulls have been preserved from the mountainous section of western Transcaucasia in the Ingur, Rion and Tskhenis-Tskhali gorges which were inhabited by the Svans.

212 Radde, it is true, wrote in 1866 that in 1864 he had observed an accumulation of horns of Caucasian goats, piled by hunters near the chapel of the village of Chibiana (Ushkul'), in the upper reaches of the Ingur. He estimated the number of horns at "several thousands." In 1948 I could

find only 7 pairs of horns and horn stems of goats (6 of Capra caucasica and 1 of C. cylindricornis) in the altar of the chapel in the village of Zhabeshi and in the altar of the Lamardiya monastery above Ushkul'. No confirmation ofthe past existence of "thousands of goat horns" could be obtained from old residents or from the local authorities. But it seemed that the hunters of this village used to store horns and blade bones of Caucasian goats and chamois under the roofs of their observation towers. By 1948 the collections were mostly abandoned or given away and no new material was introduced due to the extermination of the animals.

TABLE 49. Species and number of Holocene bones of mammals from pellets of eagle owls in the Tskhali-Tsiteli gorge

Species	Number of bones	Number of individuals
Erinaceus europaeus	37	4
Canis aureus	1	1
Lepus europaeus	2	1
Glis glis	12	3
Rattus norvegicus	74	12
Total	126	21

It was the practice of the Svans, as opposed to that of the Ossetians, to cut the goat horns off with only a small piece of frontal bone. Even now goat horns and bear paws can be seen attached to the porches of houses and embedded in the stone walls of houses made of slate.

Thus, the studies of Holocene bones in western Trancaucasia indicate an abundance in the Neolithic and later epochs of larger game animals: boar, deer, roe deer, bison and bear, as well as the European beaver found in Colchis. The appearance of new species, unknown in the Pleistocene (Paleolithic) beds (jackal, Norway rat and black rat) is highly characteristic. The composition of the domestic fauna and the nature of their deposition indicate that, in general, the landscape of Colchis and the Black Sea coast was very similar to the landscape of the beginning of the present century.

Central Transcaucasia

Reconnaissance excavations were carried out in 1952 by Lyubin above the overhangs of the natural landmarks of Saroty-Or and Sharshiat-Kadzakh near Staliniri. We have identified in Lyubin's collections bone fragments of small domestic pigs, bulls, goats and sheep, and teeth of European brown bears and foxes. Rich collections were also obtained in 1955-1957 from the Holocene beds of the Kudaro caves on the upper Rion.

In the valleys of the Kura and the Aragva rich bone material was excavated by archaeologists of the Caucasian Museum from multilayered

213 cemeteries and towns at Samtavro and Armazi, near Mtskheti.* A comparison between photographs of this material in the archives and exhibit material of the Upper Bronze Age (9th-8th centuries B.C.) show that these were bones of horses, cows, sheep, goats and boars, and amulets made of canines of European brown bear and incisors of beavers. Skeletons of martens (Martes foina) and steppe voles (Microtus socialis), which died at a later period, have recently been discovered. Objects made of red deer antlers are very common, e.g., the so-called "spear rectifiers." Elegant bronze plates and trinkets of this period from Samtavro and Armazi often depicted dogs, foxes, lions, panthers, hares, deer, goitered gazelle, rams, Caucasian goats and Bos primigenius.

Taking into account the paleontological data for Transcaucasia as a whole, these artistic representations confirm the existence of some large game animals in the Caucasus during the first millennium B.C. These animals became extinct only in the Middle Ages.

Eastern Transcaucasia

On the Kura Plain and in the foothills of the Greater Caucasus, Karabakh and Talysh, Holocene deposits of bones occur in diluvium, alluvium, caves, asphalt crusts and cultural layers of ancient settlements.

There is a record of a horn of a red deer from the diluvium of a mountain slope near the village of Alty-Agach, near the eastern margin of the Bolshoi Range (Deminskii, 1901). Many occurrences are concentrated on the Apsheron Peninsula.

Kovalevskii found in 1941 a skeleton of a striped hyena (Hyaena hyaena) at a depth of 4 m in Holocene loess loams in the lower section of the Sumgait rivulet, north of Baku. The skeleton was buried under a cultural layer containing medieval pottery and under a bone-bearing bed of an older settlement, overlain by the sediments of the Recent Caspian. From the stratigraphic position of the skeleton and its state of preservation it can be dated as Lower Holocene.

A skull of a very old striped hyena, bones of a horse and of a Caspian seal (Phoca caspica) were found by Kovalevskii in the Bailovskaya cave on the southern outskirts of Baku (Bogachev, 1938b).

We found two leg bones of goitered gazelle (Gazella subgutturosa) in blocks of asphalt-impregnated surface loams overlying the Middle Quaternary beds at Binagady. The bones are fresher and less impregnated with oil than the Pleistocene bones. In the asphalt crusts of Mount Kir-Kishlag we discovered bones of hare and wolf. Skeletons of small rodents, jerboas (Allactaga elater), hamsters (Cricetulus migratorius) and voles (Microtus socialis), which died in asphalt, also occur in this locality and at Mount Zigil'-Pirya (Vereshchagin, 1951b).

The numerous Holocene settlements and burials of Azerbaidzhan (Passek and Latynin, 1926) are responsible for the rich bone collections from the cultural layers.

Gummel' (1948), who excavated the Bronze Age mounds on the sloping plain west of Khanlar (formerly Helenendorf), mentions numerous bones of

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* This material remained unidentified and was subsequently lost.

Bos, sheep, goat and domestic pig. The number of horse bones was negligible.

Excavations of the settlements and the burial near **ancient Mingechaur** on the right bank of the Kura, near a hydroelectric power plant, revealed cultural layers dating from the second millennium B.C. to the early Middle Ages. The very rich bone material from this locality has not yet been completely identified. Our preliminary study of these materials indicated the presence of numerous bones of horses, asses, cows, sheep, goats and, more rarely, domestic pigs. The wild animals are represented by red deer (Cervus elaphus), goitered gazelle (Gazella subgutturosa) and boar (Sus scrofa), all of which were until recently quite common in the region.

We found a particularly interesting burial near Mingechaur with bones of black rat (Rattus rattus) and horse, ass, large cattle and boar buried in jugs. This type of burial, which included sacrificed domestic goats and grain, is usually dated as middle of the last millennium B.C. In view of the fact that the burial field has been covered for many centuries by a semidesert saltwort vegetation, the rats could only have inhabited the field during a time when it was settled and irrigated or at the time when the cult of mass burial flourished. Their occurrence verifies assumptions of the early appearance of black rat in Transcaucasia (Vereshchagin, 1949c).

TABLE 50. Species and number of mammal bones from ancient settlement near Sumgait

Species	Number of bones	Number of individuals
Domestic		
Horse	6	1
Large cattle	11	3
Sheep	12	3
Subtotal	29	7
Wild		
Lepus europaeus	2	1
Gazella subgutturosa	3	1
Subtotal	5	2
Total	34	9

A very old settlement was discovered by Kovalevskii in 1941 in Holocene loams near the **mouth of the Sumgait rivulet**. Food remains were found at a depth of 3 m under the cultural layer containing medieval pottery; they were well preserved under the very dry burial conditions. The species found are given in Table 50.

215 At the same locality ten fragments of bones of mute swan (Cygnus olor L.) and goose (Anser anser L.: three specimens) were found.

According to Kovalevskii, the bone-bearing bed is overlain by sediments of the present-day Caspian and therefore antedates the last Holocene transgression of the Caspian, i.e., early first millennium B.C.

Large collections of bones were made in 1953-1954 by archaeologists of the Azerbaidzhan Academy at the excavations of the fortress Uren'-Kala (Bailakan) in the center of the Mil'skaya steppe. We observed the layers from the Middle Ages at this locality to be characterized by sheep, large cattle, goat and horse, with a small admixture of goitered gazelle (Gazella subgutturosa).

TABLE 51. Species and number of mammal bones from the medieval settlement on the Baku Fortress hill

Species	Number of bones	Number of individuals
Domestic		
Dog	3	3
Cat	1	1
Horse	39	10
Ass	15	5
Camel	3	2
Large cattle	111	14
Sheep	202	29
Goat	3	2
Small cattle (no closer identification)	223	15
Subtotal	600	81
Wild		
Phoca caspica	1	1
Vulpes vulpes	1	1
Equus hemionus	1	1
Gazella subgutturosa	48	18
Subtotal	51	21
Total	651	102

Bone material from beds of the Middle Ages was also obtained by Leviatov in excavations of the Shirvan-Shah Palace courtyard in Baku. The excavations revealed that small settlements successively occupied the hill of the contemporary **Baku Fortress**. The beds which have been studied are dated by the pottery as 9-13th century A.D. This is the time of the end of the Arabic caliphate, the age of Nisami and the beginning of the Mongolian invasions into eastern Transcaucasia. Part of the bone material buried at the site probably resulted from epidemic death among the cattle, since complete scapula and forelimb bones are common. However, most of the bone fragments are food remains which were well-preserved in the dry ground.

216 Bones of domestic animals — sheep, cows, horses and asses — characteristically predominate. Bones of wild species — goitered gazelle, kulan, fox and seal — are not numerous (Table 51).

FIGURE 99. Ruins of Chukhur-Kabala fortress

Photograph by author, 1951

From the same beds the following birds have been identified: Cygnus sp., Anser sp., Otis tarda L., O. tetrax L., domestic fowl, totalling 21 fragments of 10 individuals. In addition bone identification was made of the following fishes: Acipenseridae (25 fragments of 4 individuals) and Cyprinidae (58 fragments of 8 individuals).

Most of the goitered gazelle bones occur in the 10--11th-century beds. The metatarsus of a kulan was found in the 13th-century bed.

The findings in ancient Baku confirm an abundance of goitered gazelle and kulans in eastern Transcaucasia. The hunting of seals and aquatic birds, and fishing in the Baku bay have also been established.

Bones and complete skulls of rats (Rattus norvegicus) are common in recent layers, dated 15-16th century A. D. However, the contemporaneity of the bones and the beds is not established, since rats may often penetrate the deep layers by descending through crevices and holes in the ground.

We studied bone material from the beds of the ancient **Chukhur-Kabala fortress** (Figure 99), located on the northern margins of the Kura Plain in the Alazan-Agrichai valley and destroyed by the Mongolians in the 14th century (Krymskii, 1934). The ruins of the fortress and the towns are located between two left tributaries of the Turyan-Chai in thick broadleaf forest. During the period of the maximum development of these towns the trees were probably felled, since fragments of square bricks
217 and pottery occur in the vicinity, particularly in the beds of the Kara-Su springs which flow through the alder and wing nut thickets.

Bones of wild and domestic animals, mixed with pottery, bricks, ash and earth, fill deep wells in the fortress, which are at present being actively eroded from the east by the Kara-Chai rivulet. The identified bones of domestic and wild animals which we collected in the talus of the cliff and in the rivulet bed are given in Table 52.

TABLE 52. Species and number of mammal bones from the Chukhur-Kabala fortress beds (Middle Ages)

Species	Number of bones	Number of individuals
Domestic		
Ass	1	1
Horse	3	2
Large cattle	13	2
Buffalo	1	1
Small cattle	38	5
Subtotal	56	11
Wild		
Cervus elaphus	1	1
Capreolus capreolus	1	1
Subtotal	2	2
Total	58	13

Special excavations would undoubtedly increase the number of wild species specimens. In 1946-1947 we collected bones of small animals on the northern margins of the Kura Plain and in Apsheron from owl pellets. The material was collected between **Aldzhigan-Chai** and **Geok-Chai** in short-lived caves in the cliffs of the Tertiary hills which separate the Alazan-Agrichai valley from the Kura Plain. Study of the fossil material showed that it was identical with the modern assemblage of insectivores and rodents known from samples obtained with traps (Table 53).

We obtained more complete materials in a study of past and present distribution of small mammals on the Apsheron Peninsula, which enabled us to compare the composition of the present and the Pleistocene faunas.

A narrow crevice (Figure 100) which had been occupied for several centuries by little owls was discovered by Burchak-Abramovich in 1944 in the limestone rock east of **Cape Bil'gya** on the northern coast of the Apsheron. Bones of insectivores, rodents, birds, reptiles and amphibians, and chitin of beetles from decayed pellets formed a layer 10-12 cm thick
218 in the cavern. The bones in the upper layer were brown in color; those in the lower layers were gray-brown. Gromov, in 1944, and I, in 1945, collected up to 5,500 bones of mammals in the crevices. There were fewer bones of birds, lizards and toads.

TABLE 53. Species and number of bones of small mammals in owl pellets from Geok-Chai

Species	Number of bones	Number of individuals
Hemiechinus auritus	2	1
Crocidura russula	33	7
Dyromys nitedula	4	1
Cricetulus migratorius	5	2
Microtus socialis	106	19
Mus musculus	16	6
Apodemus sylvaticus	36	9
Meriones erythrourus	15	1
Total	217	46

FIGURE 100. Resting place of little owls in the rocks of Cape Bil'gya

As old and plentiful as the accumulations found in owl prey are, they contain an essentially modern faunal assemblage, very similar to that which occurs at present on the northern Apsheron and is known from extensive samplings obtained with traps (Table 54).

In both the owl-pellet accumulation and the trap samplings, there is a disproportionate representation of certain rodent species, which reflects in the one case the selectivity of the owls and in the other the specific instructions under which the personnel of the anti-plague station operated.

There is no doubt that the ecological assemblage of smaller mammals of the Apsheron remained relatively stable over the last part of the Holocene. The study of the distribution of Recent mammals showed that 219 the European hedgehog, forest dormouse, field mouse and steppe vole are relict species which have survived in a few sections of the peninsula from a more humid climatic stage, as have some other vertebrates, in particular Rana ridibunda L. and the pond turtle Emys orbicularis L. (Vereshchagin, 1949c) (Figure 101).

TABLE 54. Species and number of smaller mammals on Apsheron

Species	Caught by owls in the last three to four centuries	Trapped in 1939-1940
Erinaceus europaeus	—	Rare
Hemiechinus auritus	—	Common
Crocidura russula	8	Common
Pachyura etrusca	2	Not recorded
Dyromys nitedula	—	Rare
Cricetulus migratorius	147	73
Microtus socialis	83	115
Meriones erythrourus	63	2,123
Allactaga elater	1	8
A. williamsi	33	50
Mus musculus	20	81
Apodemus sylvaticus		6
Rattus norvegicus	—	2
Total	357*	2,458

* The number of individuals is estimated from the number of lower jaws.

The graphic art of nomadic tribes provides indirect evidence of the occurrence of large mammals in the historical epoch in eastern Transcaucasia.

A number of ancient campsites of nomads occur under the cliffs of Apsheron limestone in Kabristan, southwest of Baku. Ancient craftsmen have left line drawings of lions, red deer, wild and domestic goats, domestic bulls and horses on the picturesque rocks and overhangs of Mount Kyzyl-Kum, Beyuk-Dag and Dzhangir-Dag, which were probably also religious sites (Vereshchagin and Burchak-Abramovich, 1948). Some of the drawings are probably Neolithic, some Bronze Age and some belong to the present era (Figure 102).

The studies of Holocene burials in eastern Transcaucasia may be summarized as follows. In the postglacial epoch the following species appeared in eastern Transcaucasia: wild forms — striped hyena and possibly lion; rodents — black and Norway rats; hoofed mammals — kulan and goitered gazelle. A number of large mammals, characteristic of the Middle and Upper Pleistocene, disappeared from the area probably at a somewhat earlier stage.

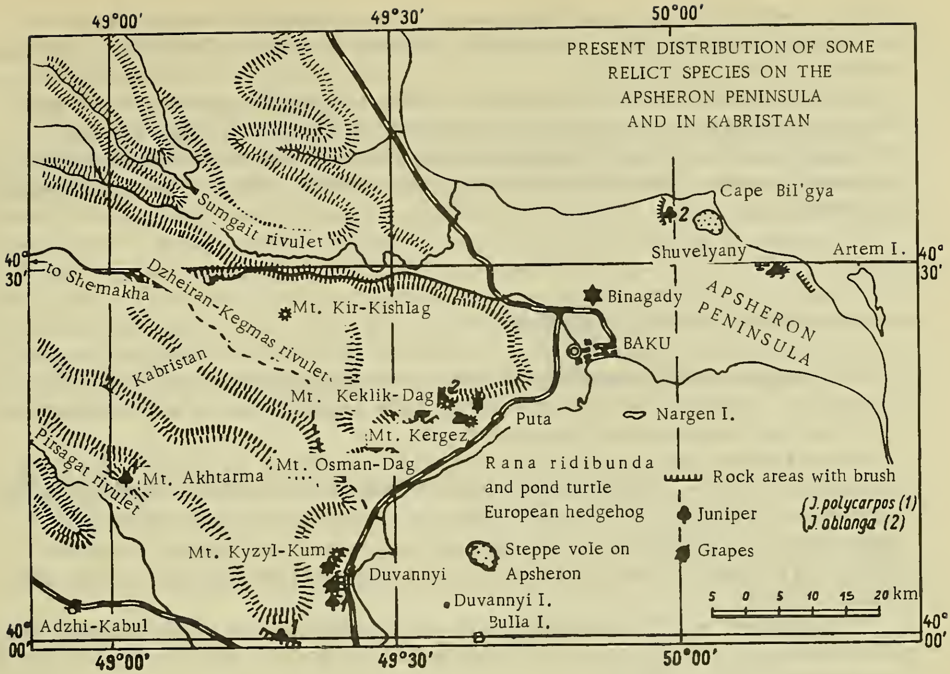

FIGURE 101

(220)

FIGURE 102. Drawing of goats and other animals on rocks of Dzhingir-Dag

Until recently some ungulates (e.g., deer and goitered gazelle) were much more abundant; the deer inhabited the tugai forests of the middle reaches of the Kura River.

221 The occurrence of relict species (European hedgehog, fat dormouse, field mouse, Rana ridibunda and pond turtle) on the Apsheron indicates that the climatic regime remained relatively stable during the historical epoch. Their distribution also reflects changes in the landscape caused by man.

Lesser Caucasus Upland

Postglacial mammals of the Armenian Plateau occur in diluvial sediments, tuffaceous conglomerates, lake sediments, caves, cultural layers of settlements and burial grounds.

Localities in diluvium on the shores of Lake Sevan. As early as 1926 Shelkovnikov brought to the ZIN rounded fragments of a bison skull (Bison bonasus subsp.), collected from postglacial, tuffaceous conglomerates at the Zanga source in Lake Sevan (Gromova, 1935c). The state of preservation of this material shows that it may be Bronze Age.

A large deer skull with excellently preserved antlers was collected from the diluvium of a slope near the village of Kabakhlu in the Azizbekov area in Armenia (Dal', 1947a).

A fragment of the skull of a suslik (Citellus cf. xanthoprymnus) was collected from the alluvial loams on the right bank of the Zanga, 6.5-7.0 m below the surface, in the vicinity of Arzni. The loams overlie a lava flow, presumably of the third to second millennium B.C. The time of the suslik is considered to be somewhat more recent (Dal', 1949a). The present eastern boundary of the suslik range is 40 km to the west.

Many animal bones were deposited in the littoral zone of Lake Sevan, some from animals which fell through the ice and drowned, some brought by the mountain streams. A large proportion of the bones are food remains of ancient hunters and cattle herdsmen who lived in pile dwellings along the lake shores. From the vicinity of such structural remains at the Zanga source two pairs of large antlers of red deer were collected and transferred to the Caucasian Museum (Bayern, 1871). Pile structures were also found near Novo-Bayazet and near Lake Gilli (Lalayan, 1929).

In 1947-1948, when the level of the lake started to fall, Dal' (1950b) collected numerous bone fragments on the exposed part of the northern shelf of the lake. The material included bones of deer, European wildcat, boar and bear. A large collection of fragments of antlers and skull fragments of boars and turs was obtained from a 1.5-m depth in the shallow-water bay in the Artanishskii Gulf.

Material from the gray river sands of the Sevan coast (the lower reaches of the Gavaraget River, near the Agbulakh rivulet and Cape Sary-Kai) appeared to be older; it included fragments of antlers, fragments of skulls and vertebrae of large bulls, similar in size to Bos primigenius and bison. A fragment of skull of a dwarf tur (Bos cf. minutus) was collected from the same sediments near Cape Sary-Kai (Dal', 1950a).

At our request Khaveson collected some bones on the Lake Sevan shores, mostly on the northwestern shore near Shordzha, and on the southern shore near Cape Noraduz and Sary-Kai.

222 We studied both collections. Most of the fragments in Dal's collection are brown and light brown in color; in Khaveson's collection the material is mostly of a light color. The bones seem heavy and permineralized, which, however, is only due to the limey deposit on the surface. Bones from the surf zone are strongly rounded and beige in color; those from the sediments in quiet water and from silt are complete and of a dark color. The deer remains mainly consist of antlers, often in a state of decomposition due to their exposure to water and subsequent weathering on the shore. Complete metapodia and jaws of domestic bulls and buffalos have been found. From the degree of coloration and loss of organic matter the material can be subdivided into two age-groups. The species identified and their proportions are given in Table 55.

TABLE 55. Species and number of bones of mammals from Lake Sevan shores

Species	Semifossil	Recent	Subtotal
Domestic			
Dog	12	8	20
Cat	1	—	1
Horse	61	23	84
Pig	6	2	8
Camel	3	3	6
Large cattle	70	67	137
Buffalo	5	2	7
Small cattle (no closer identification)	13	14	27
Subtotal	171	119	290
Wild			
Vulpes vulpes	1	1	2
Ursus arctos	1	—	1
Meles meles	—	1	1
Sus scrofa	5	—	5
Cervus elaphus	19	33	52
Subtotal	26	35	61
Total	197	154	351

The occurrence of dromedary is particularly interesting. The state of preservation of the forearm, scapula and mandible (Figure 103), which are colored light brown to a depth of 4-5 mm, indicates that the bones are quite old (3,500-4,000 years).

Khaveson (1954b), on the basis of teeth indexes, identified the jaw of the camel as belonging to a wild form — Camelus dromedarius dahli. Confirmation of this identification based on more complete material would indicate an extensive development of xeromorphic landscapes of the Armenian Highland at some early stage of the Holocene.

223 It seems very doubtful that wild camels could migrate into a mesophytic landscape of the present upland type in the vicinity of Lake Sevan. Other wild forms (bear, boar and deer) are more characteristic of the mesophytic, i.e., meadow and forest, environment than of the upland steppe and desert.

Material from burials and settlements. It has been possible to date more accurately the bones from burial grounds and ancient towns on the Lake Sevan shores, the Karabakh plateau, the Zanga shores, Debed-Chai ravine and the upper reaches of the Khram, near Tsalka on the Trialet ridge.

According to Piotrovskii (1949, p. 92), the oldest Holocene site is the Eneolithic, on **the bank of the Zanga River** near Shengavit, which was excavated by Baiburtyan in 1936-1938. The site was dated as second half of the third millennium B.C. Dal' has identified in the site material bones of wild goats, horses and fish; the horses were probably wild varieties.

Remarkable material, including antlers of red deer, was collected by Kuftin (1939) in 1930 from Eneolithic (third millennium B.C.) mound burials on the Trialet ridge in the upper reaches of the Khram.

A lower molar of a bear (Ursus arctos meridionalis) was collected by Kuftin from an Upper Eneolithic single burial near the village of Ozny in the Tsalka area.

FIGURE 103. Lower jaw of Camelus cf. dromedarius from the shores of Lake Sevan

More recent burials from the middle of the second millennium B.C. contained fragments of skulls, metapodia and phalanges of giant bulls, nearly the size of Bos primigenius, as well as bones of dogs, horses, boars, sheep and goats. All the bones are stained with humus; they are dark brown in color, and partially decayed. Kuftin thought that venerated human remains were carried on bull-drawn carts to the grave site. The bulls were then slaughtered and eaten, and the skins, skulls and limb bones were buried with the corpse. These mounds yielded a silver bucket depicting red deer and chamois and a gold goblet depicting lions.

The same type of burial with remains of a bull was found in 1948 in **Kirovakan** (Piotrovskii, 1950). The skull, better preserved than the one at the Trialet locality, indicates that the primitive tribes who built burial sites of this type had begun the domestication of Bos primigenius. A pair of roaring lions, similar in style to Hittite drawings, are depicted on a gold cup found in the grave.

224 It is known from Resler's (1896) descriptions "of the sites of huge fires" that "great accumulations of ashes and burnt animal bones — horses, rams, dogs, boars, buffalos, and bulls — " occur in the mounds and burial sites at Archadzor near the village of Khodzhala on the Karabakh Plateau. The presently accepted date of these monuments, which are related to the Assyrian culture, is early first millennium B.C. (Piotrovskii, 1949). Skulls of horses, bones of rams, camels and wild animals were found in the dolmens excavated by Belek and Ivanovskii in Karabakh and near Kedabek (Sysoev, 1925).

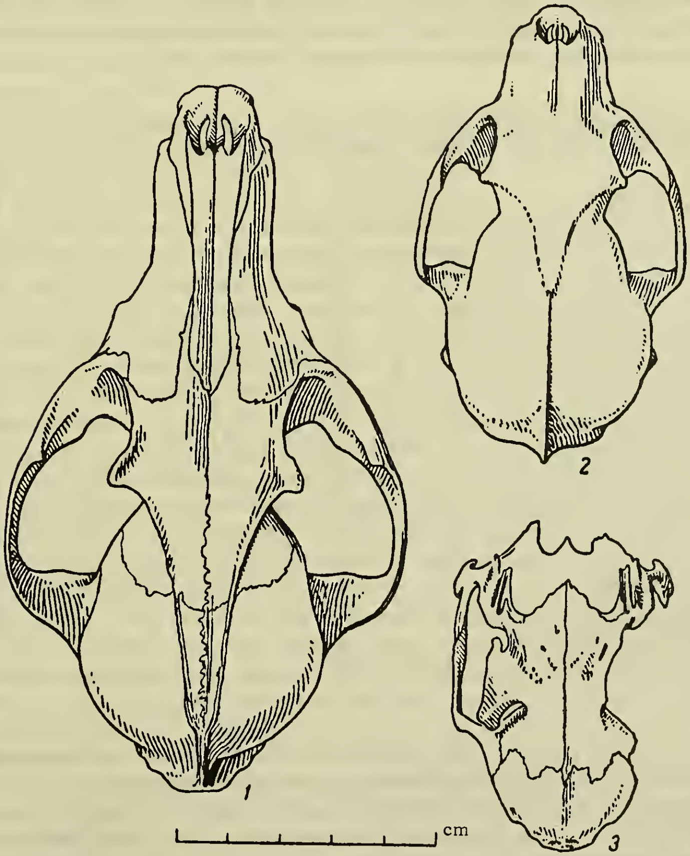

FIGURE 104.

Skulls: 1 — Vulpes vulpes; 2 — Martes foina; 3 — Lepus europaeus from Urartu burials on the shores of Lake Sevan

The excavations of the Urartu fortress Tsovinar on the southern shore of Lake Sevan (Piotrovskii, 1944) revealed bones of domestic pigs, domestic bulls and sheep. Large Urartu burial fields on the eastern shore of Lake Sevan near the village of Zagalu were excavated in 1905-1908 by Lalayan (1929). Big earth mounds of three types, which cover stone mausoleums used for common burials, were found there and near the villages of Nor-Bayazet and Adiaman. By the transitional Bronze-to-Iron-Age material found there, these burials have been dated as early first millennium B.C.
225 (Piotrovskii, 1949, p. 86). The sites contained skulls of martens (*Martes latifrons* = *Martes foina*) and badgers (*Meles urartuorum* = *Meles meles minor*) (Satunin, 1907b). From the same sites, Shelkovnikov in 1930 collected a mandible of a horse, a skull of a young pig, two skulls of foxes (*Vulpes vulpes*), four skulls of martens (*Martes foina*) and a skull of a hare (*Lepus europaeus*), all of which he donated to the ZIN.

The burial of the bodies of wild and domestic animals was of ritualistic importance to the Urartus. Lalayan mentions that he invariably found skeletons of horses, large cattle, sheep and goats in Urartu graves which he disposed of at the site. It is not known whether complete bodies of wild animals or only their skulls were buried (Figure 104).

TABLE 56. Species and number of mammal bones from Urartu fortress Teishebaini

Species	Number of individuals
Domestic	
Dog	3
Horse	8
Ass	6
Pig	6
Large cattle	22
Buffalo	2
Sheep	25
Goat	7
Subtotal	79
Wild	
Crocidura russula	4
Hemiechinus auritus	1
Martes foina	1
Felis lybica	1
Cricetulus migratorius	2
Mus musculus	2
Apodemus sylvaticus	4
Meriones sp.	1
Capra aegagrus	1
Ovis gmelini	1
Gazella subgutturosa	2
Cervus elaphus	4
Subtotal	24
Total	103

Ornaments from the graves usually depict red deer. A running bear is engraved on a sard seal collected in one of the graves.

Excavations of the Urartu *fortress Karmir-Blur* (Teishebaini) on the Zanga River near Yerevan (Piotrovskii, 1944, 1949) produced bone material which reflects some features of the animal husbandry and the faunal peculiarities of the Armenian Highland in the middle of the first millennium B.C.

Teishebaini, an important administrative center of the Urartus, was conquered in the 7th century B.C. by the Scythians who invaded Transcaucasia. Domestic and wild animals and various objects were buried under falling roofs and walls as the fortress burned. Dal' (1952), who has studied 4,667 bones from the Teishebaini excavations, listed the species given in Table 56.

From his knowledge of the conditions of the burial and his personal observations at the excavation site, Dal' concludes that gerbil and long-eared hedgehog migrated to the ruins of the fortress at a later time. The stone marten (Martes foina) and the spotted cat (Felis lybica) might have been domesticated species which were used to control rodents.
226 White-toothed shrew, hamster, field and house mice belong to the local synanthropic forms which at that time invaded human dwellings. Bones and objects made of horns of wild goat, ram, deer and goitered gazelle give some idea of the hunting traditions in the northern part of Urartu. This incidence of goitered gazelle bones is the first documented evidence of the occurrence of this gazelle in the middle section of the Araks valley.

Material from shelters of predators. New paleontological materials of the postglacial epoch were found by zoologists during studies of accumulated food remains of predators in the caves and smaller caverns of the Lesser Caucasus upland.

Polyakov (1882), in his survey of the caves along the shores of Lake Sevan in 1879, found a skull of a weasel, jaws of voles, mice and ducks in a cave at Mount Peschanaya Gor.

In his study of the present vertebrate fauna of the Saraibulakh (Urtskii) ridge, Dal' (1940b, 1954a) collected and identified the remains of animals accumulated by preying eagle owls and wolves in four karst caves. (Some of the bones belonged to animals which entered the cave and died there.) The richest material was collected in a cave in the third gorge from the west, in the western part of the ridge, above the village of Shagaplu. The entrance into the cave is on the right wall of the gorge, 11 m above the ravine floor (1,750 m above sea level). The combined length of the sections of the cave which were studied is 41.5 m. The animal bones were scattered and were mainly found in depressions and chambers, occurring in large numbers in the clayey surface layer. In this cave, 1,850 bones, belonging to at least 660 individual reptiles, birds and mammals, have been collected.

The state of preservation and the age of the bones vary. Some bones of domestic animals which remained on the surface were better preserved than those which were embedded in the ground. The bones are grayish yellow in color. Calcareous crusts up to 1.3 mm thick and stalagmites up to 5 mm high formed on some of the bones. The oldest bones dissolve completely in hydrochloric acid. Dal' estimates their age from 2,000-4,000 years. They include bones of jackal, domestic dog, fox, stone marten, tiger polecat, badger, hare, ass, horse, deer, bull, wild goat and Armenian mouflon.

We have studied the skulls of badgers from this cave (Vereshchagin, 1951b) and found them to be closer to that of the Urartu form of badger than those from the Sevan burials. This fact makes it seem possible that some of the bones are older than the age assigned to them by Dal'. The jaws of a large pika, found in the far corner of the cave, are among the oldest bones. The remains of white-toothed shrews, Myotis, foxes, weasels, martens and rodents are of modern types. Most of them were washed out of the pellets of eagle owls by water.

The identification of the material from the four caves resulted in the long list of species given in Table 57. Bones of larks, chough, pigeons, Hungarian and rock partridges, Ophisaurus apus and lake frogs were also found.

The location of the caves in a transitional landscape zone and the ways by which the animal remains were introduced into them preclude their usefulness as a basis for any far-reaching conclusions on changes in the climate and landscapes during the Holocene.

The list of wild species of the Saraibulakh ridge shows that large species (jackal, bear, pika, kulan and deer) do not occur there in the present;
227 their disappearance can undoubtedly be attributed to man.

TABLE 57. Species and number of mammal bones from caves on the Saraibulakh (Urtskii) ridge

Species	Number of bones	Species	Number of bones
Domestic			
Dog	11	Meles meles	14
Horse	8	Felis lybica	1
Ass	11	Lepus europaeus	98
Large cattle	15	Ochotona sp.	3
Sheep	28	Allactaga williamsi	9
Goat	26	Meriones persicus	135
Subtotal	99	Cricetulus migratorius	135
		Mesocricetus auratus	794
Wild		Microtus socialis	140
		M. nivalis	6
Erinaceus europaeus	1	Arvicola terrestris	2
Crocidura russula	1	Ellobius lutescens	323
Myotis oxygnathus	3	Equus hemionus	4
Canis aureus	3	Cervus elaphus	24
C. lupus	4	Capra aegagrus	85
Vulpes vulpes	35	Ovis gmelini	76
Ursus arctos	16		
Mustela nivalis	3	Subtotal	1,931
Martes foina	15		
Vormela peregusna	1	Total	2,030

Taken as a whole, the faunal complex of the region, even in the oldest times, was very close to the present faunal complex, which is characteristic of the arid plateau landscape of southwest Asia.

In southeastern and central Armenia, Sosnikhina (1947, 1948) did a thorough study in 1946-1949 of bones from eagle owls' pellets in three different altitudinal vegetation zones and landscapes. These were: 1) zone of spiny tragacanth formations (1,500-1,600 m above sea level); 2) zone of upland fescue steppe and arid thin forests (2,100-2,200 m above sea level) in the Azizbekov area and near Lake Sevan; 3) zone of mountain meadows

(2,600 m above sea level) in Nakhichevan A.S.S.R. The material, consisting of several thousand bones, illustrates very well the distribution of small mammals on the high plateaus and the effects which changes in climate and landscape can have on formation of ecological assemblages. These data are summarized in Table 58.

Most of the bones studied probably accumulated during the last centuries, possibly only during the last decades.

The two main assemblages of small mammals, the xerophilous and the mesophilous, either replace or supplement each other, reflecting in part the landscape of the region and in part the distribution and hunting behavior of eagle owls.

These data also indicate some etiological features of the behavior of eagle owls: the length of time they occupy their shelters, their habits of preying on a wide variety of species, choosing their prey in various biotopes, and leaving their pellets near the hunting ground. In the winter some of the eagle owls probably migrate from the highlands to the valleys, and, 228 in the absence of shelters on the hunting grounds, they may migrate to another area to find day resting places.

TABLE 58. Species and relative abundance (in %) of mammalian bones in pellets of eagle owls of Armenian Plateau

Species	Chirakhan ravine (1,500-1,600 m above sea level)	Southern slope of Sevan ridge (2,000-2,100 m above sea level)	Dzhagri ravine (2,200 m above sea level)	Slopes around Lake Aknalich (2,600m above sea level)
Erinaceus europaeus	—	—	0.7	2.4
Crocidura russula	—	—	1.5	—
C. leucodon	—	—	1.1	—
Sorex minutus	—	—	0.3	—
Neomys fodiens	—	—	0.3	—
Myotis oxygnathus	—	—	0.3	—
Mustela nivalis caucasica	—	—	0.3	1.2
Lepus europaeus	4.5	2.5	0.7	—
Ochotona sp.	4.5	—	—	4.7
Allactaga williamsi	—	—	1.2	—
Dyromys nitedula	—	—	0.3	—
Apodemus sylvaticus	—	2.5	5.0	—
Meriones sp.	31.9	—	—	—
Cricetulus migratorius	9.1	2.5	9.6	—
Mesocricetus auratus	18.2	82.5	22.5	17.3
Microtus arvalis	9.1	10.0	44.2	62.5
M. socialis		—		—
M. majori	—	—	4.9	2.4
M. nivalis	4.5	—	4.9	2.4
Arvicola terrestris	—	—	0.7	4.7
Ellobius lutescens	18.2	—	2.0	2.4

The occurrence of pika bones is of interest, sinces this species has probably become extinct in modern times on the Armenian Plateau.

In the upland semidesert of the Araks valley, bones from the pellets of owls and eagle owls were collected by Sosnikhina (1950b) in a cave of the volcanic Mount Karakhan (900 m above sea level), near the village of Novyi Shakhvarut, west of Yerevan. In 1947 we collected material in caves and under overhangs at the foot of the rock formations known as Alindzha-Dag, Ilyanlu-Dag and Darry-Dag, and in caves near the village of Klit, east of Ordubad, at the beginning of the Araks gorge.

The present-day landscape of the Abrakunis area consists of plateau-like spurs, covered with spiny astragalus bushes, mountain saltwort and weakly developed ephemeretum. The relict shrub vegetation, which had persisted in the valleys, consists of almonds, buckthorn and ephedra. This vegetation indicates that a xerophytic landscape existed in the region even before cattle husbandry. The plateau-like spurs are cut by dry canyons with rock-covered areas and caves, which are the resting sites of owls and eagle owls. There has been a survey of one such cave in the "Hyena ravine" Kyaftar-Dara (Figure 105).

On the left wall of the Araks gorge we surveyed three karst caves located between the Ordubad and Megri stations near the village of Klit.

These caves were visited in 1879 by Polyakov (1882) on his reconnaissance
229 of Paleolithic sites. In a trench in the anterior chamber of the middle cave, at a depth of 1.5 m, Polyakov found two pelvic bones of wild goat (Capra aegagrus), leg bones of European brown bear (Ursus arctos), several bones of hare (Lepus europaeus), "femur of a small carnivore similar to a dog" and bones of a pigeon. The excavations revealed the following sequence from top to bottom: a layer of flaky clay and excreta of bats, 35 cm thick, clayey beds with excreta and bones of bats.

All three caves are located in a wall of dolomitized limestone on the eastern slope of one of the small valleys in the Araks ravine. There are other caves in this limestone which, however, are not easily accessible. The biggest cave is the middle stalactitic cave "Dlinnokryly", described by Satunin (1915a). The entrance slopes downward into a cavern, from the middle of which the floor slopes upward to a long, narrow corridor with calcitic encrustations. From the posterior part of the cavern another twenty-meter-long corridor leads to the left into a lower chamber, 15 m wide, and to yet another corridor, this one proceeding a length of 50 m to a dead end. The combined length of the cavern and the long corridor is 250 m.

230 The height of the first chamber is 12-18 m; some sections are higher. In the talus left by Polyakov's excavations bones of Miniopterus schreibersii were observed. In the left corner of the cave, near the resting place of some carnivore (panther?), we found 14 gnawed bones (horse, ass, sheep, tur) showing a recent mode of preservation, and several bones of Miniopterus schreibersii covered with calcitic crust. Bones of a young panther (Panthera pardus) and stone marten (Martes foina), also showing a recent type of preservation, were found in the stone-covered middle section of the cave.

Of the present cave inhabitants, we caught only one greater horseshoe bat (Rhinolophus ferrum equinum) and counted only ten flying Miniopterus. Satunin in 1893 counted Miniopterus in the thousands. Footprints of panthers, martens and white-toothed shrews occur in the ancient dust.

(229)

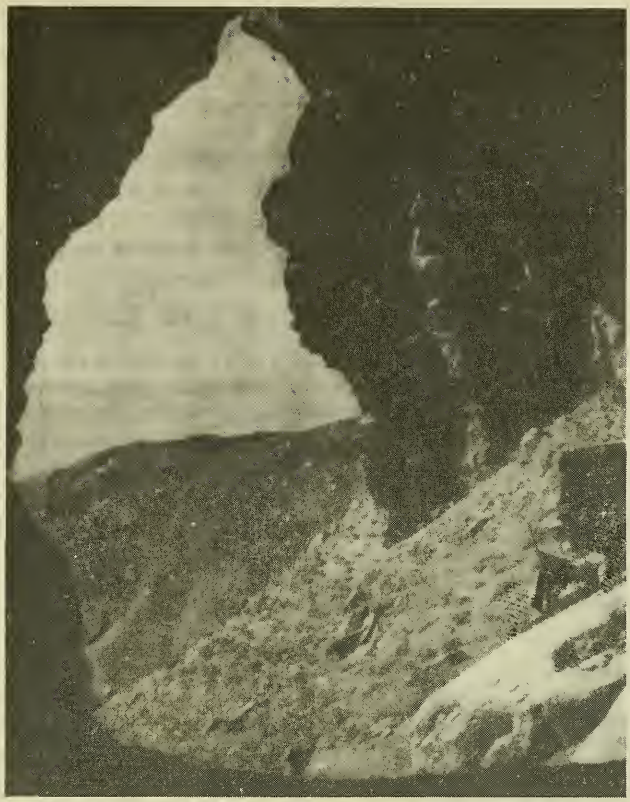

FIGURE 105. Entrance to cave inhabited by eagle owl in Kyaftar-Dara ravine

Photograph by author, 1947

Some rodent bones from the pellets of eagle owls were collected near the mouths of the two marginal caves.

Comparison of Sosnikhina's collections of small species with ours indicates a considerable increase — from west to east — in the xerophilous fauna and a concomitant species impoverishment in the small-mammal complexes (Table 59).

All of this material from the Arals valley — up to 1,500 bones from owl pellets — was collected from the surface and generally shows a recent type of preservation. It gives no indication of the appearance or the disappearance of any species in the semideserts in our time. A similar composition of the fauna was established through sampling with traps. However, in the interests of accuracy, it is necessary to mention that a mouse-like hamster was discovered as recently as 1938 on Mount Darry-Dag near Ilyanlu-Dag, and that bones have been found of Asia Minor hamster which does not inhabit the upland semidesert zone at present.

231 Talysh and El'brus upland

No bones of the postglacial epoch are known from the northern foothills of the Talysh Mountains and the Lenkoran Plain; neither are food remains known from the Talysh highland steppe. However, ancient burial mounds, in southern Mugan, as yet untouched by archaeologists, are evidence of ancient human habitation of the region.

(230)

TABLE 59. Incidence of species (in %) in mammal remains from pellets of owls and eagle owls in caves of the middle Araks Valley

Species	Novyi Shakhvarut, Mt. Karakhan	Abrakunis, Kyaftar-Dara cave	Ordubad, Dlinnokryly cave
Erinaeus europaeus	—	3.1	—
Hemiechinus auritus	25.2	—	—
Crocidura russula	1.2	3.1	—
Miniopterus schreibersii	0.6	—	—
Mustela nivalis	0.6	—	—
Lepus europaeus	3.7	6.4	6.7
Allactaga williamsi	4.9	6.4	—
Allactaga elater	14.2	—	—
Mus musculus	4.3	3.1	6.7
Apodemus sylvaticus	0.6	6.4	—
Meriones blackleri	14.2	40.0	—
M. persicus	—		80.0
Mesocricetus auratus	0.6	—	6.7
Cricetulus migratorius	4.3	6.4	—
Calomyscus bailwardi	—	6.4	—
Arvicola terrestris	1.2	3.1	—
Microtus arvalis	17.8	—	—
M. socialis	—	6.4	—
Ellobius lutescens	0.6	9.2	—

In 1945 I collected rodent bones in small caves inhabited by owls located in three sections of upland steppe, covered with grass and spiny astragali, in the upper reaches of the Vilyazh-Chai, near the Dymanskii post and in the upper reaches of Vassaru-Chai, near Kelakhan and Kel'vyaz.

TABLE 60. Species and number of mammal bones from owl pellets in upland steppe of Talysh

Species	Number of bones	Number of individuals
Hemiechinus auritus	2	1
Lepus europaeus	1	1
Allactaga williamsi	53	9
Meriones persicus	2	1
Cricetulus migratorius	35	14
Mesocricetus auratus	111	17
Microtus socialis	76	15
M. arvalis	1	1
Ellobius lutescens	13	7
Total	294	66

The age of these bones is not more than 200-300 years. In most cases, they were not protected by soil and consequently were subject to weathering. The combined data for all the three sections are given in Table 60.

All the small mammals listed still inhabit the region, forming the Recent assemblage characteristic of the upland steppes of the northwestern Iranian Plateau and the Armenian Highland. The list does not include the European hedgehog, long-tailed shrew, steppe mouse and snow vole. These species are very rare in the region. (Relict snow voles occur higher in the mountains.) The similarity of our list to Sosnikhina's (1947, 1948) list, given for the tragacanth-covered steppe areas of the Armenian Highland, proves a considerable degree of affinity between the faunas and between the landscapes of the two regions.

On the adjacent Iranian Plateau, Coon (1951) collected Holocene mammals from the eastern part of the Elburz Range, 50 km from Asterabad, in Mesolithic and Neolithic beds of the Belt cave. Among the 1,170 fragments of bones, 18 species have been identified. The most abundant is goitered gazelle (Gazella subgutturosa, 67%), followed by Bos primigenius (18.8%), goat (Capra sp., 5.7%), ram (Ovis sp., 4.4%), Caspian seal (Phoca caspica, 3.1%) and dog (Canis sp., 1.7%). Also mentioned are individual occurrences of Vulpes sp., Felis sp., Viverridae, Citellus sp., Castor fiber, Hystrix sp., Mus sp., Equus asinus, Sus sp., Cervus elaphus and Cervidae.
232 Identification of the bones of the Viverridae, European beaver and Bos primigenius needs to be confirmed. The remaining species are to some extent similar to the present assemblages of mammals on the hot plateaus of northwestern Iran and humid, wooded Asterabad.

These studies of the various types of Holocene deposits of the Armenian Highland, Araks valley, and Talysh and El'brus highlands show that a number of large animals (bison, Bos primigenius, kulan, goitered gazelle) inhabited the region in the not-distant past. They also reveal shifts in the areas of distribution of some smaller species (suslik and Asia Minor hamster).

The results of the studies of Holocene localities on the Caucasian Isthmus can be summarized as in Tables 62-63.

In our studies of the bone collections from the post-Paleolithic cultural beds and from diluvial sediments, we were able to trace the appearance of some species of large mammals in the Caucasus in postglacial time. The species migrated to the Caucasus from adjacent areas. Extinction of many of the Pleistocene species was also revealed by the studies. The rapid development of animal husbandry and its characteristic regional features, as well as the steady increase in the proportion of domestic over wild species in food remains from the Neolithic to the present, could be traced through the bone material. Studies of bone material from the day resting places of eagle owls produced a more precise delineation between past and present distribution of many insectivores and rodents. The rarity of multilayered Holocene deposits of small bones and the abundance of younger bones in small caves and under rocky ledges might indicate a discontinuity in the availability of shelters and in the accumulation of food remains of owls. It is possible, however, that rapid mechanical weathering of the exposed rodent bones and the frequent collapse of small caves might have created the appearance of such a discontinuity.

The studied Holocene material consists of 77 species of mammals which inhabited the Caucasus at the end of the Upper Paleolithic, some of which became extinct toward the 20th century.

Comparison of the lists of the Holocene and Pleistocene species indicates pronounced changes in the compositions and distribution of the mammalian fauna of the Caucasus, occurring mainly at the Pleistocene-Holocene boundary (Table 61).

Thus, the Holocene in the Caucasus is characterized by the complete disappearance of proboscideans* and apes while perissodactyls and artiodactyls decreased catastrophically. The increase in the number of rodents in the Holocene beds is accounted for by the differences between excavated and open sites.

TABLE 61. Number of mammalian species from the Pleistocene and the Holocene in the Caucasus

Species	Pleistocene	Holocene
Insectivora	6	9
Chiroptera	2	3
Primates	1	—
Carnivora	21	14
Lagomorpha	1	2
Rodentia	26	33
Proboscidea	2	—
Perissodactyla	6	2
Artiodactyla	18	14
Total	83	77

Reliable conclusions on the appearance or disappearance of species in the Holocene can be drawn only with respect to the mass species. Overall, the species complexes and locations of the Holocene deposits exhibit a nearly modern faunal composition and distribution pattern.

233 A review of paleontological material on post-Pleistocene fauna shows the following changes:

Insectivora — At least five species crossed the Pleistocene-postglacial boundary: mole, white-toothed shrew, water shrew, long-eared and European hedgehog. In addition, three species of white-toothed shrew (Crocidura suaveolens Pall., Crocidura leucodon Hermes, Suncus etruscus) occur in the Holocene; these species probably inhabited the Caucasus in the Pleistocene also.

Chiroptera — Greater horseshoe bat (Rhinolophus) is known from the Pleistocene beds. The Holocene beds in the caves of the Lesser Caucasus uplands commonly contain bones of Myotis and Miniopterus.

Primates — There are no data on the occurrence of Holocene macacas.

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* In view of the finds of geologically young mammoths in Pyatigor'e and in the Gori depression, the question of their possible survival through the Pleistocene in the Caucasus deserves further investigation and requires additional corroborative material.

Carnivora — Of the 21 species known in the Pleistocene, only 15 have been recorded in the Holocene. In the Holocene of the Caucasus there are no steppe or cave bear, cave hyena, Panthera leo or cheetah and probably no glutton. Jackal and striped hyena occur for the first time in the Holocene. It seems possible that at this period a number of other southern carnivores (jungle cat, lion and tiger) migrated to the Caucasus although their remains have not yet been found. The absence of lion, tiger and cheetah bones from postglacial deposits can be accounted for by their scarcity in the historical epoch.

Lagomorpha — European hare is the only species known from the Pleistocene. The Holocene deposits contain remains of European hare and large pika which probably existed in the Lesser Caucasus in the Pleistocene.

Rodentia — A number of important changes in the composition and distribution of the rodent fauna occurred during the Holocene. The porcupine and the Apsheron vole became extinct; the Asia Minor hamster retreated from the Apsheron and from Imeretia; the areas of distribution of the suslik of Asia Minor on the Armenian Highland and of the Caucasian snow vole in Ciscaucasia decreased. The finds of remains of black rats in Neolithic beds on the Black Sea coast and in Kura Plain beds of the middle of the first
244 millennium B.C. are a basis for assuming that the species was autochthonous and that it survived through the Pleistocene on the warm, humid lowlands near the Black and southern Caspian seas. A similar conclusion, if applied to the Norway rat, would be open to question. The occurrence of European beaver in Neolithic times in Colchis has been confirmed.

Most of the other findings fill in details of the distribution of extant species.

Perissodactyla — The materials studied give no indication that the woolly rhinoceros and the Equus hemionus survived in the Caucasus through the Pleistocene. The occurrence of the modern kulan in the Holocene of eastern Trans- and Ciscaucasia has been recorded. There were undoubtedly wild horses in the Holocene, but it has not yet been possible to distinguish their bones from the bones of domestic horses of various origins. Wild and domestic horses were the main animals used in sacrifices and for food by the Caucasian tribes during most of the historical epoch.

Artiodactyla — Boar were widely distributed in the Caucasus. In the Holocene the species was one of the primary game animals. Bos primigenius were also abundant in the Lesser Caucasus. So far there is no evidence of the existence of wild camels in the Caucasus in the Holocene.

The wide distribution of red deer has been traced over nearly the entire Caucasian Isthmus from the Pleistocene to the 19th century. Roe deer and elk inhabited the lower Don valley, the river valley forests and reed jungle of the Kuban and the wooded lowlands of Ciscaucasia and Colchis to the end of the 18th century. No Holocene remains of Cervus pliotarandoides and fallow deer are known.

The occurrence of bison has been established for the Bronze Age in the Lesser Caucasus, and for the Middle Ages of the present era on the middle and lower Don. Saiga disappeared from eastern Transcaucasia in the Lower Holocene. Remains of goitered gazelle begin to occur in beds dated second millennium B.C. in eastern Cis- and Transcaucasia. They are particularly abundant in the Apsheron Peninsula beds of the Middle Ages.

234 TABLE 62. Species and stratigraphic location of mammal bones from the Quaternary of the Caucasus

Orders and species	Pleistocene			Holocene					
	Lower	Middle	Upper	Mesolithic	Neolithic	Bronze Age	Iron Age	Middle Ages	Present time
Insectivora									
Erinaceus europaeus L. (s. lato)	—	+	+	—	—	+	+	+	+
Hemiechinus auritus Gmel. (s. lato)	—	+	—	—	—	+	—	+	+
Sorex minutus L.	—	—	—	—	—	—	—	—	+
S. araneus L.	—	—	—	—	—	—	—	—	+
Neomys fodiens Schr. (s. lato)	—	+	—	—	—	—	—	+	+
Crocidura leucodon Herm.	—	—	—	—	—	+	—	+	+
C. russula Pall. (s. lato)	—	+	—	—	—	+	—	+	+
Suncus etruscus Savi	—	—	—	—	—	—	—	+	+
Talpa caucasica Sat.	—	—	+	—	—	—	+	+	+
T. sp	—	+	—	—	—	—	—	—	—
Chiroptera									
Rhinolophus ferrum-equinum Schr.	—	—	+	—	—	—	—	—	+
Myotis oxygnathus Mont.	—	—	—	—	—	—	—	+	+
Miniopterus schreibersii Kühl.	—	—	—	—	+	+	+	+	+
Chiroptera gen	+	+	—	—	—	—	—	—	—
Primates									
Macaca sp.	+	+	—	—	—	—	—	—	—
Carnivora									
Canis aureus L.	—	—	—	—	—	+	—	+	—
C. lupus L. (s. lato)	+	+	+	—	+	—	—	—	—
C. lupus apscheronicus N. Ver.	—	+	—	—	—	—	—	—	—
*C. tamanensis N. Ver.	+	—	—	—	—	—	—	—	—
Canis sp.	—	+	—	—	—	—	—	—	—
Cuon sp.	—	+	—	—	—	—	—	—	—
Vulpes corsac Pall.	—	+	—	—	—	—	—	—	—
V. vulpes L. (s. lato)	—	+	+	—	+	+	+	+	+
V. vulpes aff. alpherakyi Sat.	—	+	—	—	—	—	—	—	—
Ursus arctos L.	—	—	+	—	+	+	+	—	—
U. arctos binagadensis N. Ver.	—	+	—	—	—	—	—	—	—
U. spelaeus Rosm.(s. lato)	+	+	+	—	—	—	—	—	—
U. rossicus Boris.	—	+	—	—	—	—	—	—	—
Hyaena hyaena L.	—	—	—	—	+	—	+	—	—
Crocuta spelaea Goldf.	+	+	+	—	—	—	—	—	—
Martes foina Erxl.	—	—	—	—	+	+	+	+	+
M. foina latifrons Sat.	—	—	—	—	—	+	—	—	—
M. cf. foina Erxl.	—	+	+	—	—	—	—	—	—
M. cf. martes L.	—	—	+	—	—	—	—	—	—
Vormela peregusna Güld.	—	+	—	—	—	+	+	—	—
235 Lutra lutra L.	—	—	—	—	—	—	+	—	—
Mustela nivalis L. (s. lato)	+	—	+	—	—	—	+	—	—

* Species of the transitional Upper Pliocene-Lower Pleistocene period on the Taman Peninsula are marked with an asterisk.

TABLE 62 (continued)

Orders and species	Pleistocene			Holocene					
	Lower	Middle	Upper	Mesolithic	Neolithic	Bronze Age	Iron Age	Middle Ages	Present time
Meles meles L. (s. lato)	+	+	+	+	+	—	+	+	—
M. meles urartuorum Sat.	—	—	—	—	—	+	—	—	—
M. meles aff. minor Sat.	—	+	—	—	—	—	—	—	—
Meles sp.	+	—	—	—	—	—	—	—	—
Gulo aff. gulo L.	+	—	+	—	—	—	—	—	—
Felis silvestris Schr. (s. lato)	—	+	+	—	+	—	—	—	—
F. lybica Forst.	—	—	—	—	—	+	—	—	—
F. aff. lybica Forst.	—	+	—	—	—	—	—	—	—
F. lynx L. (s. lato)	—	—	+	+	—	+	—	—	—
Panthera pardus L.	+	+	+	+	+	—	+	—	—
P. spelaea Goldf.	+	+	+	—	—	—	—	—	—
* Panthera sp.	+	—	—	—	—	—	—	—	—
Acinonyx aff. jubatus Schr.	—	+	—	—	—	—	—	—	—
Lagomorpha									
Ochotona sp.	—	—	—	—	+	+	+	—	—
Lepus europaeus Pall.	—	—	+	+	—	—	+	+	—
L. europaeus gureevi I. Grom.	—	+	—	—	—	—	—	—	—
L. cf. europaeus	+	+	—	—	—	—	—	—	—
Rodentia									
Marmota sp.	—	+	+	—	—	—	+	+	+
Citellus pygmaeus Pall.	—	—	—	+	+	—	—	+	+
C. aff. citellus xanthoprimnus Benn.	—	—	—	—	—	+	—	—	—
Castor fiber L.	—	—	+	—	+	+	—	—	—
* C. tamanensis N. Ver.	+	—	—	—	—	—	—	—	—
* Trogontherium cuvieri Fisch.	+	—	—	—	—	—	—	—	—
Hystrix cf. leucura Sykes	—	+	+	—	—	—	—	—	+
H. vinogradovi Arg.	—	+	—	—	—	—	—	—	—
Dyromys nitedula Pall.	—	+	—	—	—	—	+	+	+
Glis glis L.	—	—	—	—	—	—	—	+	+
Sicista subtilis Pall.	—	—	—	—	—	—	—	—	+
S. cf. caucasica Vin.	—	—	+	—	—	—	—	—	—
Allactaga jaculus Pall.	—	—	—	—	—	—	+	+	+
A. jaculus bogatschevi Arg.	—	+	—	—	—	—	—	—	—
A. williamsi Thos.	+	—	—	—	—	+	+	+	+
A. williamsi dzhafarovi I. Grom.	—	+	—	—	—	—	—	—	—
A. cf. williamsi	+	+	—	—	—	—	—	—	—
A. elater Licht.	—	+	—	—	—	—	—	+	+
Spalax microphthalmus Güld.	—	—	—	—	—	+	+	+	+
S. giganteus Nehr.	—	—	—	—	—	+	—	—	—
Micromys minutus Pall.	—	—	—	—	—	—	—	+	+
Mus musculus L. (s. lato)	—	+	—	—	—	+	+	+	+
Apodemus agrarius Pall.	—	—	—	—	—	—	—	—	+
A. sylvaticus L. (s. lato)	—	+	—	+	—	+	+	+	+
Rattus rattus L.	—	—	—	—	—	+	+	—	—
R. norvegicus Berk.	—	—	—	—	—	—	—	+	+

TABLE 62 (continued)

Orders and species	Pleistocene			Holocene					
	Lower	Middle	Upper	Mesolithic	Neolithic	Bronze Age	Iron Age	Middle Ages	Present time
Cricetus cricetus L.	—	—	+	—	—	+	+	+	+
Mesocricetus auratus Water.	—	—	—	—	—	+	+	+	+
M. aff. auratus Water.	+	-	+	—	—	—	—	—	—
M. auratus raddei Nehr.	—	—	—	+	—	—	+	+	+
M. auratus planicola Arg.	—	+	—	—	—	—	—	—	—
Cricetulus migratorius Pall.	—	—	—	—	—	+	+	+	+
C. migratorius argiropuloi I. Grom.	—	+	—	—	—	—	—	—	—
Calomyscus bailwardi Thos.	—	—	—	—	—	—	—	—	+
Meriones erythrourus Gray.	—	—	—	—	—	—	—	+	+
M. erythrourus intermedius I. Grom.	—	+	—	—	—	—	—	—	—
M. blackleri Thos.	—	—	—	—	—	—	+	+	+
M. persicus Blanf.	—	—	—	—	—	—	+	+	+
Lagurus lagurus Pall.	—	—	—	—	—	—	—	—	+
Arvicola terrestris L. (s. lato)	—	+	—	+	—	+	+	+	+
Microtus arvalis Pall.	—	+	—	—	—	—	—	—	—
M. socialis Pall.	—	+	—	—	—	+	+	+	+
M. cf. roberti Thos.	—	—	+	—	—	—	—	+	—
M. nivalis Mart.	—	—	—	—	—	+	+	+	+
M. aff. gud Sat.	+	+	—	+	—	—	—	—	—
M. aff. majori Thos.	+	+	—	—	—	—	—	+	—
M. apscheronicus Arg.	—	+	—	—	—	—	—	—	—
Prometheomys aff. schaposchnikovi Sat.	+	+	+	—	—	—	—	—	—
Ellobius talpinus Pall.	—	—	—	+	—	—	—	—	+
E. lutescens Thos.	—	—	—	—	—	—	+	+	+
E. aff. lutescens Thos.	—	+	—	—	—	—	—	—	—
Muridae gen.	+	+	—	—	—	—	—	—	—
Proboscidea									
*Elephas meridionalis Nesti	+	—	—	—	—	—	—	—	—
*E. antiquus Falc.	+	—	—	—	—	—	—	—	—
E. trogontherii Pohl.	+	+	—	—	—	—	—	—	—
E. primigenius Blum.	—	—	+	+?	—	—	—	—	—
Perissodactyla									
Equus hemionus Pall.	—	—	—	—	—	+	+	+	—
E. aff. hidruntinus Reg.	—	+	+	—	—	—	—	—	—
E. caballus L. (s. lato)	—	+	+	+	+	+	+	+	+
E. caballus gmelini Ant.	—	—	—	—	Not distinguished from domestic horses				
*E. aff. sũssenbornensis Wüst.	+	—	—	—	—	—	—	—	—
*E. stenonis Cocchi	+	—	—	—	—	—	—	—	—
Rhinoceros tichorhinus Fisch.	—	—	+	—	—	—	—	—	—
Rh. cf. mercki Jaeger	+	+	—	—	—	—	—	—	—
Rh. binagadensis Dzhaf.	—	+	—	—	—	—	—	—	—
Rh. sp.	+	+	—	—	—	—	—	—	—

Orders and species	Pleistocene			Holocene					
	Lower	Middle	Upper	Mesolithic	Neolithic	Bronze Age	Iron Age	Middle Ages	Present time
*Rh. cf. etruscus Falc.	+	—	—	—	—	—	—	—	—
Elasmotherium sibiricum Fisch.	—	+	+	—	—	—	—	—	—
*E. caucasicum Boris.	+	—	—	—	—	—	—	—	—
Artiodactyla									
Sus scrofa L. (s. lato)	+	+	+	+	+	+	+	+	+
S. apscheronicus Bur. et Dzhaf.	—	+	—	—	—	—	—	—	—
*S. tamanensis N. Ver.	+	—	—	—	—	—	—	—	—
*Hippopotamus sp.	+	—	—	—	—	—	—	—	—
Camelus dromedarius dahli Chav. (ferus?)	—	—	—	—	+	—	—	—	—
C. knoblochi Nehr.	—	+	—	—	—	—	—	—	—
*Paracamelus gigas Schloss.	+	—	—	—	—	—	—	—	—
*P. cf. kujalnikensis Chom.	+	—	—	—	—	—	—	—	—
Cervus elaphus L. (s. lato)	—	+	+	+	+	+	+	+	+
*Eucladocerus sp.	+	—	—	—	—	—	—	—	—
*Cervidae gen.	+	—	—	—	—	—	—	—	—
Dama cf. mesopotamica Brooke	—	+	—	—	—	—	—	—	—
Megaceros euryceros Aldr.	+	+	+	—	—	—	—	—	—
*Megaceros sp.	+	—	—	—	—	—	—	—	—
Alces alces caucasicus N. Ver.	—	—	—	—	—	+	—	+	+
A. aff. alces L.	—	—	+	—	—	—	—	—	—
*Tamanalces sp.	+	—	—	—	—	—	—	—	—
Capreolus capreolus L. (s. lato)	+	+	+	+	+	+	+	+	+
Saiga tatarica L.	—	+	+	—	—	+	+	—	—
Gazella subgutturosa Güld.	—	—	—	—	+	+	+	+	—
*Gazella sp.	+	—	—	—	—	—	—	—	—
*Tragelaphus sp.	+	—	—	—	—	—	—	—	—
*Strepsicerotini gen. et sp.	+	—	—	—	—	—	—	—	—
Rupicapra rupicapra caucasica Lyd.	—	—	+	+	+	—	—	+	+
Capra cylindricornis Blyth.	—	—	—	—	—	—	—	+	+
C. caucasica Güld.	—	—	—	—	—	—	—	+	+
C. aff. caucasica Güld.	+	+	+	+	—	—	—	—	—
C. aegagrus Gmel.	—	—	—	—	—	+	+	—	+
Ovis gmelini Blyth.	—	—	—	—	—	—	+	+	—
O. cf. gmelini Blyth.	—	—	+	+	—	—	—	—	—
O. cf. ammon L.	+	+	+	—	—	—	—	—	—
Bos minutus Malsb.	—	—	—	—	+	—	—	—	—
B. primigenius Boj.	—	—	+	—	+	+	—	—	—
B. trochoceros Leitn.	—	+	—	—	—	—	—	—	—
B. mastan-zadei Burtsch.	—	+	—	—	—	—	—	—	—
Bison bonasus caucasicus Sat.	—	—	—	+	—	+	—	+	+
B. priscus Boj. (s. lato)	+	+	+	—	—	—	—	—	—
*B. cf. schoetensacki Freud.	+	—	—	—	—	—	—	—	—
B. sp.	+	+	—	—	—	—	—	—	—
*Bison and Bos	—	—	+	—	—	—	—	—	—

TABLE 63. Stratigraphic summary of main localities of Quaternary mammalian index species in the

Subdivision of Quaternary			Marine beds	Black Sea region		Climate and landscape from the composition of mammalian fauna
				Western Ciscaucasia and Russian Plain	Western Transcaucasia	
Holocene	Upper	Present time	Recent sediments	Sarkel fortress, 9-13th centuries European brown bear European beaver kulan elk red deer saiga bison CI-284*		Recent climate and increasing influence of man on landscape
		Iron Age		Semibratnoe site at Kuban estuary wolf otter boar deer		Development of broad-leaf forest in foothills
	Middle	Bronze Age			Huts of Colchidians at Anaklia and Ochamchiri jackal boar roe deer red deer	
		Neolithic		Mud-hut settlement at Gelendzhik lynx hare red deer dolphin CI-417		
					Akhshtyrskaya cave, upper beds European brown bear badger black rat roe deer CI-460	
	Lower	Mesolithic				Strong warming and development of steppes in foothills; waning of valley glaciers

* Calcination indexes of bones (CI) by collagen analysis (Pidoplichko, 1952); analyses done in I.G.

Marine beds	Caspian region		Lesser Caucasus upland and northern Iranian Plateau
	Eastern Ciscaucasia and Russian Plain	Eastern Transcaucasia	
Recent sediments	Dzuars of North Ossetia 15-19th centuries red deer roe deer Caucasian elk east Caucasian goat chamois Caucasian bison	Settlements near Baku, 9-13th centuries fox kulan goitered gazelle seal	
	Settlements of Sunzha valley, Isti-Su, Alkhan-Kala kulan red deer		
	Settlements at Kayakent and Dzhemikent fox bear kulan goitered gazelle CI-275	Burials in jugs at Mingechaur and settlement at Sumgait striped hyena black rat boar red deer goitered gazelle	Karmir-Blur fortress stone marten Armenian mouflon wild goat goitered gazelle
			Pile dwellings and burials on Sevan shores stone marten badger boar red deer dwarf tur CI-207
			Belt cave at Asterabad porcupine red deer goitered gazelle Bos primigenius seal
	Sosruko grotto on the Baksan hare little suslik boar red deer Caucasian goat CI-241		
	Chokh site in Dagestan hamster mouflon CI-317		

Pidoplichko's laboratory in Kiev.

240 TABLE 63 (continued)

Subdivision of Quaternary			Marine beds	Black Sea region		Climate and landscape from the composition of mammalian fauna
				Western Ciscaucasia and Russian Plain	Western Transcaucasia	
Pleistocene	Upper	Upper Paleolithic	Neo-Euxine	Bone-bearing alluvium of late terraces of Don fox small pika little suslik great jerboa water vole horse elk red deer reindeer saiga	Gvardzhilas cave mole European brown bear glutton Asia Minor hamster *Prometheomys* Caucasian goat bison CI-512	General strong cooling and probable displacement downslope of landscape zones following glaciation of high ridges
			Karangat		Sakazhia, Devis-Khvreli, Mgvimevi caves cave bear horse European beaver elk chamois Caucasian goat argali CI-580	Major uplift of the mountain ranges
	Middle	Middle Paleolithic	Uzunlarskoe	Il'skaya site at Krasnodar cave hyena mammoth boar red deer saiga *Bison priscus* CI-518		Altitudinal zonation of modern type
			Ancient Euxine	Bone-bearing alluvium of early terraces of Don Siberian polecat little suslik jerboa *Allactaga sibirica saltator* Eversmann *Spalax* red deer	Akhshtyrskaya cave, lower beds wolf cave bear common hamster red deer giant deer *Bison priscus* CI-706	

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Marine beds	Caspian region		Lesser Caucasus upland and northern Iranian Plateau
	Eastern Ciscaucasia and Russian Plain	Eastern Transcaucasia	
Khvalynsk stage	Diluvium in Yankul' gulley on upper Kalaus horse saiga		Diluvial loams at Marāgheh wolf cave hyena horse rhinoceros argali
	Upper travertine complex of Mt. Mashuk in Pyatigor'e mammoth horse roe deer	Bituminous loams Kir-Maku and Artem I. wolf horse red deer saiga European tur CI 158-208	Tamtama and Bisotun caves in northern Iran jackal cave hyena panther gerbil red deer goitered gazelle
	Bone-bearing sands of Terek, terraces at Mozdok Bison priscus	Bituminous sands at Binagady on Apsheron Peninsula long-eared hedgehog corsac fox Ursus arctos binagadensis tiger polecat cheetah red-tailed gerbil porcupine Rhinoceros binagadensis red deer saiga tur CI 450-520	Zurtaketi site on upper Khram horse ass mouflon Bison priscus
Khazar stage	Bone-bearing alluvium of ancient extended Volga valley cave hyena Panthera leo mammoth woolly rhinoceros horse Camelus knoblochi giant deer long-horned bison CI-484		

TABLE 63 (continued)

Subdivision of Quaternary			Marine beds	Black Sea region		Climate and landscape from the composition of mammalian fauna
				Western Ciscaucasia and Russian Plain	Western Transcaucasia	
Pleistocene	Lower	Lower Paleolithic	Chauda beds	Bone-bearing sands at Girei and Krasnodar, middle beds *Elephas trogontherii* long-horned bison bear	Kudaro cave on upper Rion, lower beds macaca Siberian red dog wolf cave bear panther Asia Minor hamster marmot *Prometheomys* vole porcupine rhinoceros boar roe deer argali CI-914	In Transcaucasia strong development of steppes on the plateaus, resulting in migration of southwest Asian species to Caucasus
				Bone-bearing sands at Girei and Ivanovskaya, on Kuban, lower beds southern elephant *Elephas antiquus* deer bison		On Ciscaucasian plains climate temperate and dry; broadleaf forests in foothills
Pliocene	Upper	Eolithic	Krasnodar beds	Conglomerates and sands at Kuchugury, Sinyaya gulley and Tsimbal on Taman Peninsula *Trogontherium cuvieri* *Castor tamanensis* southern elephant *Elephas antiquus* *Elasmotherium caucasicum* horse *Cervus pliotarandoides* camel antelop bison Cl 913-1203	Fauna unknown	
				Sands and gravels of ancient terraces of Kuban at Voskresenskaya and Psekups at Babinskaya and Saratovskaya southern elephant *Equus stenonis* *Rhinoceros etruscus* *Cervus pliotarandoides* CI-1033		On Ciscaucasian plains; warm climate; savannah and gallery forests

Marine beds	Caspian region		Lesser Caucasus upland and northern Iranian Plateau
	Eastern Ciscaucasia and Russian Plain	Eastern Transcaucasia	
Baku stage			Bone-bearing sands of Adzhi-Eilas near Yerevan Elephas trogontherii fallow deer tur Paleolithic sites on middle Zanga and at the foot of Alagez; fauna unknown Bone-bearing sands at Leninakan, upper beds Elephas trogontherii horse Rhinoceros mercki giant deer Camelus knoblochi Bos primigenius
	Bone-bearing sands of upper terraces of Kuma and Podkumok near Georgievsk southern elephant Equus stenonis deer Bos CI 1073	Marine coquina at Khurdalan on Apsheron Peninsula horse rhinoceros	
		Sub-Khazar beds at Binagady Elasmotherium sibiricum	
			Bone-bearing sands at Leninakan, lower beds Mastodon arvernensis
Upper Apsheron	Bone-bearing sands at Podlesnyi and Divnyi near Manych southern elephant Elasmotherium caucasicum	Marine coquina at Kishla on Apsheron Peninsula hyena Equus stenonis Diluvium at Tsinandali Rhinoceros etruscus	Nurnus on Zanga small Mustilidae hare Rhinoceros etruscus Oryx
	Tash-Kala near Grozny Elephas planifrons Equus stenonis	Yenikent on Alazan Trogontherium cuvieri	

TABLE 63 (continued)

Subdivision of Quaternary			Marine beds	Black Sea region		Climate and landscape from the composition of mammalian fauna
				Western Ciscaucasia and Russian Plain	Western Transcaucasia	
Pliocene	Upper	Eolithic	Krasnodar beds	Bone-bearing sands at Khapry and Rostov on Azov Sea coast *Elephas planifrons* *Mastodon arvernensis* *Hipparion* *Equus stenonis* camel CI 1056-1142	Fauna unknown	Warm climate; savannahs and gallery forests in the southern part of the Russian Plain

245 Paleontological studies of Holocene mammals lead to a number of general conclusions on faunal and landscape changes in the Caucasus which have occurred since the end of the Upper Pleistoce. The absence from the Holocene beds of those mammals which lived during the stage of maximum cooling indicates that a discontinuity in ecological conditions promoted their extinction.

The paleontological materials indicate that the ecological assemblage of the piedmont plains was the one most affected in postglacial time; mountain fauna was probably affected to a much lesser degree.

Inasmuch as species such as cave bear, cave hyena, *Panthera leo*, *Equus hemionus*, giant deer and others lived in the cold climate of the Upper Pleistocene, it may be assumed that the main reasons for their extinction were abrupt warming and increasing drought. The development of xerothermal landscapes must have affected the fauna of the lowlands and foothills to the east much more pronouncedly than the fauna in the western part of the Caucasian Isthmus. A number of relevant examples of the retreat of mesophilous species have been given under the discussion of the Binagady locality.

The Holocene deposits, like the Pleistocene, do not contain any northern cold-climate forms (reindeer, blue hare, arctic fox). No Holocene remains of these species were found on the lower Don either. It becomes clear that in the Holocene the ranges of distribution of these species moved north, rather than closer to the Caucasus. Development of isolated pockets inhabited by mountainous mesophilous rodents also indicates the advent of a warm climatic phase, which resulted in shifts in the landscape zones. Examples of such isolated pockets are: pine vole on the meadows of the Stavropol Plateau, Transcaucasian mole vole on Mount Razvalka in Pyatigor'e, Asia Minor snow vole on Mount Kelakhan in the dry Zuvanda valley of the Talysh Mountains, and steppe vole on the Apsheron Peninsula. These and other examples of disrupted ranges of distribution are reviewed in more detail in a separate section under the discussion of the history of the development and the present state of areas of distribution of some species.

The new developmental stage in Upper Quaternary faunal complexes is marked by the appearance in the Caucasus of new species of mammals not found in the "universal" paleontological record of the bituminous Pleistocene beds of the Apsheron Peninsula. The occurrences noted in the Holocene of jackal, striped hyena, kulan and goitered gazelle and their present habitation of the area* indicate that their ranges in the Caucasus are relatively young. The southern origin and the migration of these species to the Caucasus in recent times can be deduced from the fact that the main areas of their distribution are to the south and east of the Caucasus, as well as from the fact that the species cannot survive deep and prolonged snow cover. In this species list, jungle cat, lion and tiger (so far unknown in the Caucasus as fossils) must probably be included. (This is discussed in more detail in Chapter III.)

246 Our paleontological materials indicate only one cycle of warming and development of xerothermal landscapes, which reached its maximum at a fairly early stage of the postglacial epoch.

It seems possible that the fossil mammals of a country as highly diversified geomorphologically as the Caucasus may not reflect the minor climatic changes which might have occurred within the Holocene.

The existence of a xerothermal stage was recognized by geobotanists Maleev (1939b, 1946), Yaroshenko (1956), Grossgeim (1948) and Takhtadzhyan (1941). According to these authors this stage was responsible for isolated occurrences of xerophilous plants in western Transcaucasia and in some places in the Lesser Caucasus uplands among more mesophytic areas.

The xerothermal stage has also been mentioned by pedologist Yakovlev (1914) and Zakharov (1935), geomorphologist Shchukin (1925), zoologist Sviridenko (1927, 1937) and geologists Gerasimov and Markov (1939).

The changes in the landscape caused by man in the last stage of the historical epoch are also traceable in the osteological material.

The abundance of boar, deer, elk and roe deer in the food remains in the Sarkel beds of the Middle Ages indicates that extensive forests were developed in the Don River valley. By the 18th century, these forests had been exterminated and the result was the disruption of the ranges of distribution of some European species in the Caucasus.

Occurrences of semifossil deer in the Stavropol area and the occurrences of boar and deer in some sections of the Armenian mountain-steppe (now arid) may to some extent provide confirmation of far fewer wooded areas in that country in Upper Holocene time.

Studies of coals from the cultural beds of settlements of the second millennium B.C. (Tsalka) and the 12th century A.D. (Gandzha) have proved the existence of extensive forests in the present woodless areas of the uplands of western Georgia near the villages of Dabi and Gomi, in southern Georgia near Tsalka, and in Azerbaidzhan on the barren ridges of Kirovabad (Yatsenko-Khmelevskii and Kandelaki, 1940, 1941a, b).

Our studies of the ritual collections of skulls in the mountain valleys of North Ossetia also indicated, through the disappearance of skulls of elks and bisons, that the forests on the sloping piedmont plains of eastern Ciscaucasia were exterminated by the 18th century.

The paleontological materials studied provide many other data on changes in the ranges and dispersion of synanthropic species and on extinction of animal game through direct extermination by man and through the indirect effects of radical anthropogenic changes in the landscapes.

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* With the exception of the extinct kulan.

247 *Part Two*

ANALYSIS OF THE ORIGIN OF CAUCASIAN QUATERNARY MAMMALS IN RELATION TO THEIR DISTRIBUTION, ECOLOGY, AND MORPHOGENESIS

249 *Chapter III*

REVIEW OF THE EARLY AND CONTEMPORARY POPULATIONS AND RANGES OF SOME MAMMALS

The patterns of zoocenose formation can be traced in any given country most easily by an investigation of range development, with consideration of the ecology of separate species. Well-defined ranges form the basis of zoogeographical division.

The existing range of a Palaearctic species may be only a relict of an ancient range, e.g., from the Quaternary period.

Therefore, in order to reach a conclusion on species dispersal, its ecology must be considered against a background of paleographic and paleontologic data, current zoogeographical conditions and man's influence during historical times.

The various factors which determine species survival or extinction divide into those of major influence and those of lesser influence.

The investigations of the Binagady asphalt deposit (Chapter II) have shown that peculiarities of early and recent ranges of eastern Transcaucasian mammals depend primarily on the evolution of the Quaternary landscape. To a lesser degree these peculiarities are also dependent on morphological evolution and biocenotic interrelationships. It is thought that the phytophagous mammals behave autonomously during the development and extinction of ranges. The influence of predators on Herbivora is probably of secondary importance to their distribution.

Theoretically the explanation of the origin and development of the range is more easily accessible from observation of colonial species — Carnivora, Proboscidea, Rodentia, Ungulata — remains of which are frequently found in various deposits. Ideally, these species should be comparatively stenotopic, that is, associated with a certain type of topography having a small number of biotopes. Species thus widely distributed leave more fossil material and more recent evidence of early ranges than narrowly distributed species endemic to their relict ranges. Eurytopic animals yield excellent paleontological data, particularly if the investigator has a consecutive chronological series of deposits to study.

250 The origin of other species, the fossil remains of which are rare, particularly the Insectivora and Chiroptera, may only be proved by means of zoogeographical mapping, analysis of present-day ranges, ecological analogy and extrapolations on the basis of more fully investigated specimens of Carnivora, Rodentia and Ungulata.

An attempt has been made to trace the early and recent distribution of both living and extinct Caucasian mammals and the factors pertaining to their range and numbers. An investigation has also been made to determine when these species appeared in the Caucasus and the routes taken by immigrant species. The examples selected include various orders and species.

Order INSECTIVORA

The paleontological age of generic series belonging to this order is quite ancient. The Insectivora fossils are known from the Eocene. Radial adaptation and the diversity of its relationships to the landscape are complex in the Insectivora. The earliest aquatic and widely specialized forms belong to 3 genera: Desmana (desman), Talpa (mole) and Crocidura (shrew) which were found in the Lower Pliocene complex of the Stavropol area (see Chapter II). Remains of 5 species belonging to 5 genera — Erinaceus, Hemiechinus, Crocidura, Neomys and Talpa — are known from the Pleistocene deposits.

The contemporary fauna of the Caucasian Isthmus includes 15 species of Insectivora belonging to 8 genera and ecologically to three categories: fossorial, 1 genus and 3 species (mole); amphibious, 2 genera and 2 species (desman and water shrew); and the remainder which are more or less specialized and associated with various biotopes (e.g., hedgehog, shrew).

Family ERINACEIDAE

European hedgehog — Erinaceus europaeus (s. lato). Fossil remains of Erinaceus species are known in Europe from the Miocene. Remains of the European hedgehog have been found in the Caucasus in the Middle Pleistocene strata of the Apsheron Peninsula and in Upper Pleistocene strata of western Transcaucasia. The hedgehog is widely distributed today (Map 1), found from the Caspian Sea level to an altitude of 2,500 m throughout the isthmus. The hedgehog is absent from alpine meadows, semisteppe, semidesert, open desert and permanent bogs and is rarely seen in upland forests; it is most frequently observed in the lowland forests of Transcaucasia and the sparse forests and shrubbery of the rolling Ciscaucasian plains.

This hedgehog lives in tugai thickets, gardens and oases of the semideserts in eastern Ciscaucasia and Transcaucasia. The range diminished in the Pleistocene over large areas of eastern Transcaucasia; the remaining
251 ranges in the Apsheron Peninsula are attributed to the postglacial dryness of the area (according to Vereshchagin, 1949c).

The origin of European hedgehog on the Caucasian Isthmus remains uncertain. Its range extends far to the north and south to the Caucasus. The absence of the hedgehog from open desert, semidesert and lowland steppes indicates its mesophilous character, its ancient associations with forest and its probable descent from Pliocene ancestors living in mesophytic environs of the eastern Mediterranean. Hedgehog remains from Middle Pleistocene deposits in Transcaucasia also confirm its presence in the Lower Quaternary, or more extactly pre-Quaternary, and the early distribution of this species in the Caucasus.

Today the European hedgehog is spreading rapidly over the plain concomitantly with the development of steppe and desert irrigation.

Long-eared hedgehog — Hemiechinus auritus Gmel. Remains of this species were found in Middle Pleistocene strata of the Apsheron Peninsula, and in Upper Pleistocene deposits of the northern Caspian lowland (Vereshchagin and Gromov, 1952). Hedgehog remains are known in the southwest from Paleolithic layers of Palestinian caves. Bones of the long-eared hedgehog carried into the caves by eagle owls have been found by the author in Holocene deposits in many areas of Ciscaucasia and Transcaucasia.

Its contemporary range includes the dry lowlands of Ciscaucasia and of eastern Transcaucasia and the high plateaus of the south (Map 1).

In the foothills of the Greater Caucasus, the hedgehog is found in the area between sea level and an altitude of 300-350 m. In southern Transcaucasia and Talysh it lives in the mountain-steppe and semidesert to altitudes of 1,600-1,800 m. The animal is absent from the mountain and lower forest zone. The largest population of the species is observed in the semidesert zone, i.e., the Kura-Araks lowlands.

The adaptation of the long-eared hedgehog to a semidesert and steppe environment is expressed in its food specialization: mollusks, locusts and beetles, and, to a lesser extent, small reptiles and rodents. Low water requirements, the ability to endure high temperatures and its use of turtle, gerbil, suslik, fox and badger burrows associate this hedgehog with a southern xerophilous fauna.

Extensive vertical distribution of the hedgehog in southern Transcaucasia and the relocation of the range southward indicates the probable penetration of the species from southwest Asia during the Upper Pliocene.

The present range of the hedgehog is increasing somewhat with the aridity of the foothills, which has been brought about by man.

Family TALPIDAE

Mole — Talpa caucasica Sat., T. orientalis Ogn. The remains of the genus Talpa are known in Europe and North America from the Miocene (Trouessart, 1898-1899a; Simpson, 1945). The earliest remains of small moles (Talpa sp.) in the Caucasus were in Pliocene strata near Stavropol.

Remains of the recent species T. aff. caucasica are found in Pleistocene strata of western Transcaucasia.

In Holocene sites they are very common, especially in the Ciscaucasian lowlands.

252 Considering the early isolation of Caucasian moles from the European mole (Talpa europaea L.) and the Mediterranean mole (Talpa coeca Savi) (cf. map by Bobrinskii, Kuznetsov and Kuzyakin, 1944), we class them as separate species (following Ognev, 1926a, 1928). The morphological adaptations of both species are similar; their sympatry is shown in Map 2. A recent study of species' ranges shows that Ciscaucasia, the Greater Caucasus and the Lesser Caucasus are inhabited by the Caucasian mole, with the subspecies T. caucasica ognevi Str. on the Rachin and Trialet ridges, whereas the eastern mole is found living in the Colchis lowland and the Talysh area.

The present distribution of the Caucasian mole is significantly related to the country's topographical development, as can be seen from the following features of its ranges.

In western Ciscaucasia, the animal inhabits the Don, Yeya, Chelbas, Yegorlyk and Kuban river valleys whereas in the Kuban Plain the population declines during arid years and survives only in more humid depressions.

There is an insular distribution of a large and varied population in the meadows and forests of the Stavropol Plateau.

In the northern Caucasus, the mole is widely distributed in the foothills, but inhabits only the river valleys of the Taman Peninsula and Kabarda Plain, and is totally absent from the steppelike plains. The species is found in oak forests of Pyatigor'e and in the Podkumok valley as far as Georgievsk, and to the north along the Kuma River to Budennovsk, becoming rare east of Ordzhonikidze.

The mole is common in upland forests of the northern slopes of the Greater Caucasus from the upper reaches of the Afips Basin to the Argun, especially along the humid Chernye Gory. It has been observed on the southern slopes of the Greater Caucasus from Gelendzhik to Zakataly and inhabits slopes covered by fir—maple forest in the Tsebelda, Inguri and Tskhenis-Tskhali ravines.

In western Transcaucasia, the species inhabits the terraces of the Black Sea coast, along riverside ridges in swampy Colchis, and to the west on the northern slopes of the eastern Taurus Mountains.

The mole is found at medium altitudes on the Surami ridge and in South Ossetia but not in the dry Gori depression.

In the Lesser Caucasus, the range is widespread in the zone of broadleaf forests and subalpine meadows on the northern slopes of the Adzhar-Imeretian and Trialet ridges in Dzhavakhetia, and on the Bambakskii and Bezobdalskii ridges.

Although the mole occurs in forests at altitudes of 400-1,700 m in Talysh, it is rare because of the marked aridity in summer. (In July 1945, the Vilyazh-Chai, Vassaru-Chai and Vasharu-Chai ravines yielded only 3-4 moles per day from 100 traps.)

It is probable that the mole lives on the northern slopes of the Elburz Range and it survives in certain parts of the northern slope of the Sevan Range in the upper reaches of the Dzegam and Shamkhor rivers.

Unexpectedly, it also survives in the semidesert zone of the Karayazy Plateau east of Tiflis, from a more humid epoch (Vereshchagin, 1940a). Here it lives in oak forests and motley-grass meadows along the banks of the spring-fed rivulets of the Kara-Su River. (Near this area steppe vole and red-tailed gerbils inhabit the solonchak meadows of sea lavender and arboreal saltwort (Figure 106); this is a remarkable example of the mosaic structure of biotopes and coexistence of hygrophilous and xerophilous animals.)

At the upper reaches of the Akstafa-Chai and Debed-Chai, Dal' (1944a) observed the maximum density — 42 moles per hectare — in a mixed beech — hornbeam forest at an altitude of 1,770-1,800 m. The author observed moles on the Karabakh Upland in the forested Terter-Chai ravine at an altitude
254 of 700-1,600 m, but they were relatively scarce.

The mole is not found in the dry longitudinal valleys from El'brus to Dagestan or in the interior of Dagestan. Its absence from the eastern part of the Main Range is principally attributed to the steepness of the slopes, the thin layer of soil covering the bedrocks of the upland and the marked aridity in the lower part of the beech—hornbeam forest zone which results in an irregular food supply.

The Alazan-Agrichai lowland, which is humid in winter but arid in summer, is also characterized by an absence of mole, as are the environs of Sevan and the Daralagez ridge.

There are no data on the presence of the mole on the Iranian Plateau and in eastern Anatolia. Blanford (1876) did not mention moles. Radugin (1917b) included the mole in his list of animals at the Khoi oasis (an altitude of approximately 2,000 m), probably mistaking the mounds of the mole vole for mole hills.

(252) Loginov (1949) obtained the following data on the relative density of the mole population from animals caught in July 1937 in various vertical zones (Table 64).

TABLE 64. Comparative population of the mole in different environments of the northwestern Caucasus

Zones	Number of moles caught per day with 100 traps
Forest-steppe of foothills	40
Broadleaf forests	30
Dark coniferous forests	5
Alpine meadows	10

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FIGURE 106. Habitats of the mole (in oak forests) and red-tailed gerbil (on meadows with sea lavender and saltwort) in the Karayazy forest of the Kura valley

Photograph by author, 1958

This survey of the collective range of Caucasian moles indicates that their distribution is more closely associated with a landscape of broadleaf forests and mesophilous meadows, and less so with a landscape of motley-grass steppes. The mole's existence depends on narrowly limited physical properties of the soil, particularly humidity and food reserves, i.e., a considerable biomass of invertebrates. Migrations of the mole through dry steppe and semidesert are improbable; it is more likely that the now separated ranges of the Greater Caucasus, Lesser Caucasus and Talysh were formerly connected. The collective range of Caucasian moles indicates that the areas of their distribution shared a uniform landscape only in the Tertiary. The Caucasian mole range (most of which lies within the western regions) was already established by the Upper Pliocene following the early development of arid zones in eastern Ciscaucasia and Transcaucasia. The present discontinuity of mole ranges in the Caucasian Isthmus is a result of the "struggle" between mesophytic and xerophytic environments during continuous climatic changes and of orographic peculiarities in the Pliocene and Pleistocene.

The mole migrations from the Russian Plain to the Caucasus and back obviously took place in the Neogene and Upper Pleistocene through the Trans-Kuban Plain and the Stavropol area. However, the Caucasus was also an independent focus of mole species formation.

The ranges in Ciscaucasia, on the Armenian Highland and in the Kura River valley near Karayazy are probably of postglacial origin. The broken range in Talysh-Karabakh may be of an earlier, pre-Quaternary age.

The contemporary range of the mole in the Caucasus has been reduced by forest felling and the xerophytization of the foothills and mountain regions during grazing and plowing. Only in the western Caucasian foothills is the direct effect of trappers on moles noticeable (Graph 1). Pelt trade does not reflect variations of population.

Desman — Desmana moschata L. The desman bones recorded from Pleistocene strata of southern and central Europe have been described (Trouessart, 1898-1899a; Wolf, 1938, 1939) as subspecies of the modern D. moschata hungarica Kormos, D. moschata fossilis Lartet and D. moschata magna Owen.

In the Caucasus remains of Desmana sp. (mandibular fragment in gravel) were found in the ancient alluvium of a Pliocene river in the vicinity of Stavropol. Pleistocene remains are known from Paleolithic settlements in the Ukraine and from Quaternary alluvium of the Dnieper, Don and Volga rivers.

The present range of the desman includes the basins of the Don, Volga and Ural. Only a small part of this area along the Don valley, from the
255 Manych to the Don estuary where the animal has always been rare, is today adjacent to the Caucasian Isthmus (Map 2).

The pronounced morphological and physiological adaptations of the desman to an amphibious existence in floodplain lakes supplied with Invertebrates indicates its ancestral evolution in river basins with a very stable hydrologic regime peculiar to rivers in extensive plains.

The desman probably could not exist in mountain rivers of the Pliocene and Pleistocene Caucasus because of heavy floods and continuous erosion. Therefore we may consider the Eastern European species as a rather early, Upper Pliocene settler, but only in western Ciscaucasia near the Yeya and Chelbas rivers, probable tributaries of the paleo-Don.

In fact some floodplain lakes are suitable for the desman, the lower Kuban, for instance, near the Cossack village of Grivenskaya and in the basins of the Colchis rivers Tsiya, Tsiva and Pichera.

Order CARNIVORA

The origin and age of the range area of most Caucasian Carnivora can be determined more or less from paleontologic data and from the peculiarities of the range. The small number of species and the rarity of mass destruction did not provide conditions for the formation of natural deposits of Carnivora. However, remains of predators are found in kitchen middens of Paleolithic man and in later settlements where these animals were hunted for their pelts. Gromov (1948) submitted a valuable stratigraphic analysis of the remains of Quaternary Carnivora. Fossil Canidae, Ursidae, Hyaenidae, Mustelidae and Felidae are known from the Cenozoic deposits of the Caucasian Isthmus. The species of these families form the present fauna of Caucasian Carnivora.

Family CANIDAE

From Pleistocene fauna of the Caucasus 5 species of Canidae of the genera Canis and Vulpes are known; of these two are becoming extinct. There are 5 existing species of the Holocene fauna.

Jackal — Canis aureus L. The remains of the jackal are often found in fossiliferous cave deposits in southern Europe (France, Italy, Rumania), north Africa and southwest Asia.

The difficulty of analyzing small Canidae according to their skeletons throws any identification of small Pleistocene European dogs with contemporary African and Asian jackals in doubt, especially since remains of Pleistocene jackals have not been found in Eastern Europe and Soviet Central Asia. Fossils in Acheulean and Mousterian cave deposits in Palestine, Lebanon and Syria may be considered closely related to the present species (Bate, 1937). In Pleistocene strata of the Caucasus, jackal remains have not been found, indicating that the jackal appeared on the Isthmus recently (Vereshchagin, 1949c, 1951b). Later remains of jackals were found in early Bronze Age settlements near Anaklia, in caves near Kutaisi and in the vicinity of the Saraibulakh ridge in Armenia (Dal', 1940b).

The contemporary jackal is mainly restricted to the plains (Map 18).
256 In western Ciscaucasia the jackal is rare; in eastern Ciscaucasia it inhabits the valleys of the Terek and Sunzha from Mozdok and Grozny. On the Black Sea coast the jackal is numerous from Gelendzhik to Batumi, but is not found at altitudes higher than 400-500 m. The jackal is particularly numerous in alder thickets of the lower reaches of Colchis rivers. Eastward the range passes through the Surami which only a few animals traverse. The largest population in eastern Transcaucasia is observed on the plains of Zakataly-Ismailly, Khachmas and Lenkoran. In winter jackals are numerous in tugai thickets and margins of reedgrass bogs of the middle Kura and lower Araks. In fall when jackals feed on fruit, in particular

medlar, they are found at altitudes to 1,000 m in the Greater Caucasus. They also inhabit the forest zone of Talysh to its upper edge at 1,700-1,800 m.

In summer the jackal lives in the open semidesert while feeding on locusts but winters there only if small hibernating bustards are plentiful.

The high arid plateaus of northern Iran and Armenia are not inhabited by the jackal; it is also rare in the deep ravines.

Despite its apparent adaptation to a moderate climate, the jackal is a thermophilous predator, unable to endure deep snow. Its southern origin becomes apparent during strong snowfalls in the Kura Lowland, when the animal becomes helpless and unable to move or to procure food, and often perishes from exhaustion and cold (Vereshchagin and Dyunin, 1949). The presence of the jackal among the Holocene fauna of southern Europe and its absence from the Russian Plain are probably explained by the difference in the thermal and snow regimes.

The jackal is now vigorously hunted everywhere, but the population remains large. In the 1930's, 113 jackal pelts were obtained per 1,000 km^2 in Azerbaidzhan, 32.4 in Georgia and 10 in Dagestan (Vereshchagin, 1947). In the last 25 years there has been a considerable increase in the pelt yield over that recorded in 1934 (Graph 2). In 1949 the pelt yield increased 2.5 times because of the higher premium placed on the jackal as a menace to cattle and an unbalancing factor in the economy. This fact demonstrates that the jackal thrives in the existing environment of Transcaucasia.

Wolf — Canis lupus L. (s. lato). Small wolves belonging to the polymorphic group C. lupus existed in the Upper Pliocene and Lower Pleistocene of Europe. Remains of a large wolf (C. lupus have been found in strata of the period of maximum glaciation. Those found in Germany and Austria are especially characteristic of the Würm age (Freudenberg, 1914).

In the Caucasus the most ancient evidence, a mandible belonging to a small wolf (C. tamanensis), comes from Lower Pleistocene conglomerates of the Taman Peninsula. The relationship of this species to contemporary C. lupus is uncertain.

Remains of large wolf appear in this locality from the Lower Pleistocene on, and are common even now (Map 19).

South of the Caucasus, C. cf. lupus remains are found in Mousterian layers of Palestinian caves (Bate, 1937) and in Upper Pleistocene talus of northwestern Iran.

In the north the remains of large Middle and Upper Pleistocene wolves are common on the banks of the Dnieper, Don, Volga and Ural and in Paleolithic settlements of the Russian Plain and the Crimea.

The present-day distribution of the wolf on the Isthmus is general although not uniform.

257 According to State figures of pelt yields, the greatest number of wolves obtained per land-unit area is from western Ciscaucasia and eastern Transcaucasia (Map 19). In the 1930's the yield of wolf pelts per 1,000 km^2 was as follows: Azerbaidzhan — 11.6, Armenia — 9.9, northern Caucasus — 6.7, Dagestan — 6.7, Georgia — 0.8.

Most pelts delivered to the State depots came from the plains and were taken from animals killed in winter.

The lower reaches of the Terek, Sulak and Kuma rivers and the Kura lowland coast of the Kyzyl-Agach Gulf are densely populated by wolves which feed on domestic cattle, wild boar and fish.

In the alder bogs of Colchis the wolf is common in the lower reaches of the Gagida, Okum and Pichera rivers.

In the mountain regions of the Caucasus a large wolf population can be observed in the Caucasian, Borzhomi and Zakataly-Lagodekhi reservations. The wolf populations settled in these areas, like those that live among the bulrushes of the Caspian coast, make predatory expeditions uphill and cross-country after wild ungulates. The wolf is distributed almost uniformly in all zones of the Caucasian Reservation, but in winter it is widely concentrated in the broadleaf forest zone. At this season large populations of boar, roe deer and deer abound. The zonal distribution of wolves found in the reservation (expressed in percentages) is as follows: alpine zone — 30%; dark coniferous forests — 32%; broadleaf forests — 38% (Teplov, 1938b). According to Teplov, the loss of young boar, deer, roe, chamois and Caucasian buck killed in the reservation by wolves ranges from 34-61% in a five-month period. In addition to the wild hoofed mammals, the wolf kills hundreds of domestic animals on lands adjacent to the reservation.

The abundance of wolves in the Borzhomi area was noted by Dinnik (1914a). The wolf is endemic in the Zakataly Reservation as in the Caucasian Reservation (Markov and Mlokosevich, 1935; Vereshchagin, 1938a).

In other areas of the Isthmus, especially in the east, the wolf makes regular predations after herds of domestic animals as they graze — in the mountains during the summer and in the lowlands during the winter. In spring the greatest concentration of wolves is observed in arid foothills where there are gulleys and rock shelters; here the young are reared.

The fluctuation of the wolf populations on the Isthmus during the Holocene can only be represented in a general outline.

The number of wolves decreased in proportion to the decrease of wild Ungulata on the plain but gradually increased with the development of cattle breeding. The improvement of firearms and methods of capture and the breeding of large dogs for herd protection have probably reduced the number of wolves.

The sharp increase of wolf pelts after World War II when the bounty was raised showed the stability of Caucasian populations of this animal (Graph 3).

The Holarctic distribution of the wolf in the Quaternary, its poorly investigated geographical variability and the imperfect paleontological data leaves its center of origin unqualified. It is considered a Pliocene dweller of the Caucasus.

258 **Fox** — Vulpes vulpes L. (s. lato). The Holarctic genus Vulpes dates from the Upper Miocene. Remains of Pliocene foxes, V. meridionalis Nordm. and V. moravicus Wold., attaining the size of the present central Russian fox, are known from Eastern Europe.

Remains of Lower Pliocene foxes have not yet been recorded from the Odessa catacombs and the Upper Pliocene strata of the coast of the Sea of Azov. On the Caucasus remains of V. khomenkoi with a dentition resembling that of red and arctic foxes were found in fossiliferous strata

(Middle Pliocene) of the Apsheron Peninsula (Bogachev, 1938c, 1944; Vereshchagin, 1951b). An isolated fox premolar was found in Pliocene strata near Stavropol.

The remains of foxes of the V. vulpes group are commonly found in various types of Pleistocene and Holocene deposits of Western and Eastern Europe, the Crimea and the Caucasus, including Paleolithic encampment sites.

South of the Caucasus remains of foxes have been found in Paleolithic strata of northern Iran (Coon, 1951), Syria, Lebanon and Palestine, from which Picard (1937) recorded V. alopex for the Mousterian and Aurignacian, V. cf. niloticus Rupp. for the Acheulean and Mousterian, and Canis vulpes for the Aurignacian and Mesolithic.

The present-day distribution of the fox in the Caucasus is general (Map 20). The greatest density of the fox population is observed in the zones of semidesert, steppe, foremontane forest steppe and highland steppe; the density is least in alpine meadows. Foxes are rare in the mountainous beech forests of the southern slopes of the Greater Caucasus. Dinnik (1914a) refers to the thinned forests on the foothills and plateaus of the northern Caucasus when discussing the fox population in Caucasian forests. In the Caucasian Reservation the largest number of foxes, up to 43.1%, inhabits the broadleaf forests throughout the year; a smaller number, up to 31.8%, is found in the spruce—fir forest zone, and the smallest number, up to 25.1%, in the alpine and subalpine zone Khonyakina, 1938). This distribution generally corresponds with the particular food supply: Muridae, birds, insects and berries. A different situation exists in Transcaucasia.

In 1935-1936, we found indications of fox distribution on the southern slopes of the Greater Caucasus in Azerbaidzhan in the form of fresh footprints and feces. The distribution according to the vertical ecological zones in which the foxes were found is given in Table 65.

(259)

TABLE 65. Frequency of foxes found and their tracks in different zones of eastern Transcaucasia

Land types in eastern Transcaucasia	Number of foxes and their tracks recorded on a 20 km walk			
	1935		1936	
	June	January	June	January
Virgin semidesert	2	4	8	12
Lower forests of the Agri-Chai valley	—	1	4	6
Beech—hornbeam mountain forests	—	—	1	2
Alpine meadows	—	1	1	2
Rocks and taluses of passes	—	—	—	—

In the semidesert zone the slopes of gulleys and foothills are densely populated in spring, whereas the seashore and foothills are populated in winter.

The basic food in summer consists of grasshoppers, and in winter of beetle larvae, caterpillars, steppe vole and gerbils. The seashore attracts the foxes because of its abundant food supply: dead birds, fish, crayfish. The contemporary fox distribution according to biotopes is greatly affected by man's agricultural activity (cf. Chapter VI).

The yield of fox pelts during 1930-1940 showed the densest population of foxes inhabiting the plains of Ciscaucasia and eastern Transcaucasia. The following numbers of pelts were obtained per 1,000 km^2 of territory: northern Caucasus — 276; Azerbaidzhan — 268; Armenia — 158; Dagestan — 138; Georgia — 74.

The number of foxes is inversely proportional to the degree of afforestation and to the mountainous relief of the country (Vereshchagin, 1947). The fox is especially rare in western Transcaucasia which is rich in forests and mountains.

259 According to Bakeev's records, the density of the fox population in the Spitsevka area of the Stavropol region during the period 1938-1941 was 12.5 animals per 1,000 hectares in summer and 10.3-16.5 in winter (Chirkova, 1952).

During historical time the range and population of foxes in the Caucasus has apparently thrived under the favorable influence of agriculture, and even concentrated gathering has failed to reduce their numbers.

The data on pelt supply during the last 25 years show sharp variations in the number of pelts for Ciscaucasia and fewer variations for Transcaucasia. Transcaucasia is more diverse ecologically and topographically and therefore the fox population is more resistant. From the pelt yields of 1925-1952, three peaks in population increase can be noted — 1927, 1936 and 1946 — with corresponding decreases in 1931, 1941 and 1951 (Graphs 4 and 5).

Considering the presence of similar factors in the Middle Pliocene of the Caucasus and the marked polymorphism of the present species in the Isthmus (Chapter IV), the fox should be included in the local eastern Mediterranean species of the Upper Tertiary.

Corsac fox — Vulpes corsac L. The range of the corsac during the Pleistocene extended over a wide steppe belt from Western Europe to North China. Remains of this fox have been found in caves of Switzerland and Czechoslovakia. They are known also from a series of Paleolithic encampments in the Russian Plain and particularly from the Kodak and Crimean caves.

On the Caucasian Isthmus corsac remains were found in large numbers but only in the Middle Pleistocene sands of Apsheron. To the south, particularly in Syria, Palestine and Iran, the corsac has not been observed. Here it was replaced by other mountain-desert forms of small foxes. By the 20th century the corsac was widespread in the Caucasus, and particularly in the northeastern part of the Isthmus (Map 21).

The reduction of the western part of the species range probably began in the Upper Pleistocene but has only been apparent during the last 150 years because of the pelt trade. Since the Middle Pleistocene the corsac range on the west coast of the Caspian Sea has receded to the north for a distance of 700 km.

Why the range diminished in Europe and the Caucasus since prehistoric times is still open to question. The data available indicate that the changes
260 in group structure of small steppe predators occurred in the Middle Pleistocene. In Western Europe, for instance, a series of small wolflike and jackal-like Canidae became extinct without leaving a trace.

At the time of the Binagady asphalt trap the corsac population was still fairly large in the biocenosis of the semisteppe of eastern Transcaucasia, but was subsequently depleted. The number of corsacs in relation to fox and wolf (as calculated by the authors for the Quaternary from bone remains and pelt yields) is presented in Table 66.

TABLE 66. Comparative numbers of Quaternary Canidae (in %)

Date and locality	Corsac	Fox	Wolf
Holocene, 20th century. Mean annual pelt yield in the Northern Caucasus for the period 1935-1940 — 63,600	0.06	97.5	2.4
Holocene, Sarkel, 8th-13th centuries A.D. Total number of the specimens trapped by Khazars and Slavs — 44	6.8	77.3	15.9
Middle Pleistocene, Binagady. Total number of specimens trapped in asphalt lakes — 327	25.6	37.7	36.7

The corsac has long been a less vital form than fox or wolf, although in those regions most favorable for it the corsac population still exceeds those of fox and wolf even now. For example, south of Akmolinsk in the grass—wormwood steppe 37 corsac burrows, 3 fox burrows and 1 wolf burrow were found in 1947; in 1948, 42 burrows were observed, 34 of which belonged to the corsac and 8 to the fox (Chirkova, 1952, p. 402).

The corsac apparently originated in the steppe region of Kazakhstan. It is a steppe-desert animal, feeding on small rodents, birds, reptiles and insects.

The corsac was common in the steppes of the western Manych area and could still be found near Salsk between 1900-1910 (Dinnik, 1914a; Bogachev, 1918). At present only a few pelts are obtained from this region (Graph 6). Steppe plowing and man's agricultural activity exerts an adverse influence on the corsac; now the animal is common only in the region of the Terek-Kuma sandy plains.

The range of the corsac, considered from both its contemporary ecology and paleontological data, indicates that this species was a typical middle Pleistocene migrant from the Russian Plain to the Caucasus. The migration must have occurred during the maximum southward advance of the cold-steppe landscape.

Family HYAENIDAE

Hyenas and Ichthytheriinae remains are known in Eurasia from the Upper Miocene (Simpson, 1945). They are especially characteristic of Mediterranean Pliocene deposits.

261 Three or four fossils and one living species of hyena are known from the Caucasus. Earlier remains were found in a Middle Miocene deposit near Belomechetskaya (Map 21).

Two specialized lines emerged in the Upper Miocene: Crocuta, with carnassial teeth resembling those of large cats, and Hyaena, more primitive and with less powerful teeth.

In the Quaternary there were two species. Their exact relationship to the Tertiary forms is not clear.

Cave hyena — Crocuta spelaea Goldf. This species is known from two localities in the Caucasian Isthmus where it apparently lived during the Pleistocene: the Middle Pleistocene strata of the Apsheron Peninsula (Binagady) and the Upper Pleistocene deposits of the Kuban Plain (Il'skaya).

North of the Isthmus the distribution range of this hyena encompassed enormous areas of Eurasia in the Pleistocene (Pidoplichko, 1951).

To the south the remains of this animal have been observed in the Upper Pleistocene of northwestern Iran (Brandt, 1870; Coon, 1951).

The Middle Pleistocene Crocuta spelaea Goldf. of the Russian Plain was considerably larger than the Transcaucasian species (Vereshchagin, 1951b), and corresponds to the larger sizes of Herbivora of these regions, such as bison and horse.

According to cranial features and body size, the Binagady hyena occupied an intermediate place between the Crocuta spelaea Goldf. and the extant C. crocuta L. of Africa. A direct relationship is quite possible.

The distribution of Crocuta spelaea Goldf. decreased rapidly in the Upper Pleistocene, moving southwestward to Africa, but it is possible that a modified species inhabited an area south of the Isthmus in the Holocene. Thus Crocuta crocuta L. inhabited Palestine in the Mousterian, in the Aurignacian and in the Holocene "Natufian" with the reappearance of the xerothermic climate (Bate, 1937).

This animal's extinction in Eurasia is of particular interest; undoubtedly one factor was the gradual extinction of Proboscidea and large Ungulata in the Upper Pleistocene. Paleolithic man could scarcely have effected the disappearance of this hyena; even the present-day hunter with his modern arms has not wiped out the species. Pidoplichko (1951, p. 160) states that the anthropic factor is negligible in the extinction of hyena from Europe and Asia. The Mediterranean Sea area can be considered the native country of Crocuta spelaea Goldf. The expansion of its range should be investigated as well as the distribution of the mammoth fauna. The advance of the postglacial xerothermic period was marked in the Caucasus by the migration from the south of a less specialized species, the striped hyena.

Striped hyena — Hyaena hyaena L. Fossils of the striped hyena were found in Paleolithic caves of Palestine, Morocco, Algeria and Portugal. The finds reported in France are doubtful (Wolf, 1938, p. 59). Pidoplichko (1951), following Sharff (1918), assumes that the striped hyena arrived in Europe in the Pliocene from the southwest because land extended from Africa to the British Isles in the Pliocene. There is no proof to date that H. prisca Mars. de Serres and H. monspessulana Croiz. et Job.
262 from the Pleistocene in southern France and H. antiqua Lankest. from the Pliocene in England are ancestral to the contemporary species.

Remains of the striped hyena have never been found on the Russian Plain or in Siberia. Only in Soviet Central Asia, south of Samarkand, in the Paleolithic strata of the Aman-Kutan cave have fragments of bones and teeth of this species been found (collection of the Zoological Institute of the Academy of Sciences, U.S.S.R.).

The absence of striped hyena remains from Pleistocene deposits of the Russian Plain, the Crimea and the Caucasus, especially from the Binagady

complex, verifies that it penetrated the Isthmus comparatively late. Striped hyena fossils are found on the Caucasus but only in Holocene deposits of the Apsheron Peninsula. The present-day range of a number of subspecies of this hyena embraces Soviet Central and southwest Asia and Africa. The range areas have a characteristically xerothermic climate. The underfur of this hyena is only slightly developed, another indication of its southern origin. Its ranges on the Caucasus are principally in the hot semidesert of lowlands and intermontane valleys (Figure 107) in eastern and southern Transcaucasia. At the close of the last century hyena was still found in eastern Ciscaucasia, between Derbent and Makhachkala (Dinnik, 1914a; Satunin, 1915a). Occasionally animals were observed near Vladikavkaz (now Ordzhonikidze) (Bogdanov, 1873). In the years 1861 — 1869 many hyenas were killed near Tbilisi, Yerevan and Nakhichevan (Radde, 1899). Prior to 1930 the hyena was found in small numbers and only in the sparsely populated areas of western Azerbaidzhan and in the western areas of Georgia (Vereshchagin, 1942b). From 1930 to 1940 the yield was 26 hyenas; from 1940 to 1950 only 5 or 6 animals were caught. Today a small number of
263 hyenas can be found in the discontinuous desert ranges of the Kartalinia Plateau, near Udabno and Geredzhi.

The typical habitats of the hyena in eastern Transcaucasia are the eroded clayey areas grown with thickets of juniper and pistachio.

During the last fifty years the range and population of hyenas have decreased very rapidly, mainly because of a planned extermination campaign provoked by hyena attacks on children.

(262)

FIGURE 107. Habitat of striped hyenas in the Middle Araks valley (Abrakunis)

Photograph by author, 1947

Family **URSIDAE**

From the Cenozoic strata of the Caucasus two representatives of Ursidae are known: Ursavus and Ursus.

Ursavus is a Middle Miocene genus found in Belomechetskaya. Ursus is a lower Pliocene genus known from a Pliocene deposit near Stavropol in the Caucasus (Maps 22 and 23).

The Quaternary fauna of the Caucasian Isthmus includes three species of bear, genus Ursus, of which only one lives today.

Ursus (Spelaearctos) rossicus Boris. was reported in 1931 from five skeletons recovered from sandy deposits of ancient alluvial flows (Middle Pleistocene) near Krasnodar (Figure 108).

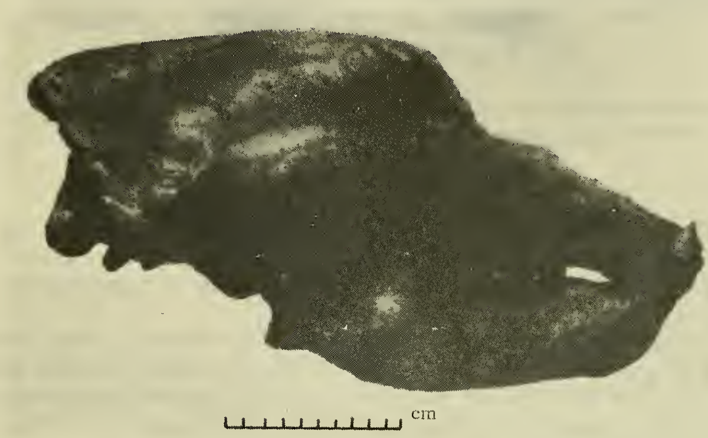

FIGURE 108. Skull of Ursus (Spelaearctos) rossicus Boris., from Krasnodar

The remains of Ursus (Spelaearctos) rossicus Boris. were also observed near Kherson (Borisyak, 1931), in the basins of the Greater Irgiz (Belyaeva, 1935, 1939a) and the Ural rivers (Vereshchagin and Gromov, 1952) and are now reported to be in caves of the northern Urals. Since remains of this species do not occur in Paleolithic strata of the caves of western and central Transcaucasia and in the bituminous strata of the Apsheron Peninsula, we can assume that the southern limit of its range was somewhere in the Ciscaucasian foothills. Ursus (Spelaearctos) rossicus Boris. probably lived in river valleys and steppe ravines and on slopes of foothills and was not as closely associated with karst topography as Ursus (Spelaearctos) spelaeus. The broad molar cusps indicate the preeminently phytophagous nature of the animal.

264 We consider this bear to be a Lower Pleistocene settler in the Russian Plain; it probably became extinct during the Upper Pleistocene.

Cave bear — Ursus (Spelaearctos) spelaeus Rosenm. During the second half of the Pleistocene the cave bear was a species associated with the landscape of Western Europe and north Africa.

It is known from the remains of the Il'skaya camp site near Krasnodar in the Caucasus and from eastern Transcaucasian caves (Figure 109). Reports on the presence of this bear in the Binagady complex by Bogachev (1939, 1940b) and Gromova (1948) are erroneous (Map 22).

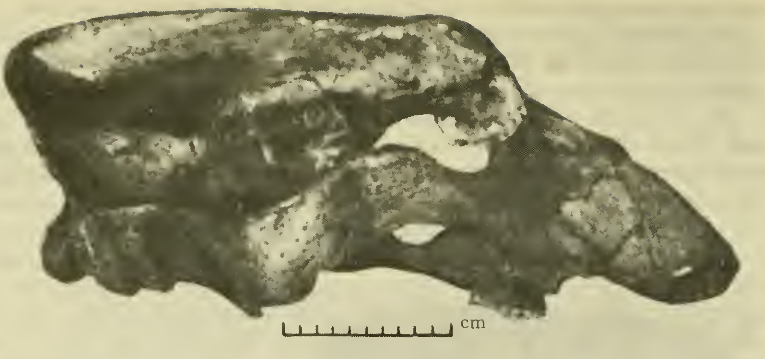

FIGURE 109. Skull of Ursus (Spelaearctos) spelaeus Rosenm. with shortened facial part from Ablaskira cave

The slight fossilization of the remains of the cave bear from the Vorontsovskaya cave near Khosta is very interesting. It is possible that a small cave bear population survived the Pleistocene in northeastern Transcaucasia.

The remains of this species are unknown in the Russian Plain, except north of the Black Sea. Near the Samara Bend, however, a small cave bear existed in the Pleistocene which according to the skull and dentition was intermediate between the small and large cave bear.

On the Lesser Caucasus, in Talysh and south of the Isthmus in Kurdistan and in Syria, cave bear remains have not been found. Therefore western Transcaucasia must be considered for now as the southern limit of the species range in the eastern Mediterranean.

The affinity between this species and the small cave bear should be further investigated; there is no reason, however, to consider this Upper Pleistocene species ancestral to the small cave bear because fossils of both forms exist within close geological proximity. From its origin, the large cave bear can be classified as a local eastern Mediterranean species.

European brown bear — Ursus arctos L. (s. lato). In comparison with the cave bears the European brown bear represents a more progressive branch which at the same time retains a number of primitive features. No less than ten forms are recorded from the Pleistocene cave deposits of Western Europe, north Africa and southwest Asia (Syria).

The European brown bear was widespread on the Caucasian Isthmus
265 during the Upper Pleistocene; this is substantiated by fossils found in the caves of Imeretia and in Apsheron Peninsula talus.

North of the Isthmus the remains of Ursus arctos L. (s. lato) were found in Pleistocene sands and pebbles in the river valleys of the Don, Volga and Kama, and in the diluvium of several Paleolithic encampments on the Russian Plain. Paleolithic U. cf. arctos and U. syriacus have been substantiated in Lebanon, Syria and Palestine (Picard, 1937).

While remains of the European brown bear are rare in Holocene deposits of the Caucasus, the species is nevertheless found as a regular replacement of the large brown bear in multilayered deposits indicating its broad dispersal during the postglaciation (Map 23).

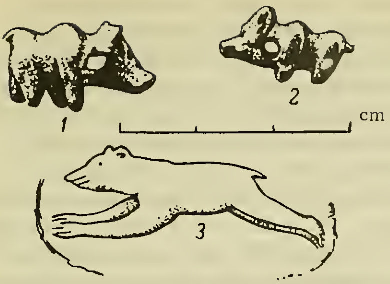

FIGURE 110.

1–2 — bronze pendant — bear figure (1:1) from the Kobanian burials of Ossetia (according to Uvarova, 1900); 3 — picture of a running bear (× 2) on a carnelian seal from Urartu graves (Orig.)

Pictures of bears are comparatively rare in the ancient art of the Caucasian people. In Kobanian burials of North Ossetia pendants and seals of bronze representing a bear were found. A running bear is shown on a carnelian seal (Figure 110) from an Urartu grave on the shore of Lake Sevan. A bear climbing a tree is figured on a silver container from the Maikop burial.

The contemporary range of the bear in the Caucasus is still extensive. On the northern slope of the Greater Caucasus it extends from Novorossiisk in the west to the upper reaches of the Dzhengi-Chai in the east, wherever there are forests, mountain shrubs and meadows. The greatest population of this animal was observed in the Caucasian Reservation. On the Stavropol Plateau the bear was exterminated in the last century and is only rarely observed in the forests of Pyatigor'e. There are few bears in the Kabardian A.S.S.R. and in northern Ossetia, and none in the largest part of central Dagestan, but they are still seen in the Deshlagar forests. The bear was exterminated about 30 years ago in the lowland forests of Samur and on the gently sloped Kusary Plain.

On the southern slope of the Greater Range there are now more bears than on the northern slope. Bears are common in wooded Abkhazia and Imeretia. There are no bears in the Colchis swamp. In Svanetia and South Ossetia the bear is common in reaches of the Kodor, Ingur and Rion, despite energetic attempts by the local population to exterminate the animal. In Azerbaidzhan it is numerous in the basins of the Belokan-Chai, Katekhi-Chai, Kakhi-Chai and other rivers, as far as the upper reaches of the Gerdyman-Chai in the east.

In September and October when chestnuts and walnuts ripen, the bears concentrate in forests and gardens of the Alazan-Agrichai valley. The animals congregate on the upper forest edge when beechnuts and acorns are abundant in fall. On the low Kartalinia, Iora and Adzhinour plateaus it lives in the sparse forests of juniper and Turkish terebinth where it feeds on terebinth berries, juniper and grasses, and especially on astragali. The bears track through gulleys and along precipices. Recently bears inhabited the tugai floodplain forests of the Kura, especially the section between Mingechaur and the Alazan estuary.

266 At present the bear is uncommon on the Lesser Caucasus where it has been nearly exterminated. It is not found in woodless Dzhavakhetia. On the Armenian Highland it inhabits sparse juniper forests and relict oak forests and it is rare in mountain forests of Talysh.

The greatest yield of recorded bear pelts was from eastern Transcaucasia. From 1930 to 1940 the average yield per 1,000 km^2 was as follows: Azerbaidzhan — 1.5, Armenia — 1.5, Georgia — 0.9, northern Caucasus — 0.9 and Dagestan — 0.2. Most of the pelts, however, were retained by the local population.

The European brown bear of the Caucasus was probably of endemic Pliocene origin. This local origin is substantiated by Pliocene finds near Stavropol, by its abundance in the area and by the diversity of its forms. In different parts of the country, however, new genetic influences from the northern and southern neighboring populations were possible. The recent Holocene relationship of the range areas of boreal and Caucasian bears existed in the Don valley, the steppe ravines and the scarps of western Ciscaucasia; this may explain the resemblance of the northwest Caucasian bear to the European bear (Smirnov, 1916a).

Man's activity, which wrought changes in the landscape, also affected the population and range of the bear. The pelt yield increased somewhat in 1930 then dropped and increased again in 1941 (Graph 8).

The future of the bear on the Caucasus is not promising because of continual forest felling and hunting of bear as a trade animal and cattle-breeding pest.

Family MUSTELIDAE

Remains of Mustelidae emerge in Eurasia in Lower Oligocene strata. From the Pleistocene fauna of the Caucasus 6 species of mustelids are known, one of which probably became extinct in the Holocene.

Glutton — Gulo aff. gulo L. Glutton remains have been found in many caves from the Upper Pleistocene of the southern and middle belts of Western Europe. In the U.S.S.R. glutton remains were found in Crimean and Ukrainian Paleolithic strata on the Kama banks and in the Altai and Urals caves.

A fragment of glutton mandible was found in the Upper Paleolithic strata of the Gvardzhilas cave and in the Lower and Middle Paleolithic strata of the Kudaro I cave. This was the most southeastern habitat of the Pleistocene species.

Smirnov (1923-1924) considered the glutton a mountain animal and explained its extinction on the Eurasian plains by the disappearance during postglaciation of compacted snow on which this animal could overtake average-size ungulates.

Pidoplichko (1951) explained the withdrawal of the glutton range to northeastern Europe and its rapid extinction by "anthropic factors." It is interesting that a similar decrease in range is recorded for the arctic fox, the reindeer and other arctic animals. In contrast, the range of the glutton shows a wide gap between its early Mediterranean focus and its northern part, added during the Pleistocene. The Caucasian focus of the species became extinct only slowly because food was abundant and mountain topography and therefore snow conditions were diverse. Many factors were responsible
267 for the extinction of this animal in the Caucasus, the most important reason being decline in reproduction in the present-day phase of species evolution.

The glutton is an autochthon of the mountain margins of the Mediterranean area; from this focus the animal dispersed northward and can be observed today on this new range.

Exactly when the glutton became extinct on the Caucasus is as yet not determined. It is, however, possible that it became extinct there later than in southwest Europe, perhaps in the Bronze Age.

Stone marten — Martes foina Erxl. The genus Martes is known in Eurasia from the Lower Pliocene. If we include the real martens in genus Mustela, we can assume that this collective group developed in the Holarctic by the Upper Miocene. Mustela filholi Goudry and Putorius sp. were reported by Bogachev (1938c) from the Caucasus in the Pliocene deposits of the Armenian Highland.

Fragments of Martes sp. were collected by archaeologists in the Middle and Upper Pleistocene strata of western Transcaucasian caves: Akhshtyrskaya and Sakazhia. On the Russian Plain we found jaws of Martes sp. in the Pleistocene sands of the lower Kama. This species is probably related to the pine marten. Real martens were not found in lower streams of Russian Plain rivers, but in the Crimea they were common in Paleolithic strata. From the Palestine Paleolithic, a M. palaeosyriaca Nehr. similar to M. foina has been recorded. The marten of Urartu time from the Sevan shores was incorrectly recorded as M. latifrons Sat.

The contemporary range of the stone marten is enormous: it spreads from the shores of Spain along the middle latitudinal belt as far as northern China and Manchuria. The Caucasian subspecies M. foina nehringi Sat. inhabits forested foothills, mountain forests and woodless plateaus (Map 24). On the Stavropol Plateau and on the undulating plains west of Stavropol it inhabits shrub-grown ravines and scarp lines of Sarmathian limestones. There is an annual yield of pelts from the middle reaches of the Kuma in the area of Budennovsk, and the Greater Caucasian foothills, the anterior valleys and central Dagestan are also inhabited by the stone marten. It is widely distributed in the basins of the left tributaries of the Terek, the Sunzha and the Manas, and in the Gunib District. An excellent pelt yield was taken from the lower forests of Samur. We found this marten near Baku, near the base of the Apsheron Peninsula.

The stone marten is absent from the fringing forests of the Kura-Araks lowland.

In western and eastern Transcaucasia Martes foina Erxl. dwells primarily in the foothills and lower mountain forests; it is very numerous in the lower forest areas, e.g., in the Alazan-Agrichai valley, where pelts are generally obtained. On the Armenian Highland and in Talysh the stone marten is widespread wherever there are small shrub thickets and forests. It lives in colonies in the upper mountain zone. However, even in desert intermontane valleys, e.g., on the middle Araks, the animal inhabits only large rocky placers and valleys, and ravines of isolated summits such as Ilyanlu-Dag, Darry-Dag and others.

Judging from its ecological distribution the Caucasian stone marten is an early Pliocene dweller originating in the south.

The activity of man, especially trading, affected it less than the following species.

268 **Pine marten** — Martes martes L. The remains of the pine marten are common in Pleistocene deposits of Western European caves (in England, France, Italy and Hungary). They are also recorded from Mousterian strata of Palestine (Bate, 1937). It is difficult to distinguish the bones of this marten from the bones of the stone marten which probably lives in some Paleolithic encampments of eastern Transcaucasia.

The present-day range of the Caucasian subspecies M. martes lorenzi Ogn. is very peculiar; it mainly inhabits full-grown beech forests on the northern and southern slopes of the Greater Caucasus, gradually disappearing in the east. On the Lesser Caucasus it inhabits the northern slopes of the Adzhar-Imeretia ridge, and on the Trialet ridge it is found from Borzhomi and Bakuriani to the Belyi Klyuch. To the west, the range extends from the northern slope of Taurus to Asia Minor (Map 25). East of Debed-Chai and Akstafa-Chai the marten is very rare if it exists at all. No marten pelts have been obtained from Karabakh forests during the last 25 years.

Satunin (1907b) recorded a skull of a young marten from a site located on the eastern shore of Lake Sevan as M. martes (?). His diagnosis was based upon delicate features and small size; this skull, which is now in the Georgian Museum, is in fact that of a stone marten.

The range of Martes martes L. had not reached Lake Sevan by the middle of the first millennium B.C. From the seven marten skulls taken from the Urartu graves not one belonged to Martes martes L.

The species is absent from Talysh despite the abundance of forests and of the fat dormouse, a very important food. Ellerman and Morrison-Scott (1951, p. 245) incorrectly claim the presence of the pine marten near Asterabad.

The absence of the pine marten from the eastern part of the Lesser Caucasus and the Talysh Mountains may be attributed to the late appearance of the species in the Caucasus and the presence of an ancient woodless barrier in the Khram basin. The competition of the stone marten in the southeastern regions of the country should also be taken into consideration.

The greatest number of pine martens is observed in the western Caucasus. Pelt yield per 1,000 km^2 for both martens* is given by pelt supply stations for the 1930's: Georgia — 37.8, Armenia — 30.3, Azerbaidzhan — 19.4, Dagestan — 10.3 and northern Caucasus — 7.8.

The high number of martens in Georgia is explained by the heavy afforestation of the country. In Armenia the entire pelt yield was from stone martens.

Donaurov (1949) observed the pine marten in the Caucasian Reservation between 1935 and 1936. (Its summer excrements and winter snow tracks were found distributed according to Table 67.)

Such a distribution is the result of an abundant supply of vegetable and animal foods: during summer months — Muridae and insects; in fall and winter — mountain ash, whortleberry, common yew and rodents.

The small population of pine marten in the lower forest is probably a result of its replacement by the stronger stone marten. On the southern slopes
269 of the Greater Caucasus the distribution of the animal is somewhat different.

Table 68 shows the frequency of encounter of the marten activity in the Zaketaly Reserve and adjacent lands, according to our data of 1935—36.

Our data and those of Donaurov for the lower and middle zones also pertain to the stone marten.

According to Mlokosevich's observations (Markov and Mlokosevich, 1935) made over several years in the Lagodekhi and Zakataly regions, the pine marten inhabits the upper mountain forests and is unable to compete successfully with the stronger stone marten of the foothills. It is absent from the woodless plains.

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* The State Yield Supply recorded both marten species together.

TABLE 67. Frequency of pine marten tracks in the western Caucasus (in %)

Habitat	Summer	Winter
Broadleaf forests	0.7	6.9
Fir—beech forests without vacciniaceous plants	16.9	9.4
Fir—beech forests with underbrush and vacciniaceous plants	37.8	51.8
Upper forest edge	40.9	30.9
Subalpine meadows	3.7	1.0

TABLE 68. Frequency of pine marten tracks on the southern slopes of the Greater Caucasus (in %)

Habitat	Summer	Winter
Beech—hornbeam forest of the lower zone	12.5	13.2
Beech forests with mazzard cherry and filbert of the middle zone	30.6	47.8
Thinned oak—beech forests of the upper zone	50.0	39.0
Subalpine meadows	7.9	—

The pine marten is a more specialized and phylogenetically younger species than the stone marten as shown by its morphology and ecology. The separation of pine marten probably occurred in Europe in the Lower Pleistocene since it was a distinct species by the Middle Pleistocene. The ecology of the pine marten's contemporary range confirms the relatively late (Upper Pleistocene) migration from Europe through the Balkans and Asia Minor.

The direct and indirect influence of man on the population and range of Caucasian martens became visible in the last century.

Ancient Circassia produced a heavy yield of pine martens. There are references in Dubois de Montpéreux (1843) of the yield of pelts in this area in the 18th century and Radde (1866) records an annual yield of 500 marten pelts from upper Svanetia in the middle of the last century. Marten-hunting for pelt-trading was taken up in the 1860's following the settlement of the 270 northern Caucasus (Dinnik, 1941a; Turov, 1937). The clearing of significant areas of forest land over the past centuries in Dagestan and Azerbaidzhan could have brought about a reduction in the marten range. Records of the last 25 years show a decrease in pelt yield in 1930-1931, an increase in 1937 and another in 1947. Some drop in trade in Abkhazia was observed in the 1930's as an apparent result of the development of the fat dormouse trade (Markov, 1938; Graph 9).

Family **FELIDAE**

At least 10 forms of cats have been identified from Neogene deposits of the Caucasus and adjacent areas. Machairodus sp. is known from Sarmatian deposits near Armavir and a medium-sized Felis sp. from the Maraginsk Upper Pleistocene site in northwestern Iran. More fragmentary bone findings of Felis and Panthera have been reported from the Lower and Upper Pliocene of Stavropol and the Taman Peninsula.

Six species have been recorded from Caucasian fauna of the Pleistocene: Panthera spelaea Goldf., panther, lynx, European wildcat, spotted cat and cheetah. And finally from the Holocene there have been nine species identifications; of these nine, three have become extinct in historical time.

Cave lion — Panthera spelaea Goldf. Remains of this species of large cat have been discovered in Middle and Upper Pleistocene Eurasian strata — from England to the New Siberian Islands (Trouessart, 1904-1905). It is a characteristic index species of the Pleistocene mammoth fauna of the Russian Plain and of the Crimea (Gromova, 1932a; Gromov, 1948; Pidoplichko, 1951). The southern distribution limit of P. spelaea Goldf. was probably somewhere in the Mediterranean area. Remains of Paleolithic cat from Lebanon, Syria and Palestine probably belong to the real lion (Picard, 1937). There have been no findings of P. spelaea Goldf. in Iranian caves. On the Caucasus remains of a large Pleistocene cat were discovered in the Sakazhia cave, in loamy talus deposits in the vicinity of Sochi and in asphalt sands of the Apsheron Peninsula (Figure 111; Map 33).

Gromov's assumption (1948) that Panthera spelaea became extinct on the Caucasus just before the Bronze Age, which would have been later than in other regions, is open to question. In all probability, it became extinct simultaneously with the cave bear, woolly rhinoceros and mammoth. Related species, such as lion and tiger, appeared on the Caucasus as postglacial immigrants from the south.

Lion — Panthera leo L. The subject of the lion's place in the Caucasian Holocene fauna and of its relationship to the Pleistocene Panthera spelaea is very complicated. The majority of paleontologists considered P. spelaea the direct ancestor of the contemporary lion. Without going into details, Pidoplichko (1951) claimed that the large Pleistocene cat was also a lion. However, as our investigations have shown (Vereshchagin, 1951b), Panthera spelaea possessed more specialized feline cranial features than the contemporary African lion.

A number of West European paleontologists have recorded lion remains in caves in England, France, Spain, Germany, Italy, Poland, Sweden, Czechoslovakia, Hungary, Morocco and Rhodesia, mostly from Holocene strata (Wolf, 1938, 1939).

271 Lion remains were reported by Picard (1937) in Acheulean and Mousterian strata in Palestine.

Gromova (1932a) mentioned teeth and metapodia of lion found in an ancient Greek cave in Olvia; however, these remains may have come from a lionskin rug brought from the south and not, as reported, from an animal caught on the north coast of the Black Sea.

Spendid low- and high-relief representations of lions found during the excavations of ancient Sumer, Babylon and Nineveh verify that the lion was very common in southwest Asia in the third to first millennia B.C. Another series of representations of lions executed on stone by the Hittites in the central part of Asia Minor was published by Osten (1929-1930).

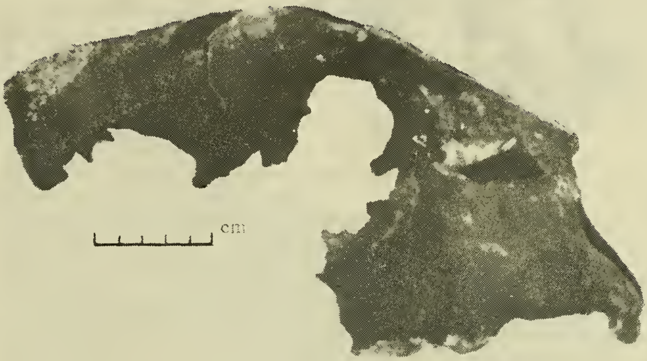

FIGURE 111. Skull of Panthera spelaea Goldf. (female) from Binagady asphalt

Lions are known on the Caucasus only from pictures and legends. Among them are the following noteworthy findings: relief representations of two lions on the gold plating of a beaker from the Trialet mounds, 2nd century B.C. (Kuftin, 1941); contour images of two lions on a gold cup from a Kirovakan burial, second millennium B.C. (Piotrovskii, 1949); contour images of lions on rocks in Kabristan from the first (?) millennium B.C. (Vereshchagin and Burchak-Abramovich, 1948); contour images of lions on silver containers and sculptures on gold plates (Figure 112) found near Maikop, second millennium B.C. (Farmakovskii, 1914); relief representation of a lion on the gold plating of a quiver from burials on the Taman Peninsula (Figure 113).

Representations of lions and lionesses dismembering fallow deer and wild asses were found on a gold vial from the Solokh burial in southern Ukraine (6th century B.C.). Mantsevich (1949) concluded that this vial was made by Ionian craftsmen, but (despite our advice) erroneously classified the wild asses as horses and the lionesses as leopards.

We do not exclude the possibility that the lion penetrated into Ciscaucasia and the Russian Plain in the xerothermic period. Pogrebova (1950) formed the reasonable opinion that most of the artistic works and representations of animals found in the Scythian mounds were executed locally and were, 272 therefore, modelled on the local fauna. The find, in the strata of ancient Tanais, of a plate of local raw limestone (43×56 cm) depicting a lion supports this theory. This stone is kept in The Hermitage (Knipovich, 1949).

Later likenesses of lion appear on many relics of Armenian, Arabian and Iranian culture in Armenia, Azerbaidzhan and Georgia. Lion heads appear on the walls of the Old Derbent fortress which dates from the time of the Arab caliphate, and on the fortress gate in Baku, which was erected in honor of Shah Abbas in the 17th century.

Lion images are frequently found in the medieval art of the Dagestan mountain region (Bashkirov, 1931). In Iran at the time of the Safawids, hunting rugs were designed with lion images (Kverfel'dt, 1940).

FIGURE 112. Gold plates with figures of lions from a Maikop burial

Both the earlier and later representations of lions found on the Caucasus could be easily accounted for by the influence of Hittite, Assyrian, Babylonian, ancient Iranian and Arabian cultures, and even by the importation of finished articles from southwest Asia, But a comparison of the pictures on Kabristan rocks with Scythian articles of Ciscaucasia suggests a different explanation.

It is possible that the distribution area of the European and of the Asian lion was irreversibly reduced in historical time even in southwest Asia.

Herodotus and Aristotle mention the presence of lions in the Balkans in the second half of the first millennium B.C. The lion figures in Homer's Iliad. A Greek military division of the 5th century encountered north African savannah animals near the source of the Euphrates (Xenophon, 1896 edit.). These included ostriches and onagers which became extinct in the 19th century.

Surveys on the early distribution of the lion in the Near East have relied heavily on such literary references as Sundevall (1863), Keller (1909), Gromova (1928) and Körner (1930).

Lucian of Samosata (125 A.D.) reported a large cat (lion?!) which jumped on the horse of a Scythian hunter (Latyshev, 1947-1948). Zhitkov refers to the probable presence of a large cat — "a ferocious animal" — on the southern steppes in old Slavonic times in "The Lay of the Host of Igor" (Slovo o polku Igoreve, 1936, p. 229), as does Vladimir Monomakh in "Instructions" (Pouchenie). However, Sementovskii (1857) understood "ferocious animal" to mean only a wolf. Moisei Kalankatuiskii wrote (10th century A.D.; 1861 edit., p. 6) in what may be an imperfect translation: "Blessed is the country of Agvan*. . . where are wild animals:
273 lions, tigers, panthers, wild asses; and a great number of birds: eagles, falcons and their like." It is interesting that the reference to wild asses was verified by kulan bones found in 1946 during the excavation of a 13th-century settlement in Baku. At the time of the Arabian caliphate and later, eastern Transcaucasia was entirely suitable for the habitation of lions. The tugai on the Kura and Araks rivers and the

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* Ancient Albania and Azerbaidzhan.

vast reed-grown areas on the Mugan floodplains were densely populated by boar and deer and herds of kulans and goitered gazelles grazed in the open semidesert.

Herds of ungulates were attracted in spring, summer and fall to the piedmonts grown with juniper—pistachio forests and a luxuriant grass cover.

In the hunting ode "Shikhariya" dedicated to Manuchekhr, the son of Shirvan Shah, the poet Khagani (Avsaraddin), who lived in Shemakha (1120-1194), glorifies the Shah's lion hunt, mentioning the area between the Caspian Sea and Shemakha (History of Azerbaidzhan Literature, Vol. 1, 1943; Text of Arasla in Azerbaidzhan).

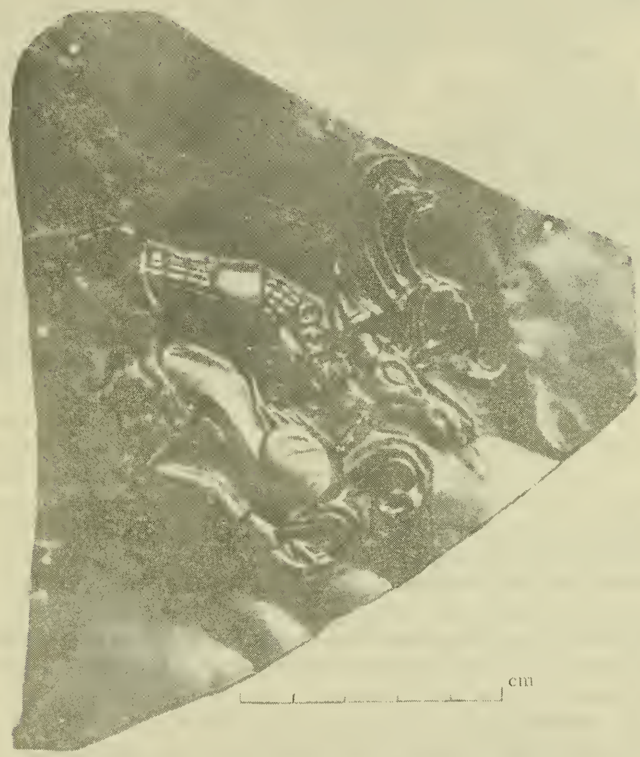

FIGURE 113. Part of gold lining of a quiver from the Semibratnoe site, showing a lion dismembering a deer

In Farsi the word "shir" means lion and we can assume that the Shirvan region derived its name not only from the ruling shahs, but also from the lions which inhabited it.

In his poems "Iskandarnama," "The Seven Beauties" and others, Nizami Ganjawi (11th-12th centuries, A. D.) constantly used the lion as a literary allusion.

Usamah ibn Munkidh (1922-1923 edit.) described lion hunts in Syria and Palestine in the 12th century when lions were as common there as hares in present-day Caucasia.

At the end of the 19th century, Blanford (1876) indicated that lions had become extinct in northern Iran, but were still living in Mesopotamia on
274 the western Zagros spurs and southeast of Shiraz. The Persian lion, P. leo persica Meyer, 1826, was described from a Teheran specimen, i.e., from northwestern Iran.

Chardin records that lions and tigers still inhabited the forests of Mingrelia and Imeretia at the beginning of the 17th century (1735, p. 51). Chopin (1852), who lived in Armenia, stated that during his lifetime lions were no longer observed there, but tigers were occasionally seen wandering from the Araks River. Danford and Alston (1880) mentioned the extermination of horses by a preying lion in 1873 or 1874 near Bilecik on the Upper Euphrates. According to Kinnear (1920), lions were no longer seen in Asia Minor by the end of the last century, but they still inhabited Mesopotamia and Arabia. After large-scale deliveries of weapons to the Near East during World War I, the number of Asian lions decreased rapidly. In the opinion of Pocock (1930, 1939) and of Harper (1945), the rapid extermination of the Asian lion was entirely a result of European colonization and wanton hunting by English officers stationed in Asia, who killed many of these animals for diversion.

Considering the above, we can assume that the lion inhabited Transcaucasia, penetrating there from the south in the Holocene. After a gradual withdrawal to the southeast and southwest (Map 33), it disappeared from this region by the end of the Middle Ages. The reduction of population and range of the tiger and striped hyena presents similar histories. Both of these animals were observed in this region until the first half of the 20th century.

Tiger — Panthera tigris L. Apparently remains of true tigers are known only from the caves of China and Java (Wolf, 1938). There are indications that findings in France and Siberia probably belong to Panthera spelaea Goldf. Tiger remains have not been found in the central Asian Paleolithic caves of Teshik-Tash and Aman-Kutan.

The absence of tiger remains in the Binagady deposit is important for an understanding of the history of the tiger on the Caucasus.

Today the tiger is distributed mainly in southeastern Asia. Like the cheetah, hyena and lion, the present-day tiger is a postglacial immigrant. The tiger spread widely in a northwesterly direction from southeastern Asia, probably only in the Upper Holocene. It is significant that this animal is not represented in the art of ancient Mesopotamia, but was depicted by the Persians, although not as frequently as the lion.

Tigers occasionally appear in ancient Persian miniatures. In the 1620's the Russian merchant Fedot Kotov colorfully described a tiger in the Shah's menagerie in Kazvin (1852).

Reviews and critiques of the literature on the distribution of the tiger on the Caucasus at the end of the 19th and the beginning of the 20th centuries have been published by Dinnik (1914a), Satunin (1915a) and Ognev (1935).

In 1947 the author presented a chart of tiger distribution on the Caucasus, showing locations where they had been captured over the previous ten years. Eastern Transcaucasia has been the extreme limit of tiger distribution up to the present time.

The tiger was so common near Lenkoran in the 1860's that some were killed there each year (Radde, 1899). The tiger was frequently encountered at the end of the 19th century on the Lenkoran Plain and in the mountain forests of Talysh where at least one tiger was killed every year (Satunin, 275 1915a). At the beginning of this century the tiger population began to decrease rapidly. In the 1920's (Figure 114) tigers were sometimes seen in eastern Transcaucasia, although they were not inhabitants of this region.

Between 1920 and 1950 only two cases of tiger-pelt yield were recorded: one in 1922 near Tiflis and one in 1932 in Talysh (Map 33).

FIGURE 114. Tiger in the jungles of Lenkoran in the first half of the 20th century

Soviet officers who lived in Gilan and Mazanderan in 1942-1943 told us of repeated reports of tigers and of their own personal observations of tiger tracks and the dismembered bodies of boars and domestic animals on the forested northern slopes of the Elburz Range.

Deforestation, the extermination of boars (the main food of the tiger) and tiger-hunting have created unfavorable conditions for tiger life on the Caucasus.

Panther — Panthera pardus L. (s. lato). Remains of P. pardus were found in the Paleolithic strata of numerous caves in Africa and India.

Remains of this species have been found in caves in Syria, Palestine and Lebanon in strata dating from Acheulean to Neolithic (Picard, 1937; Bate, 1937) and, in central Iran, it is recorded from Paleolithic strata of the Bisotun cave (Coon, 1952). Wolf in 1938 reported related fossil evidence.

It is possible that a contemporary species of panther of African-European type inhabited Western Europe during the warmer phases of the Pleistocene. Panther remains have not been observed in the Pleistocene strata of Eastern Europe, which in our opinion indicates that the limits of the range were more southerly — at the Caucasus and Kopet Dag ranges — during the Pleistocene.

A unique find of Pleistocene P. pardus remains was made in the Paleolithic strata of Kudaro I and II caves at the head of the Rion.

The remains of P. pardus found in Holocene localities may have been brought there from elsewhere, as the only other reliable reports are on 276 findings from Greek and Roman strata of Olvia and of ancient Theodosia (collection of the Institute of Zoology of the Academy of Sciences in the Ukrainian S.S.R.) and on findings in the Caucasus from the Mesolithic of the Sosruko grotto (on the Baksan) and from the "Dlinnokryly" cave (in the Araks ravine).

The absence of P. pardus from the Middle Pleistocene fauna of Apsheron indicates that it first appeared in central Caucasia, penetrating the area along with the mouflon and porcupine from the south.

FIGURE 115. Bronze heads of P. pardus from Ukraine burials

During early historic time, P. pardus was widespread. It was known by the Scythians on the Ciscaucasian Plain. Bronze heads of P. pardus have been found in the Scythian hills of the Russian Plain and in Ciscaucasia (Figure 115).

A golden figurine of a reclining panther was recovered from the Kellermess hill. A splendid small bronze statue of a panther was recently found in Samtavro excavations, west of Tiflis (cf. reproduction in: Vestnik drevnei istorii, No. 3, 1948).

At the beginning of the 20th century, the distribution of panther was limited by the foothills and mountain regions of the Greater and Lesser Caucasus, and by the lowland of eastern Transcaucasia (Dinnik, 1914a; Satunin, 1915c). During the last 50 years the number of panthers has rapidly decreased.

From 1894 to 1898 eleven panthers were captured in the Kuban hunting regions. In 1904 only two panthers were caught there, while in 1905 and 1906 none were found. The panther is rarely encountered on the Main Range in our century. In 1912 two panthers were killed in the Zakataly region; after that time, despite the abundance of goats, gazelles and deer, only occasional panther tracks were seen in the ravines of the left tributaries of the Alazan. In North Ossetia two panthers were killed at the beginning of the 'twenties. In 1949 one panther was killed in the gully of the right tributary of the Sunzha and in 1952 another panther was killed near Staliniri in South Ossetia.

Panthers have been more numerous and more enduring in Talysh and Karabakh. In the middle of the last century Radde ordered and received twelve fresh panther pelts from the Lenkoran District over a seven-week period. From 1930 to 1940, i.e., about 70 years later, the Azerbaidzhan pelt-supply base received only two panther pelts and a small number of pelts was acquired privately by individuals.

Not more than ten panthers were killed on the entire Caucasus in the 1930's, and those mainly on the Zangezur ridge and in Talysh. Regular appearances of panther in the reed-grown thickets of the central Mugan, for example on Makhmud-Chala Lake, were recorded from 1929 to 1932. Near the village of Kharmandali, a dead female panther apparently buried by the male was found in 1929. A male panther, which had fallen into a pit during a snowstorm, was killed near the village of Mashtagi on the Apsheron Peninsula on February 15, 1946 (Burchak-Abramovich and Dzhafarov, 1949). Heavy snowfalls and storms have driven the panther away from the mountains.

277 After World War II, encounters with panthers became more frequent and pelt yield increased. Fresh panther pelts were received from the Talysh Mountains, the Nakhichevan area and the Karabakh Upland. Thus, in Azerbaidzhan in 1947, the yield was five pelts and in 1948, thirty-six pelts.

This population increase is an apparent result of the migration of this animal from southwestern Iran. Present-day panther distribution on the Caucasus is limited by the forests of the Talysh Mountains and the ridges of Karabakh, Zangezur and the Nakhichevan area (Map 34).

FIGURE 116. Three-month-old panther from Talysh, showing typical spottiness of the young animal

Photograph by author, 1947

The panthers which inhabited the Greater Caucasus belonged to the pale-colored subspecies Panthera pardus ciscaucasicus, now nearly extinct.

The Transcaucasian P. pardus tullianus Val. (Figure 116) is brighter colored with an admixture of rust tints and shorter fur. The panther which was killed in Apsheron belonged to this subspecies. The rapid disappearance of panthers from the Greater Caucasus in this century is undoubtedly the result of persistent hunting of these animals. Unless panther hunting is forbidden, the animal will disappear in the next few decades from the Caucasian Isthmus.

Lynx — Felis lynx L. (s. lato). A species which is closely related to the subgenus F. lynx pardina, dating at least from the Middle Pliocene, has been found in Upper Tertiary deposits of southern Europe (in Moldavia and in catacombs in Odessa, France and Italy). A cat mandible, similar in dentition to that of a small lynx, was found in Lower Pliocene deposits near Stavropol.

Lynx fossils of the present-day type are characteristic of Lower and Upper Paleolithic settlements in the forest and forest-steppe zones of Western and Eastern Europe (Wolf, 1938, 1939; Gromova, 1948; Pidoplichko, 1951). On the Caucasus they have been found in the Sakazhia cave in western Transcaucasia.

There are no reports of lynx remains from the Paleolithic of the eastern Mediterranean (Lebanon and Syria: Picard, 1937; Bate, 1937; Iran: Coon, 1952). Thus, it can be assumed that in the Pleistocene the lynx was not distributed very far south of southwest Asia. Today the lynx range lies in plains and mountain forests and is limited by the polar circle.

During the Holocene the lynx population was considerably reduced by hunting, but even more by deforestation. The lynx does not inhabit the riverain forests of the steppe zone nor the region to the south, despite the abundance of food, e.g., hare, beaver and roe. Perhaps the flooding of 278 the area in the spring accounts for their absence; it may also account for the rarity of lynx remains in deposits found along the lower reaches of the Ural, the Volga and the Don.

The present range of the lynx F. lynx orientalis Sat. on the Caucasus includes the entire forested area of the Greater and Lesser Caucasus and of the Talysh area (Dinnik, 1914a; Satunin, 1915a; Vereshchagin, 1947d) (Map 35). In adjacent areas of Turkey and Iran the lynx is encountered in islets of mountain forests. Generally this cat is found in mountain regions even though small shrubs may be the only vegetation. For instance, on the eastern limit of the Main Range many lynx live in the shrub thickets and undergrowth near the villages of Kyzyl-Burun and Khizy where hares are numerous. The lynx is also seen sometimes in woodless Dagestan and in small islands of oak forest in the Armenian Highland, e.g., along the headwaters of the Nakhichevan-Chai near Shalbuz. The lynx originated in the ancient Mediterranean area and today still inhabits the nearly woodless landscape of Palestine (Bodenheimer, 1935). According to Pidoplichko (1951), the lynx does not always inhabit forest land in southern mountain countries.

The recent yield of lynx pelts from the Caucasus, from Ciscaucasia and from Transcaucasia has fluctuated widely. Significant increases in population were noted in 1928-1929, 1932-1933, 1938 and 1950 (Graph 15). The difficulties of mountain trade curtailed lynx extermination.

European wildcat — Felis silvestris L. Remains of small cats (F. pygmaea Lartet, F. media Lartet, F. attica Wagner and other species) closely related to the European wildcat are known from Miocene and Pliocene deposits in Italy, Austria and Greece, and are particularly associated with the Hipparion fauna. Fossils of a contemporary type are common in Pleistocene and Holocene strata of many caves throughout

Western Europe, excluding the Scandinavian Peninsula (Trouessart, 1898-1899a; Wolf, 1938). They are frequently found in Middle and Upper Paleolithic strata in Crimean caves (Puzanov, 1929; Gromov, 1948). On the Russian Plain a mandible of a small cat was recovered from Pleistocene deposits of the lower Don (Tsimlyanskaya). On the Caucasus several bones of this cat were found in Paleolithic strata of the Akhshtyrskaya and Tsebeldinskoe caves. There are records of Felis silvestris L. remains in the southeastern Mediterranean area taken from Acheulean to Neolithic strata in caves in Palestine and Syria (Picard, 1937; Bate, 1937).

We found Holocene remains of European wildcat only in the Pyatigor'e area. It is interesting that only remains of domesticated cats were found in the medieval strata of the Sarkel fortress on the Don. It would appear that the range of the Caucasian subspecies, F. silvestris caucasicus Sat., was not associated during the Holocene with the European subspecies in the Russian Plain.

Today the range of the European wildcat includes Western Europe, Asia Minor and the Caucasus. It probably became extinct in the Crimea during the Holocene. Within the Caucasus the distribution of the European wildcat gradually declines eastwards (Map 36). There are no documented data from the Talysh and Elburz mountains; there is, however, some ambiguous information concerning a kind of cat seen in the forests of Lenkoran, Gilan and Mazanderan (Blamberg, 1853; Smirnov, 1922; Bobrinskii, Kuznetsov and Kuzyakin, 1944) which has not been verified. Associations with forest biotopes are quite pronounced for this species, but in Ciscaucasia wildcat distribution is limited by the small number of surviving plots of shrubs, forests and reeds, such as those of the Kabarda lowlands, the valley of
279 the middle Kuma, the Stavropol Plateau and the Kuban River delta. In the southern part of the country, wildcat is more likely to be found in stands of forests, while on the woodless upland of the Lesser Caucasus it is practically nonexistent. In western Transcaucasia wildcats are numerous in the beech forests of the Adzhar-Imeretia Range and in the alder swamps of Colchis. Contrary to the studies made on the plain by Formozov (1946) (and repeated by Pidoplichko in 1951), the distribution pattern of wildcat does not show a relationship to the varying depths of snow cover on the irregular mountain terrain.

The largest population of European wildcat is observed in the lower third of the forest zone; the animal prefers the beech—hornbeam forests.

Caucasian Reservation data show the following distribution of 43 encounters with wildcat: 76.7% in broadleaf forests, 18.6% in dark coniferous forests and 4.7% in the subalpine zone (Teplov, 1938a). The principal pelt yield on the Caucasus is obtained from submontane forests.

According to paleontological data, the European wildcat is an autochthon of the Mediterranean area and, on the basis of present distribution patterns, can be regarded as an early Pleistocene settler from Europe which penetrated the Caucasus via the Balkans and Asia Minor.

The hunting of European wildcats for their pelts during the last 25 years has not affected this animal's population (Graph 16).

Jungle cat — Felis chaus Güld. The remains of this cat are known from Pleistocene strata of India (Wolf, 1938), According to Picard (1937), fossils have been found in Syria and in Palestine in deposits from the Mousterian to the Neolithic. Gromov (1937, p. 86) is of the opinion that

Azilian and Tardenoisian strata of the Crimean mountain regions may well contain jungle cat fossils. The finds in Western Europe (e.g., in Stuttgart travertines) are insignificant. Pleistocene and Holocene remains of this species are unknown on the Caucasus, and finds of Holocene remains on the Russian Plain are also doubtful. In the 8-13th century strata of the Sarkel fortress near Tsimlyanskaya two inferior humeral epiphyses were found which were similar in size to those of the jungle wildcat.

In the 14th-century strata of a Slavic village in Poltava an inferior humeral epiphysis of a cat resembling this species in size was reported (Gromov, 1948), but the authenticity of this report is questionable. Our later investigations of cat fossils indicate that Felis lybica lived in the Crimea and on the southern Russian Plain throughout the Quaternary, but Felis chaus did not. It is probable that Felis chaus only penetrated eastern Ciscaucasia and the southern Russian Plain late in the Quaternary (during the Holocene).

At present the main distribution area of Felis chaus is in southern and southeastern Asia, while on the Caucasian Isthmus the range is "undeveloped." This cat inhabits eastern Transcaucasia from the Caspian Sea to an altitude of 900-1,000 m. In the west it inhabits the valleys of Kura to Gori; it has not been observed beyond Surami. In the Araks River valley the cat is encountered as far as the longitude of Mount Alagez. It is common along the Caspian shore, especially near Samur and along the lower reaches of the Sulak and Terek rivers, penetrating farther through the reeds along the Berovskie knolls and to the Volga delta (Dobrokhotov, 1939).

In eastern Ciscaucasia this cat is found as far as Grozny in the Sunzha River valley and as far as Mozdok in the Terek River valley (Map 37).

280 Felis chaus is not encountered at present in western Ciscaucasia. The pelts obtained from the Krasnodar Territory were brought from the southeast. In the scientific collections from this region, the jungle cat is not represented; although the literature, beginning with Bogdanov (1873), mentions the presence of this cat on the Kuban delta, it is yet to be confirmed.

The data of Formozov (1946) on the habitation of this cat along the reed-grown banks of the lower Kuban River are erroneous. The finding he cites of a pelt and skull in the Cossack village of Grivenskaya was really of European wildcat.

FIGURE 117. Jaw of cheetah from Binagady asphalt

The greatest number of this species is observed in the lowland forests of eastern Transcaucasia. Its favorite biotopes are reed—cattail thickets beside lakes and marshes and tugai thickets along rivers and rivulets. Here the cat hunts water voles and marsh birds. It is not encountered in mountain forests, but will migrate through open places in the Transcaucasian semidesert.

Some unknown barriers impede its penetration into western Transcaucasia. At the first glance it would seem that, like the jackal, the jungle cat would prosper in the Colchis, which has a topography similar to that of Girkan, a warm climate and many swamps. The absence of the cat from the Colchis cannot simply be explained by the "newness" of the distribution area on the Caucasus. After all, the Surami Pass is sufficiently low to permit passage, and predatory communities are known to settle rapidly. The absence of jungle cat remains from the Binagady locality, the "underdevelopment" of its range on the Isthmus and, finally, the stenotopic character of the animal and its relative adaptation to warmth suggest that it is a postglacial settler of southern origin. The area of land on the Azerbaidzhan Plains inhabited by the jungle cat increased with the development of a local irrigation system and decreased with its abandonment. Most recently, the destruction of tugai forests and of bamboo groves and accelerated trade have caused a further decrease in range and population. It is difficult to discover the population dynamics of the jungle cat from figures on pelt yields because the pelts of this species and those of European wildcat are reported together.

The granting of bounties on cats sharply increased the pelt yield. This reflects a state of species well-being, although nutria breeding is thereby endangered.

Cheetah — Acinonyx jubatus Schr. Cheetah remains are known from the Upper Pliocene of southern Europe and Africa (Simpson, 1945).
281 The species is very rare in Quaternary deposits and until recent times was known only from the Upper Pleistocene of China (Pei, 1939). In the Caucasus (Figure 117) they were first revealed in Middle Pleistocene strata of the Apsheron Peninsula (Map 38). At that time the cheetah (Figure 118) could have hunted saigas, asses, horses and hares. Possibly its distribution in the Pleistocene extended to eastern Ciscaucasia. The contemporary range of the cheetah includes Africa and southern Asia as far as China. Its preferred biotopes, according to Roosevelt, Pocock (1939, 1941) and other naturalists and hunters, are low-lying plains and hilly savannahs, deserts and semideserts where the animal shelters among rocks and shrubs. In Turkmenistan and Iran it lives in the open sandy, clayey and stony desert, but prefers river valleys grown with tugai thickets where it hunts gazelles and hares.

There are no documentary data on the occurrence of the cheetah in the Caucasus in historical times. It was depicted (Figure 119) on an ornament of a silver container found in the Maikop burial (Farmakovskii, 1914). The wearing of a collar suggests the possibility of cheetah domestication by the time of the Scythian. On a 12th-century ceramic from the excavation of ancient Gandzha [now Kirovabad] there are pictures of cheetah somewhat reminiscent of those depicted by the ancient Egyptians.

The Georgian Chronicles "Kartlis Tskhovreba" place the cheetah in eastern Georgia (Kartlia) in the Middle Ages and, from this source, its

presence was incorporated into the local fiction. Some local authors made
extraordinary statements regarding its habitation of high mountains, e.g.,
K. Gamsakhurdia in "The Hand of a Great Master" (1945). Usamah ibn
Munkidh (1922-1923 edit.) mentioned that Asia Minor gazelles were hunted
282 with cheetahs in the 12th century in Syria and Palestine. In the Russian
Chronicles and also in "The Lay of the Host of Igor" (Slovo o polku Igoreve)
"parduses" are mentioned — hunting "leopards" (cheetahs) — which served
the Russian princes in the hunt during the 11th-12th centuries (Zhitkov,
1936). This practice was borrowed from the Persians or the Polovtsian
khans, according to Zhitkov. This is quite probable, because nomads of
the Russian Plain maintained military, cultural and commercial relations
with those of Ciscaucasia and Transcaucasia from the time of the Bronze Age.

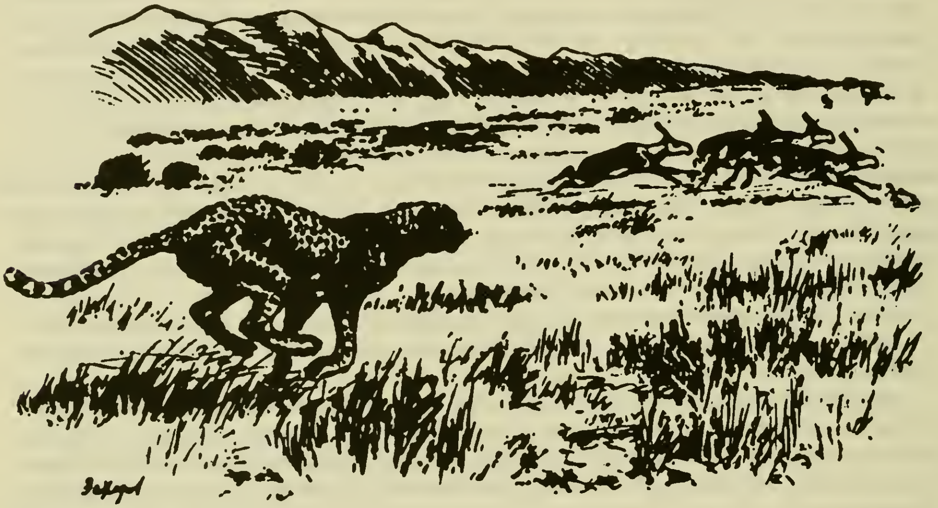

FIGURE 118. Cheetah in the Pleistocene semidesert of eastern Transcaucasia

After Aristov (1866), Pidoplichko (1951, p.178) erroneously ascribed these references to "parduses" (cheetahs) in the old Slavic records to the leopard, an animal unsuited for this hunt. The Azerbaidzhan khans and Armenian and Kartlian princes hunted with trained cheetahs up to the 14th century. In 1474 Josaf Barbaro saw the hundred hunting cheetahs of an Armenian prince.

Adam Olearius (1870 edit.) recorded that a Persian shah hunted onagers using cheetahs in the Isfahan hunting grounds. Olearius wrote (page 935) in connection with this: "There* are numerous predators, such as tigers, leopards, wolves and bears. Tigers** are so numerous there that they are sold in herds of 10-20 animals. The tigers were generally used for the hunt because they were rapid runners and became so highly domesticated that the hunter could place the tiger on the horse behind him." Later information appears on the cheetah in Mazanderan and throughout the Caspian forests (Filippi, 1865, Blanford, 1876).

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* In the Gilan area.

** Cheetahs.

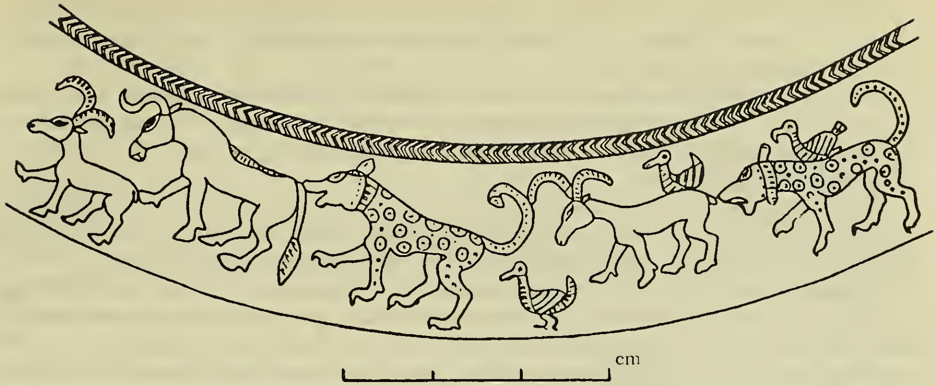

FIGURE 119. Representation of cheetahs on a silver container from Maikop burial (according to Farmakovskii, 1914)

In Asia Minor and Arabia the cheetah was rare at the end of the last century (Danford and Alston, 1880; Aharoni, 1930; Bodenheimer, 1935).

The cheetah probably remained in a wild state in the Kura-Araks lowland and in the middle Araks valley until the 18th century. This is convincingly shown by the sudden decline in cheetah range and population in present-day Turkmenistan and its recent presence in northern Iran (southern Azerbaidzhan).

The disappearance of the cheetah from Transcaucasia and southern Asia is explained by the depletion of steppe ungulates and the intensive pursuit of young cheetahs for training.

283 By tracing the contemporary range of the cheetah in Asia and Africa, Harper (1945) established the reduced area of distribution and the population decline of this peculiar cat.

Order LAGOMORPHA

Lagomorphs appeared relatively early in time. Some genera of this order, for instance Mytonolagus and Shamolagus, are known from the Eocene. In the Mediterranean, central Asia and Mongolia, Tertiary lagomorphs are represented by pikas and hares (Trouessart, 1904-1905; Simpson, 1945; Borisyak and Belyaeva, 1948).

On the Caucasian Isthmus remains of only two genera, Ochotona and Lepus, are known from the Lower Pliocene.

Family LEPORIDAE

European hare — Lepus europaeus (s. lato). The earliest fragmentary remains of small hares were found in Pliocene alluvium near Stavropol and, later, in Pliocene fluvial deposits of the middle Zanga, north of Yerevan.

Numerous L. europaeus remains from the Middle Pleistocene of eastern Transcaucasia (Binagady) belong to a species closely resembling the contemporary animal.

The Upper Pleistocene remains of European hare were found in deposits of the lower Don. In Holocene deposits on the Caucasus, European hare remains are often found in caves used by eagle owls, as well as in strata of human settlements.

The contemporary European hare inhabits almost all of the Caucasian Isthmus, from where it spread to the north and to the south. The southern limit of its range is undefined but probably extends to Mesopotamia.

The pelt yield from European hare on the Caucasus shows the following distribution per 1,000 km^2, according to state pelt-supply records over several years (Vereshchagin, 1947): northern Caucasus — 3,300; Azerbaidzhan — 770; Dagestan — 594; Georgia — 219; Armenia — 127.

Because most of the pelts are sold on the spot, the number of European hare killed in Transcaucasia is actually much greater, especially in Azerbaidzhan. The yield on the northern Caucasus is mainly from Krasnodar Territory and the Dagestan plain. In Georgia almost all of the hares are obtained from the dry eastern portion (Map 39).

The hare population of the alpine and subalpine meadows of the Greater Caucasus is insignificant. It is more common in the dry inner valleys of the northern slope of the range and on the steppelike alpine meadows of inner Dagestan. On the Gunib Plateau the European hare rests by day in relict pine and birch forests.

This species is not found at all in continuous mountain forests of beech, hornbeam and fir. It is true that they penetrate the forest zone moving upwards from the subalpine meadows along woodless slopes and ridges and along denuded ravines, but this penetration takes place mainly as man has changed the landscape.

The contemporary range of the European hare over broad areas of the Caucasian Isthmus shows upon examination that these animals generally
284 inhabit dry uplands and moderately dry ravines with shrubs or sparse forests. In discussing the biotopes of the European hare, it is necessary to distinguish between its day resting places and its feeding grounds, which do not always coincide. The natural distribution of couching and fattening places has undergone marked modifications over the millennia wherever man has engaged in animal husbandry.

On the Ciscaucasian Plain the European hare feeds and couches in the open virgin steppe only in spring and early summer. If the steppes dry out or are burned, the animals concentrate in the river valleys. In fall and winter they feed on windblown places, i.e., on the hills and southern slopes, and couch in ravines and shrubs.

In continuously cultivated regions and in regions of intensive grazing the distribution of the European hare is very complicated. Almost all types of continuously cultivated land in the Stavropol area divert the hares from virgin land, especially when the virgin land is used for cattle grazing.

Alfalfa and grass seedlings comprise the basic diet of the hare; hares also feed on ripened field melons, wheat and barley grains in stubble fields — the latter a probable result of careless combine harvesting (Kolosov and Bakeev, 1947, p. 12).

In winter the hare feeds on crops where it couches. It will often couch on fall-plowed fields, crossing the next forest belt if disturbed. Permanent fattening and couching places in the forest belts are observed only where there are very wide stands of advanced age.

The contemporary widespread distribution of the European hare in the foothills, especially on the Trans-Kuban sloping plain, is the result of man's activity, i.e., eradication of forests and swamp drainage.

The hare is rare in western Transcaucasia, inhabiting the driest plots of Black Sea terraces and only the cleared-forest foothill glades in humid Colchis.

In eastern Transcaucasia the maximum European hare population is observed in the dry foothills and on the slopes of the Kartalinia, Iora and Azdhinour plateaus living in vegetation of Christ's-thorn and beard grass. The hares are temporarily driven out of this type of land only in winter when large sheep herds and their dogs appear (Vereshchagin, 1942b). Many European hares live in sparse tugai thickets, particularly in the tamarisk zone. In the Alazan-Agrichai and Khachmas lowlands they inhabit places where the original forests have been cut and where they can couch along the edges of forest glades. In the flat semidesert of the Kura-Araks lowland the European hare is very rare even in saltwort—caper communities. The plowing of semideserts and the establishment of fields, gardens and oases immediately promotes the appearance of the hare. It is particularly common in vineyards and fallow fields. Alfalfa and cotton plantings also attract the European hare (except when the cotton fields are being watered and weeded).

On the Apsheron Peninsula the hare is found in vineyards and sand dunes where it couches among the ephedra shrubs and sand fescue. In winter when the hare is hunted, and when sheep are grazing in the vineyards, it couches on plowed fallow land and in winter barley fields, which, because of
285 their microrelief, afford better protection in the furrows or between lumps of earth than winter-sown land. In vineyards the hares eat the ripe grapes and gnaw on field watermelons when they are thirsty.

Hunting during the last decades has influenced the development of the hare population on the Apsheron Peninsula. Individuals couch during the day on stone fences or on ruins of houses from which they have a clear view of approaching danger.

On piedmont plains hares couch in dry riverbeds where they hide behind boulders in order to escape easily from jackals and foxes.

In the Talysh upland and in the Araks valley the main natural biotopes of the European hare are bottoms and slopes of ravines grown with tamarisk, common buckthorn and buckthorn thickets. In general, the habits of this small southern European hare are similar to the central Asian Tolai hare.

It is characteristic of the European hare, a species of southern, Mediterranean origin, that it reproduces the year round and maintains its largest population in the south, its litters decreasing proportionately to the distance it migrates northward (Vereshchagin, 1938b, 1942b; Kolosov, 1941; Kolosov and Bakseev, 1947).

The hare population is greatly affected by tularemia, epizootics, coccidiosis and, more rarely, early frosts (Kolosov and Bakeev, 1947). These population fluctuations affect the trade to some extent (Graphs 17-18).

The prime cause of the decline in hare population in recent years is year-round poaching at night with automobiles.

The cultivated terrain of the Caucasian Isthmus will promote an even more valuable trade in European hare in the future.

Order RODENTIA

More than 40 species of rodents are actually known from Cenozoic deposits of the Caucasian Isthmus and the southern Russian Plain. Holocene fauna of the same areas account for no less than 50 species identified as belonging to the families Sciuridae, Castoridae, Myoxidae, Dipodidae, Spalacidae, Muridae, Cricetidae and Hystricidae.

The features of the ranges and the representatives are examined below.

Family SCIURIDAE

Only four species of Sciuridae are known from the Quaternary fauna of the Caucasus. Of these, the marmot is extinct; two susliks and the squirrel still survive.

Marmot — Marmota sp. According to the finds made in the Kudaro I cave in 1957 a kind of marmot inhabited the Greater Caucasus in the Pleistocene and Holocene. Marmot bones were found in Upper Pleistocene deposits in the basin of the Khram River in the Lesser Caucasus near the village of Orozman. Some relatively "fresh" marmot skulls resembling those of the steppe marmot were obtained by geologists from the karst funnel in the Belaya river ravine (Map 40). It is possible that the Caucasian marmot became extinct in the northwestern Caucasus at the beginning of this century (Vereshchagin, Geptner, Stroganova, 1959). The find of a small suslik, Marmota (?) sp., in lower Quaternary strata near Akhalkalaki is noteworthy.

Little suslik — Citellus pygmaeus Pall. (s. lato). The origin and distribution of the suslik in the Caucasus have been studied by faunists, 286 zoogeographers and parasitologists but remain unclear. More paleontological, morphological, zoogeographical and ecological data are required for the task.

The genus Citellus is known from the Miocene and Pliocene of North America and from the Pliocene of Eurasia (Simpson, 1945).

Remains of marmots of C. pygmaeus type were determined by Büchner and also by Pidoplichko (1951) from Quaternary deposits at Nogaisk in the Zaporozhe Region.

Upper Pleistocene remains of Citellus pygmaeus have been found only within the limits of the present-day range on the Eastern European plain. Vinogradov and Gromov (1952) distinguished an earlier form — C. pygmaeus musicoides — and a more recent form — C. pygmaeus caspicus. The identification points up the probable retention of some archaic features of the mountain subspecies.

From Lower Holocene, Mesolithic strata, suslik remains are known from the first Baksan gorge. More recent bones of little susliks from eagle owl pellets were collected by the author on the outskirts of the Caucasian Range: in the upper reaches of the Kalaus, in the Stavropol area and in the vicinity of Makhachkala.

The contemporary range of the little suslik includes Eastern Europe, the northern Crimea, the Ciscaucasian plains and the plains of northern central Asia within the steppe, semidesert and desert zones.

There are reasons to consider the Neogene of these areas as the origin of this species without resorting to Pidoplichko's hypothesis (1951) of an earlier migration from the southern Caucasus.

In the 1950's, the southwestern limit of the little suslik on the Ciscaucasian Plain crossed the Manych depression in the lower reaches of the Yegorlyk and, following the Stavropol upland from the north, penetrated the upper reaches of the Kalaus far to the southeast near the village of Sultanskoe, 15-18 km from the Kursavka station. Farther eastward the southern colonies extended to the Kuma near Vorontsovo-Aleksandrovskoe and continued parallel to the latitudinal course of the Terek. From the Terek estuary to the north, the range of this rodent continued unbroken. An isolated colony is located between the lower reaches of the Terek and the Sulak.

On the right bank of the Sulak the suslik is dispersed over the foothills from Chir-Yurt to Buinaksk, while on the maritime terraces on the Caspian it penetrated southward nearly to Kayakent.

Suslik populations exist in more isolation from the main basin of the range in the latitudinal valley between the Sunzha and Terek ranges, west of Grozny, and deeper in the ravines of the upper reaches of the Kuban, Malka, Baksan, Chegem and Bezingi Cherek rivers (Map 41).

The territory between the Sunzha and Terek rivers inhabited by the suslik in the late 1930's comprised four sections with a total area of approximately 1,000 ha (Ognev, 1947).

The little mountain-dwelling suslik was recorded by Ménétries (1832) who noted the animal on the northern slope of El'brus; the range was traced and described by at least 14 zoologists from the end of the last century to the first half of the present one.

According to Sviridenko (1927, 1937) the westernmost colonies of the mountain suslik were disposed along the Uchkulan ravine and its tributaries. The uppermost somehow did not reach the estuary of Makhar and Dzhalp-Kol, and down the ravines they spread no farther than the Khudes estuary.

287 The largest habitat was and is in the upper reaches of the Malka and its tributaries: Khasaut, Garbazi and Bolshoi Taluko. This is a vast plateau, gently sloping north and east from altitudes of 1,500-2,500 m. Sviridenko (1937) followed the junction of this range with that of the right bank of the Malka at an altitude of 3,072 m through the Buruntash Pass where the animals live not far from the El'brus glaciers. From here the susliks probably entered the Uchkulan basin.

In the 1930's the suslik spread along the Khasaut to Narzan, a natural boundary, and to the Taluko Basin and the southwestern slope of Mount Kinzhal but not down into the Malka valley.

In the east the suslik colonies are at present dispersed along the ravines of the Kurtyk and the Dzhovurgen, which are the left tributaries of the Baksan. In the Baksan ravine, the suslik is found 1.5-2 km above the gorge cut by the river in the Skalistyi ridge. From here, the suslik steadily spread in 1952 along both slopes of the ravine as far as the village of Nizhnii Baksan (Figure 120), and is especially numerous near the village of Byllym.

Above Nizhnii Baksan there is another valley colonized by susliks which is separated by 8 km from the nearest colony on the left slope of the ravine. The animal's penetration into the Verkhnii Baksan ravine was probably accomplished by way of the Kurtyk River ravine, which is the left tributary of the Baksan from the west. In the upper trough of the Baksan the species was observed in 1952 in the Tegenekli area and even somewhat higher, although Sviridenko (1937) did not find suslik even at the Adyly-Su estuary.

FIGURE 120. Habitat of the little suslik in the Baksan ravine

Photograph by author, 1952

Through the valley of the Dzhigiom River, the right tributary of the Baksan, the suslik penetrated the Chegem valley in which it lives at a very 288 high altitude especially on the Bashi-Buzu-Su tributary. From the northern slopes of Mount Chegem-Bashi it spread into the Bezingi Cherek ravine.

In the Balkar Cherek, the suslik has not been encountered, although there are places suitable for it in this area, for instance, near the villages of Kunim and Zilga.

The suslik has never been found in the Urukh ravine. In 1947-1948, the author travelled through the entire Urukh area, including its tributaries, through the Balkar Cherek and the Cherek Rion pass without finding any suslik, and local inhabitants reported that suslik had never been seen in their area. Dinnik did not find them even in 1883 (1884a, 1884c). Thus the Rossikov report (1887, p. 44) of encountering a mass of susliks in mountainous Digora is probably purely imaginary. Ognev, citing Rossikov (1947, p. 139), added confusion by placing Mount Kun'-Ityg and the Zhelanoko ridge (i.e., Dzhinal) in North Ossetia, whereas they are located in the Malka Basin (i.e., the Kabarda piedmont).

The present geographic variations of the little suslik range within the Caucasian Isthmus (Chapter 4) does not account for the isolation of separate parts of the early range of this animal on the Caucasus, because we simply do not know how rapidly the formation of separate features of the species in different environmental conditions takes place.

A study of suslik distribution throughout its total range clearly shows the early adaptations of the species to artemisia semidesert. It is precisely in this zone of artemisia semidesert, clayey soils and specific plant groupings that the greatest suslik population density is observed.

Considering the Neogene origin of the artemisia semidesert landscape on the northern margins of central Asia (Lavrenko, 1938) and the mountain xerophytes of the eastern Mediterranean (Bush, 1935; Grossgeim, 1948), we may assume that the age of the indicated adaptations is at least Upper Pliocene.

Suslik penetration into the true artemisia steppe is only spotty. Birulya (1941) assumes that the factors limiting its distribution are the high, closed stands of homogeneous grass, the heavy spring thaws and the stagnant, overheated air in the feathergrasses.

He further stated — and correctly so — that during the course of evolution the animal adapted to open biotopes. On the level steppe with a low grass stand, the colony could maintain prompt signalling of mutual danger, a complex system of burrows and normal heat exchange conditioned by moving ground air. It is significant that among mountain susliks of the Caucasus these early adaptations have not disappeared but have only changed somewhat.

Susliks settling in the mountains on the moraine or on alluvial gravel have adapted to burrows dug under large boulders, thereby preventing the collapse of the burrows in the sandy ground and utilizing the friable spaces between cobblestones.

On mountain-steppe meadows the suslik generally lives in colonies in open places near rock outcrops and digs burrows through the vertical walls of paths worn by cattle grazing on the slopes. This habit of digging burrows in different kinds of vertical walls is also characteristic of the Volga-Don steppe suslik.

The arid floors of the Baksan and Chegem ravines have environmental conditions resembling those of the desert-plain and for this reason are 289 more constantly and densely populated by susliks. The immigrating population decreases rapidly in proportion to the altitude. Thus, on Baksan near Byllym (August 1952) we obtained the following data on suslik population by altitudinal zones (Table 69).

TABLE 69. Density of the suslik population in the Baksan ravine

	Artemisia-thymus grouping on the lower first terrace and in places where there are small stone heaps, stone fences and weeds; altitude 1,100 m	Festuca-artemisia grouping on the upper, third terrace on stone placers; altitude 1,200 m	Subalpine meadow with motley-grass, in some places with outcrops; southern exposure of slope approximately 30°; altitude 1,850 m
Number of burrows per ha	76	25	2

Sviridenko's data (1937) on the burrowing habits of the suslik can be explained only by his tendency to emphasize the morpholgical-ecological isolation of the mountain suslik from the plain suslik. Thus, he claims that susliks will tolerate arboreal habitats, burrowing deeply in forest glades, but digging shallower burrows in sun-warmed artemisia-grown ground.

The ages and causes of isolation of suslik colonies in Ciscaucasia are various. The isolation of the extreme southeast colonies in the Dagestan piedmont is caused by the more or less constant flow of the lower courses of the Terek and Sulak rivers. Their frequent bifurcation and meandering create fairly wide land areas, grown over with tugai forests, and reed-grown lakes which are ecological barriers for susliks. When a river changes course, the habitat of the animal population previously located on one bank is left on the other bank. It has also been experimentally proved that susliks can swim across narrow rivers (to 150 m wide) and can cross them on bridges (Sviridenko, 1927, 1937). Isolated instances are known of gravid susliks being transported alive over considerable distances by birds of prey, such as Larus argentatus.

For various reasons, the isolation of suslik colonies located between the Sunzha and Terek ranges seems to us to be quite ancient. In the first place, the susliks from the Alkhan-Churt valley are morphologically different from those of the Kuma and of Dagestan — they have been reported as subspecies C. pygmaeus boehmii Krass. Secondly, it is known that the Terek cut through the Terek gorge between Zmiisk and Terek at a period no later than the Middle Pleistocene. From the Malka estuary to the Sunzha estuary, the Terek is a powerful river with a strong and straight current and nearly devoid of oxbow lakes. Well-developed forest belts of old galleries unsuitable for suslik settlement are disposed along the Terek, and the northern slope of the Terek Range is covered by forests impassable to susliks.

The eastern approach of susliks to the Alkhan-Churt valley was barred by a wide strip of broadleaf and tugai forests on the Gudermes sloping plain and by the Argun, Gudermes and Aksai rivers.

Therefore the formation of the Terek-Sunzha colonies should be correlated with the formation of the festuca—artemisia and andropogon—
290 artemisia steppe landscape of the Alkhan-Churt valley, i.e, at least with the Middle Pleistocene.

The origin of the Elburz mountain colony of susliks is more enigmatic.

Up to the present, Shchukin's hypothesis (1925) has served to a greater or lesser extent as the basis for various modifying theories on the penetration of suslik into the mountains. Shchukin differed his hypothesis in answer to statements of Kuznetzov (1890) and Krasnov (1893-1894) on the penetration of dry mountain vegetation along the interior, longitudinal valleys of the northern Caucasus to Dagestan. He implied the penetration of suslik from the plain along the transverse ravines after the withdrawal of the glacier on the periglacial steppe, and a subsequent cutting-off of the colony from the north by the establishment of a forest strip. However, the question of the origin of the mountain suslik cannot be resolved so simply, because in Elburz the animal inhabited not only the valley floors, but also the passes of meridional ranges. Besides which, the colonies disposed along the low ridges of the Malka Basin were not cut off from the north by a forest strip; the foothills of this region have always been woodless.

Still Sviridenko (1927) assumed that, as an "emigrant from central Asia," the little suslik could have appeared on the steppes of the Volga-Don and in Ciscaucasia only after Khvalynsk time. Even from our viewpoint, the fairly recent establishment of the suslik range in Dagestan is confirmed by the absence of the species from central Dagestan where living conditions are very favorable for it. Later, after studying the peculiarities of suslik distribution in the mountains, Sviridenko (1937) concluded that they appeared in the mountains of central Caucasia during the time of the third Pleistocene maximum glaciation (Riss) — i.e., long before the Khvalynsk transgression — thus "broadening the open-steppe ranges." Sviridenko's conclusions were based on Tutkovskii's rejected hypothesis (1909) of an arid climate in preglacial time. Contrary to this view, there is no place on the Caucasus where glaciers and foehns have not formed periglacial steppe, and contemporary glaciers are often embedded directly into pine and mixed forests (e.g., in Karaugom and Tseya). The formation of a dry-steppe zone within a mountain system is associated with fringing, isolated ridges which act as rain screens, rather than with any glacial influence. For example, central Dagestan is very arid, but has no glaciers. What is of importance is Sviridenko's assumption of the survival of mountain susliks from the time of the major glaciation of the Caucasus, which contradicts earlier geologic and geomorphologic data to the effect that enormous glaciers covered places inhabited by susliks. Also of significance is Sviridenko's zoogeographical structure which coincides well with Bush's concept (1935) that the mountain-steppe vegetation of the longitudinal valleys of the northern Caucasus derives from the ancient mountain xerophilous vegetation of the entire Mediterranean area.

Ioff (1936), who accepted Shchukin's hypothesis of the postglacial penetration of the suslik into the mountains, was inclined to explain the entire history of discontinuities in the Ciscaucasian range of the suslik by extreme fluctuations in population, colonization and extermination over great expanses.

In point of fact, in the early 'fifties, the break in range between the southern suslik colonies in the upper reaches of the Kalaus
291 and the Bermamyt slopes was only 92-95 km on a straight line and that between the Kuma Steppe and the Baksan ravine colonies was only 120 km. This break may mend because the distribution of susliks to the south has accelerated in the last decades under the influences of human activity and the naturally arid climatic cycle. Previously it was thought that the mass settling of susliks on the Caucasian steppes began, as it did in the former Astrakhan Province, about 1900-1901 (Pirkovskii, 1913; Sviridenko, 1927). However the suslik probably inhabited this area earlier, but was not reported because the country was so little cultivated and, mainly, because its presence was not investigated. There could also have been local population variations as reported by Lebedev (1912) and Satunin (1920, p. 81). All of this, however, neither excludes nor contradicts the established fact of the suslik's rapid advance southward in present time (Sviridenko, 1927; Romanova, 1936; Babenyshev, Birulya, Besedin, Golosovskaya, Egorov, Korf, Yanushko, 1937).

In 1952, the author found susliks near Sultanskoe and Mironov. In the same year, Pavlov, Pushnitsa and Shiranovich together published a chart which indicates a shift of suslik range southward along the entire border for some kilometers.

The settlement is advancing southward at a rate of 2.5-3 km per year. At this rate, the plain susliks may reach the mountain colonies of the upper reaches of the Baksan and the Malka within 30-40 years!

From geological data (Vardanyants, 1939, 1948; Nikolaev, 1941) we can assume that the suslik appeared on the Greater Caucasus at the beginning of the Quaternary when the recession of the Apsheron sea and a considerable peneplanation of the ranges created areas of the Caucasian Isthmus suitable for wide distribution of steppe and desert species of flora and fauna. By concentrating in those parts of longitudinal valleys and southern cuesta scarps with mountain-xerophilous vegetation, the suslik could have survived the maximum glaciation in the mountains, although the possibility of Pleistocene and Holocene migrations cannot be excluded.

The later settlement of the suslik was dependent upon the animal's surmounting the ecological barriers which the forest and meadow zones in the Chernye Gory mountains and on the Pastbishchnoi and Skalistyi ridges presented. Suslik penetration into the mountains did not, in our view, follow the transverse ravines of the central Caucasian rivers, as proposed by Shchukin (1925). The ravines of the Skalistyi ridge east of Chegem have always been narrow and humid, and impassable to the suslik for distances of 8-10 km. These gorges became deeper with the tectonic cycles of the Pleistocene and attained maximum development in the postglaciation.

Perhaps it is because of this barrier that the suslik is not found in the xerophytic zone of the upper reaches of the Balkar Cherek, Urukh, Ardon, Fiagdon, Gizel'don, Sunzha and Argun, nor in the whole of central Dagestan, although the living conditions are certainly no worse than those below El'brus.

The suslik's presence in the Alkhan-Churt valley as contrasted with its absence in the valleys of the right tributaries of the Sunzha is especially significant.

The suslik's relatively recent appearance in the mountains is indirectly indicated by the feeble development of the eastern range along the
292 longitudinal valleys. The Balkar Cherek ravine is an example of an area which the suslik has not had sufficient time to populate.

During the time of suslik migration from the plain to El'brus, the path of distribution probably lay east and west of the forested Pyatigor'e area, which was a barrier of sorts to animal penetration southward. It is likely that suslik bones deposited by eagle could be found in caves in this area.

In 1952 we made a paleontological field trip into the Pyatigor'e area and found that no suslik bones had accumulated over the past 1,500-2,000 years in the regions of Zheleznovodsk, Pyatigorsk and Kislovodsk. This, however, does not mean that there were no susliks in the Pyatigor'e area in the postglacial xerothermic epoch or in the Pleistocene, particularly since suslik remains have been discovered in Lower Holocene strata in the Baksan gorge.

The question of the origin of susliks in the Caucasian mountains could possibly be clarified further by more intensive investigations of shelters and caves in the mountains of Razvalka and Verblyud, and the gorges of Kich-Malka, Kuma and Podkumok; the acclimatization of mountain susliks on the plain and of plain susliks in the mountains should also be investigated. During this study it should be possible to trace the rate of ecological and morphological evolution for both forms. For the present, the best estimate, based upon acknowledged facts, for the settlement in the mountains of the suslik from the Ciscaucasian plains is the relatively Upper Holocene.

In the Recent epoch, man, by his activity, has unknowingly contributed to the rapid settlement of the suslik in the mountains, as well as on the plains (see Chapter VI). Efforts at extermination and the pelt trade (Graph 20) were not enough to impede this process in its early stages.

Modern extermination methods and accelerated cultivation of the steppes, the development of shelterbelts and of artificial irrigation systems will virtually eliminate the suslik from the Ciscaucasian plains.

Asia Minor suslik — Citellus citellus L. Fossils of suslik C. citelloides Kormos have been reported from Pleistocene strata in European caves (Wolf, 1939), and Citellus sp. from the Upper Paleolithic of Syria (Wolf, 1939). In the Caucasus, only more recent remains of C. citellus L. are known from Holocene alluvial loams in the Zanga ravine northwest of Yerevan (Dal', 1949a).

The contemporary distribution of the southeastern subspecies C. citellus xanthoprymnus Benn. includes the Armenian Highland and Asia Minor.

In Armenia the suslik occupies a large area of the Araks valley, from the region of the Kara-Burun station and Alagez to the village of Illi, northwest of Leninakan; the upper valley and the Pambak River Basin to the Amamla station; and the western and northern slopes of Alagez (Map 41).

The altitudinal distribution of the animal occupies a zone approximately 1.5 km wide within an altitudinal range of 1,100 to 2,700 m (Dal', 1948b; Avetisyan, 1950). In the mountains, it lives in meadow-steppe, or even in subalpine meadows. In the Araks valley it is found in the mountain-artemisia semidesert, but not in the desert valley of the Araks.

In view of the considerable ecological variability of the Asia Minor suslik (Avetisyan, 1950) it should be considered endemic to the submontane and 293 mountain landscape of arid and relatively hot regions. The range area includes Asia Minor, the Aegean and the Balkans. The former habitat of the suslik in the Zanga ravine indicates a wider distribution during isolated epochs of the Quaternary. The present-day distribution in some areas suitable for the habitation of Asia Minor suslik was achieved only circuitously; for instance the arid Tertiary foothills bounded on the north by the Kura lowland were reached by way of land lying east of the Karabakh Mountains. The main causes of the feeble development of the Caucasian range of this species, in comparison with that of the steppe vole and the Asia Minor hamster, are its more conservative living habits and its lesser migratory ability.

The local breaks and contractions in the range of this suslik on the Armenian Highland may be a result of orogenic processes and lava flows which covered large areas. At the time of cooling and glaciation, the upper border dropped at least 400-500 m. It is possible that the suslik also inhabited southern Dzhavakhetia in the Pleistocene.

In the recent epoch the distribution of the Asia Minor suslik expanded in the upper zone and shrank in the lower as a result of pelt trading and chemical extermination (Avetisyan, 1949).

Family CASTORIDAE

Castoridae remains are known from the Lower Oligocene of Eurasia and North America. In their adaptations the beavers greatly resemble the terrestrial porcupines and, to a lesser extent, the amphibious voles and Octodontidae. Miocene-Pliocene fossils of the genera Steneofiber, Amblycastor, Trogontherium and Pliocene-Pleistocene fossils of the genus Castor are numerous along a wide belt of the northern Mediterranean and central Asia stretching from the British Isles to Mongolia.

Fossils of four beaver genera, Steneofiber, Amblycastor, Trogontherium and Castor (Map 42) have been found on the Caucasian Isthmus.

European beaver — Castor fiber L. Remains of European beaver were first found on the Caucasus in Upper Pliocene conglomerates of the Taman Peninsula. The Taman beaver, C. tamanensis N. Ver., from the Sinyaya gulley site, a natural boundary, was probably the direct ancestor of the contemporary European beaver (Vereshchagin, 1957a). Other Pliocene representatives of the family Castoridae — Steneofiber, Amblycastor and Trogontherium — also known from the Caucasian Isthmus, do not have direct affinities with European beavers.

A European beaver of a completely contemporary type lived in the Caucasus during the Upper Pleistocene and the Holocene. Its remains are found in the caves of Sakazhia (Gromov, 1948) and Uvarova in the vicinity of Kutaisi, in the Neolithic strata of the Sagvardzhile cave, and in Upper Bronze Age strata in the Samtavro burial fields in the vicinity of Mtskheti.[*]

Thus the beaver habitat in the Holocene on the Rion, Kvirila, Kura and Aragva tributaries has been documented (Figure 121).

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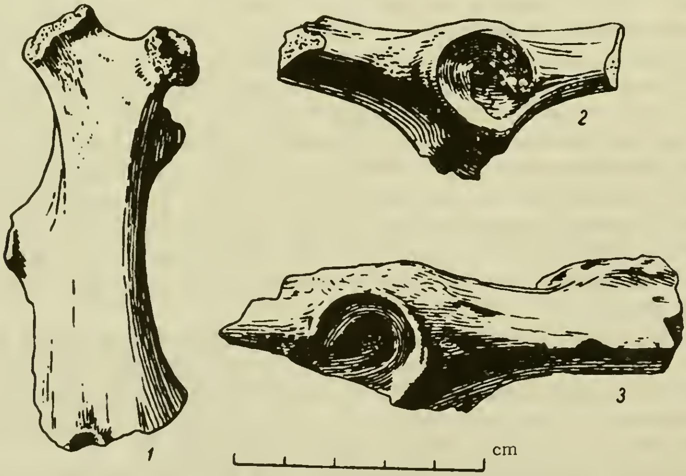

FIGURE 121. Remains of European beaver

1 — Femur from Samtavro deposits (first millennium B.C.); 2 — pelvic fragment from the Neolithic strata of Sagvardzhile cave; 3 — pelvic fragment from the Paleolithic strata of the Uvarova cave

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[*] Information on beaver fossils from Sagvardzhile and Samtavro was kindly provided by N.O. Burchak-Abramovich, Doctor of Biological Sciences.

The remains of European beaver are very common in Quaternary deposits on the Russian Plain, but in the Crimea they have been found only in strata of the Upper Scythian epoch. South of the Caucasus, there have been no validated findings of beaver remains; Bate (1937) reports none from caves in Palestine, Syria and Lebanon.

Beaver fossil identifications from Iranian caves (Coon, 1951) are doubtful because these fossils were probably mixed with porcupine remains.

The great number of recent beaver remains in the lower Don floodplain (Sarkel near Tsimlyanskaya, Novocherkassk) indicates that the contemporary habitat of this animal on the rivers of the Cis- and Trans-Kuban plains is quite probable. Until the 18th century, perfectly suitable beaver habitats were located on the Psekups and on several small left tributaries of the Kuban and even of the Terek.

Published data on the presence of beaver in the Caucasus during the present epoch are numerous and well-known.

The beavers of Scythia and Colchis were often mentioned by ancient authors (Herodotus, Strabo). More recent references to beavers in Mingrelia and generally throughout Georgia can be found in Lamberti (1654) and in Chardin (1686), in the Georgian Chronicles "Kartlis Tskhovreba," and in the "Geography of Georgia" by Prince Vakhushti (1904), written at the beginning of the 18th century. At the end of the 18th and the beginning of the 19th century beaver pelts and "castoreum" were probably important to the import-export economy of Georgia. This is apparent from the status of Tiflis as a trade center in 1803.

Güldenstaedt (1879) and Pallas (1831) recorded the probability of beaver habitation on the Kuban and the Sunzha. Ménétries sent a beaver skull, found on the bank of the Sunzha, to Academician Brandt for his collection. Rovinskii (1809) mentioned that beavers were occasionally observed on the Kuban. Nordmann (1840) recorded several beavers killed in the 1730's in the Notanebi Basin and in Colchis, and indicated the beaver's presence on the Terek. Hohenacker (1837) mentioned the Araks valley as a habitat of beaver.

295 Chopin's data (1852, p. 807) on beavers and "castoreum" obtained in Armenia, Turkey and Iran are questionable.

All these data are to be found in Brandt's monograph (1855).

The beaver skull preserved in the Zoological Institute of the Academy of Sciences U.S.S.R. under No. 6330 ("Ménétries, 1831"), represented by Brandt (1855), has no trace of water sluice, river sand or silt, and has been thoroughly prepared and scraped with a knife. Perhaps this animal was killed not long before the arrival of Ménétries in Sunzha, or was gathered by him from a northern location en route to or from the Caucasus. Ménétries himself did not mention (1832) the beaver among the Caucasian animals (!).

Radde (1866) validated beaver habitats in Upper Svanetia, in the Tskhenis-Tskhali Basin, in the vicinity of Lentekhi and in the sources of the River Kheledula. Vinogradov (1870) wrote that beavers lived in the bottomland of Malyi Zelenchuk on the Trans-Kuban Plain.

Bogdanov (1873) reported that beavers were found in the rivers of the Trans-Kuban steppe, and that the last beaver was killed in 1864 on the Laba River, not far from its estuary. Dinnik (1884b) recorded the beaver's presence near the source of the Laba. Keppen (1902) published data on two beavers killed in 1947 [sic] on the Araks and suggested some interesting possibilities of beaver habitation in the upper reaches of the Araks. Linstow (1908) published prolific but unsubstantiated data on beavers.

Satunin (1920) used Keppen's and Linstow's surveys in his history of the Caucasian beaver, observing that if the beaver lived in the Supsa Basin of Colchis in 1909, it probably survives in some uninvestigated corners of eastern Transcaucasia and the northwestern Caucasus.

Ognev's survey (1947) on the Caucasian beaver with an appended map of its former ranges (! ?) added new perplexities for future investigators.

When studying the swamps and rivulets of the Colchis in 1931 and 1944 in connection with nutria breeding, the author did not find gnawed tree stumps or remains of beaver dams, but was nevertheless convinced that beavers could have lived recently in the Rion valley from the source of the Kvirila to the Black Sea coast.

There are rivers (they now have bare banks) near the Tskhaltubo resort and in many other places in Colchis which would have been perfectly suitable for beaver.

It is difficult to establish exactly when the beaver disappeared from the Caucasus, but it was probably in the middle of the 19th century.

South of the Caucasus the beaver was known in the past century in Mesopotamia and was widespread in Iran. It inhabited the rivers of the Kyzyl-Irmak system in Turkey where an annual yield of 2,000 pelts (!) was recorded. The beaver might have lived in the swampy area between Kayseri and Inesu, south of the middle course of Kyzyl-Irmak in the last half of the 19th century (Danford and Alston, 1877, 1880).

All this data, published first by Keppen (1902) and then by Linstow (1908), looks very solid but lacks any scientific confirmation, e.g., figures, photos and collections. Radde (1866) provides another example of unscientific speculation: he "placed the beaver" on the right tributaries of the Rion in the highlands of Svanetia in small mountain fissures with turbulent streams avoided even by the otter.

296 It is difficult to imagine that the beaver could have lived in the central parts of Asia Minor and Iran considering the absence of water and forests. It is known that beavers feed on wood of poplar, aspen, willow and birch, and it is doubtful that dewberry, sea buckthorn, oleaster and smoothleaf elm, the main contemporary shrubs and trees growing along the riverbeds in Iran and Turkey, would have been sufficient food for the beaver. However, the very rapid changes in landscape of the last centuries are a further consideration. The recent discovery of beaver remains in the strata of the ancient Scythian site of Neapolis in the Crimea showed that from the middle of the first millennium B.C. beavers lived on the Salgir River on a part of the peninsula that was actually dry and completely woodless (Tsalkin, 1947). With reference to old reports of the beaver on the steppes of the southern Ukraine, Pidoplichko (1951) reasonably explained that, given the presence of fluvial forests, the beaver could have lived, and could still live, in the southern steppe zone, or even in the semidesert zone, on rivers crossing these zones. His reasoning is useful in validating the earlier distribution of beaver in Ciscaucasia. On the other hand, it is likely that the unstable regime of mountain rivers and the dry continental climate were limiting factors in the uplands of southwest Asia.

The beaver cannot live on a rapid, pebble-bedded mountain river for lack of shelter and food, even though a forest may grow along its banks. A river with a steep gradient provides no place for the beaver to burrow, and every flood will inevitably demolish the beaver dams.

Nevertheless, the beaver survived intensive orogenic disturbances in such vast intermontane valleys as the Kura and the Rion, and on submontane plains. More frequently, beavers resettled in the area after peneplanation had occurred and subsided.

The history of the beaver on the Caucasus presents a particularly interesting phenomenon: the morphological-physiological development in an animal native to warm (Mediterranean) climates of characteristics adaptive to life under ice.

These adaptations to life in freezing water bodies have often been emphasized by investigators — Linstow (1908), Fedyushin (1935), Vereshchagin (1939c) and others — who place their early development in the Lower Pliocene with the initial cooling of the climate. Swimming under ice and working incisors under water probably involved a considerably accelerated process of adaptation in the first half of the Pleistocene.

Postglacial beaver settlement progressed at a startling rate in territories free from inland ice. In view of the difficulty of migration across watersheds, the abundance of this animal in historic time in Scandinavia, on the Kola Peninsula, and on the Karelian Isthmus might be taken by opponents of the theory of a major glaciation on the European plain as substantiation for their views.

The first stage of beaver population decline resulted from excessive trading in pelts; the second stage and ultimate disappearance of the species from the Caucasus occurred because of anthropogenic alterations of the landscape. Environmental conditions changed with the cutting of fluvial forests and the acceleration of river currents, erosion and flooding as land was cleared and cattle grazed in the basins. These processes were more
297 rapid along Ciscaucasian rivers than along those of Transcaucasia. The beaver survived longest in deep marshes and water courses of the Colchis lowland.

In the 1940's some beavers were brought in pairs from Voronezh into the Karayazskii nutria sovkhoz where they reproduced in cages. They could be allowed to live out of captivity if they were placed in a suitable environment, e.g., riverbanks grown with poplar and willow trees.

We conclude the following from our survey:

1. The European beaver inhabited the Caucasian Isthmus in the Pliocene and in the Quaternary.

2. By the beginning of the 18th century, the distribution of this animal had become vestigial, surviving only in marshes and rivers of western Transcaucasia, in Colchis, and possibly on the piedmont plains of Ciscaucasia along tributaries of the Terek and the Sunzha. The beaver is not known in mountain regions of the Caucasus in historic time.

3. The final extinction of beaver on the Caucasus occurred in the middle of the 19th or the beginning of the 20th century in Colchis.

4. If water and forest regimes and hunting can be regulated in the U.S.S.R., it will become possible to breed beavers in small numbers on some of the left tributaries of the Kuban and on the rivulets of the Khachmas lowland and of Colchis. Especially suitable for breeding grounds are those spring-type rivulets ("kara-su") with a constant flow of water and plantings of poplar and smoothleaf elm on their banks. Beaver breeding, however, will not produce any marked effect on an accelerated agricultural economy.

Family MURIDAE

Remains of 15 species of this family are known from Quaternary deposits on the Caucasian Isthmus; today the Muridae of the Caucasus comprise 29 species. The emergence of the genus *Rattus* is of particular interest.

Black rat — *Rattus rattus* L. *R.* cf. *rattus* remains were known long ago from Quaternary strata of numerous Western European caves from the British Isles to the Carpathians (Woldrich, 1882; Brandt and Woldrich, 1887). They were usually found with bones of animals of the Upper Pleistocene — cave bear, woolly rhinoceros, and others — in Upper Paleolithic strata, such as Aurignacian strata of the Evelinis cave of Somerset (England). The majority of black rat bones were found along Italian coasts and generally around the Mediterranean (Wolf, 1939).

In Lebanese, Syrian and Palestinian caves black rat bones were found in the Mousterian strata in which were also found remains of *Rhinoceros mercki* and the hippopotamus (!) (Bate, 1937). Black rat remains are, as a rule, deposited contemporaneously with their enclosing strata, i.e., "in situ," but there are probably many cases of contemporary rat remains being thrown down into the bottom of excavations or of the rats themselves entering the deeper strata by fissures.

Nevertheless, the explanations are insufficient to accept the theory of postglacial, prehistoric penetration of the black rat by "importation" into Europe — a theory perpetuated in scientific articles. The black rat is probably a Pliocene relict of the Mediterranean. It survived the Pleistocene on the warm coasts of southern Europe and north Africa, and perhaps even on the Caucasus (Vereshchagin, 1947d, 1949c).

298 In the U.S.S.R. black rat bones were found in Greek and Roman strata of Olvia, in the southern Ukraine (Pidoplichko, 1938c).

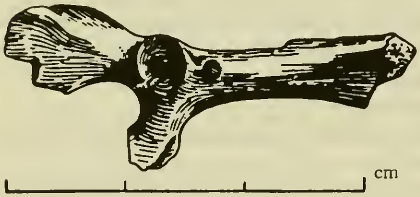

FIGURE 122. Black rat pelvis from strata of the first millennium B.C. in Mingechaur

On the Caucasus single bones of this kind were found in Neolithic strata of the Akhshtyrskaya cave and in graves with jar burials of the first millennium B.C. on the Kura near Mingechaur (Figure 122).

Actually the black rat is widespread on the Caucasus, living both "wild" and as commensals with humans. It lives within the harbor constructions along the Azov, Black and Caspian sea coasts. The black rat is not found in the mountains or plains of Ciscaucasia and probably has never lived there.

Black rat bones were not observed among the thousands of bones recovered from eagle owl pellets which were collected by Kistyakovskii (1935) and the author from the Stavropol and Pyatigor'e areas.

Black rat is widespread along the Black Sea coast from Batumi to Novorossiisk, living in gardens and forests, and infrequently on the banks of water bodies where it has been largely replaced by the Norway rat. Flerov (1927) observed it north of Batumi forest. Shidlovskii (1947, 1948, 1950) recorded the rat in many parts of Abkhazia, Mingrelia and Adzharia. He claimed that the black rat can be found in Abkhazia from sea level to 600 m and in Adzharia to an altitude of 1,500 m. The author found both the black rat and the Norway rat on Bebesyri Lake in the fall of 1946, but it has hever been observed in the bogs around the Paleostom Lake (Vereshchagin, 1941b). According to Stepanov (1931), the black rat of Batumi is less numerous than the Norway rat. In eastern Transcaucasia it lives "wild" in the forests of northern Armenia where it is also found in populated areas. In 1937 it was frequently observed in the Shamlug mine and in the mills of the villages of Kulali, Achadzhur and Marts (Shidlovskii, 1942). The animal is rare in South Ossetia and is found only in inhabited places deep in ravines. In Kakhetia and the Alazan-Agrichai valley it lives in gardens and buildings, quite often in garrets (Argiropulo, 1940a). It is common in summer in blackberry thickets bordering fields near Kutkashen and Vartashen. In the Kura lowland it lives in oases, especially in blackberry thickets along irrigation ditches.

In Baku the black rat finds refuge in structures along the littoral strip and usually is not found farther than 100 m from the bay's edge. Sixty percent of the yield of a large-scale capture was from ships in Baku port and only 9% from port buildings. The remainder of the yield was made up of the Norway rat (Vereshchagin, 1942a).

This rat is common in the Lenkoran lowland from the village of Masally to Astara, and further along the southern coast of the Caspian sea in Gilan and Mazanderan. In these areas it lives in orchards and can be found in all harbors, especially those near fisheries. Rodents from Asterabad were known to zoologists even at the beginning of the last century (Ménétries, 1832; Radde, 1886).

According to records from large-scale catches in Lenkoran and adjacent villages (late 1930's-early 1940's), the black rat comprised only 0.51%
299 of all synanthropic rodents caught (Vereshchagin, 1949d). Even here the rodent does not inhabit mountains but confines itself to lower altitudes. The ability of the black rat to exist in the wild the year round in Colchis and Asterabad and to construct burrows under tree stumps, fences and shelters in hollows substantiates its Pliocene origin in the Mediterranean area in general, and in Transcaucasia in particular.

The black rat adapted readily to the new types of shelter provided by human culture: first mud huts, and later brick, stone and wood buildings and boats and ships, in which heat and food were available. Adaptation to life within harbor constructions and on ships is, in our opinion, associated with the rat's original habitat on the warm Mediterranean coasts, where feeding along the shore was possible. Later, penetrating inland along rivers and confining itself to inhabited places, it gradually occupied the lower Transcaucasian forests.

Norway rat — Rattus norvegicus Berk. There are no proved remains of this species from the Pleistocene strata of southwest Asia, the Caucasus and Western Europe. Remains of Norway rat found in the caves of Czechoslovakia, Malta, Gibraltar and Ireland were bedded together with the remains of postglacial animals and the type of preservation does not indicate an early origin (Wolf, 1939). The bones of Norway rat are known on the Caucasus from later Middle Ages strata (15th-16th century, A.D.) of the excavation of the courtyard of the palace of the Shirvan Shahs in Baku (Vereshchagin, 1949c), and from eagle owl pellets, no more than several hundred years old, found in small caves in the Stavropol and Pyatigor'e areas and in North Ossetia and Imeretia.

The first reference to mice as being harmful to crops and trees was made by Claudius Aelianus in the 3rd century A.D. (Latyshev, 1904). Arabs probably knew of the Norway rat in the early Middle Ages (Zhitkov, 1944).

Nowadays the Norway rat is reported on the Caucasus from all inhabited places of the country which are connected by railways or roads, from coastal villages, fisheries and ports along the shores of the Caspian and Black seas, and from the rivers (Kuban, Sulak, Terek, Kura and Rion), especially from their navigable sections (Vershchagin, 1947d) (Map 52).

On the Caucasus the Norway rat is frequently found living off the land, especially in the humid foothills of Kabarda, North Ossetia and the Grozny Region. Here the Norway rat is often a real pest of gardens and field storehouses ("sapetki") (Rossikov, 1887; Bogdanov, 1936). In Kabarda and North Ossetia the Norway rat lives in mountain villages ("auls"), particularly in the vicinity of mills, almost to the upper areas of the Greater Caucasus ravines (Turov, 1926c).

There are wild populations of this rat in the Colchis swamps (Figure 123), in Asterabad and on ancient lakes of the Kura left bank in Azerbaidzhan (Vereshchagin, 1914b, 1942b, 1947d, 1949d; L'vov, 1949).

The Norway rat also lives in rock placers on the Caspian desert coast, e.g., on the Apsheron Peninsula, where it feeds on flotsam. In the Rion and Kura lowland swamps, the animal shelters in open, raised nests in reed thickets or in closed shelters constructed beneath alder roots.

In the wild, the Norway rat feeds primarily on vegetable food but its consumption of animal food is also significant.

300

FIGURE 123. Habitat of Norway rat in Colchis

Photograph by author, 1939

During periods of prolonged snow cover and hard-frozen open waters, some of the Norway rat population of reed and alder swamps in Transcaucasia die in their own habitats, and some survive in the inhabited areas along the shores (Vereshchagin and Dyunin, 1949).

This species, closely associated as it is with water biotopes, probably could not tolerate glaciation either in Ciscaucasia or Transcaucasia.

The wider contemporary distribution of Norway rat throughout the world, as compared with black rat, is consonant with its Pliocene origin, and with the Mediterranean Holocene origin of the black rat.

The Norway rat possesses a greater adaptability of physiological functions than the black rat (Ruttenburg, 1950) which has facilitated its settlement along with man's from the tropics to the Arctic. However, it is less resistant to winter conditions in the wild in Transcaucasia because of its hydrophilic nature.

In developing Zhitkov's (1944) opinions and our own main premise of the survival of the genus Rattus in the Mediterranean from the Pliocene (Vereshchagin, 1949c), it was necessary to consider the Norway rat as a postglacial newcomer into the Transcaucasian swamp fauna and to the forests of the Ciscaucasian lower mountain zone. This raised questions as to the routes and dates of its penetration into the Caucasus.

The Norway rat certainly could not have entered Europe from central Asian deserts. The more recently popularized notion that the species entered the Caucasus by way of caravan routes across the dry Iranian desert from India was properly discredited by Kashchenko in 1912. The
301 route of penetration obviously was along the sea coasts. In view of the historical fact that Egyptian and Phoenician ships crossed the Red and Mediterranean seas as early as the second millennium B.C., later sailing as far as southern Asia (Avdiev, 1953), it seems clear that the Norway rat was transported into the Mediterranean before the common era, probably first to the coast of the Black Sea in the Caucasus.

The penetration of the Caspian coast occurred later, after settlement of the Black Sea area, either by water — on the Manych — or by land — very possibly along the humid, sloped plains of Ciscaucasia.

Before urban concentrations of many-storied buildings and slaughter houses, and the development of canal, railroad and automobile transportation, the Norway rat apparently lived wild in reed-grown swamps and river deltas, as can be seen from observation of its habitats in the estuaries and lower reaches of the Danube and the Dniester (Aizenshtadt, 1950b), in the swamps of the Rion, and in the Volga delta.

Pallas [1741-1811] observed rats in the Volga delta; at that time, the Norway rat probably lived there, as did the water vole.

The new developmental stage of the Norway rat range in the Caucasus is associated with the construction of paved roads and railroads, and rural and urban centers in the 19th and 20th centuries. Slowly it extended into the populated areas of the Kura lowland along waterways (the Kura and Araks rivers and their tributaries). The rats first penetrated the Alazan-Avtaran valley by the left tributaries of the Kura: the Turyan-Chai, Geok-Chai and Alindzha-Chai. Later the population growth was accelerated by road construction — less so on the dry Armenian plateaus than elsewhere. In Yerevan and Dzhulfa, for instance, the Norway rat appeared in the 1930's after the construction of the railroad connecting these towns with Tiflis and Baku.

In the Ciscaucasian Plain the settlement of the Norway rat accelerated in the 1920's with the development of road transport. Gubarev (1941) recorded the appearance of the Norway rat in inhabited areas of the Salsk steppes.

The Norway rat was known to Satunin (1901) in Stavropol from bones contained in eagle owl pellets from Mount Strizhament, which established that the species inhabited the forested valleys of this region as early as the last century.

Kuzyakin's survey (1951) on the Norway rat's origin in northern Eurasia and its relationship to man added nothing to an understanding of the history of the animal in the U.S.S.R.

Striped field mouse — Apodemus agrarius Pall. Remains of the striped field mouse are known from Pleistocene strata of Czechoslovakian caves (Wolf, 1939). They are as yet unknown on the Caucasus, although they have been exposed in Upper Quaternary deposits of the lower Don.

The contemporary range of the striped field mouse occupies the broadleaf forest zone and the southern Eurasian taiga with discontinuities in Transbaikal and in the upper Amur Basin (Bobrinskii, Kuznetsov and Kuzyakin, 1944). The striped field mouse inhabits only the river valleys of the Russian Plain steppe zone. It is now absent from the Crimea although it has been found in Pleistocene strata. The distribution in Ciscaucasia, now isolated from the north, is confined to the humid piedmont and to the riverbeds of
302 the steppe and semidesert (Sviridenko, 1944). Striped field mouse has been reported from the Black Sea coast south as far as Sukhumi (Shidlovskii, 1947, 1950).

The species inhabits the Stavropol Plateau and the tugai forests of the Kuma, Terek and Sulak rivers. An isolated range is situated to the southeast in the forests of the Khachmas lowlands from the lower reaches of the Samur to Khachmas (Beme, 1928; Vereshchagin, 1944).

Its vertical distribution is insignificant: the upper parts of inhabited mesophytic meadows and fields in the northwest Caucasus between altitudes of 950-1,000 m; in the Nalchik area, to an altitude of 700 m; and near Ordzhonikidze and in Alagir, between 800 and 850 m.

Sviridenko (1944) observed that striped field mouse distribution is related to the amount of precipitation. The animal becomes eurytopic only if the annual precipitation is above 500 mm. In more arid regions the rodent inhabits only humid biotopes like the lowland forests of the Khachmas depression near the Caspian coast. Here the striped field mouse lives in the humid bottoms of afforested valleys and on the banks of spring-fed brooks under cover of alder and blackberry growth interspersed with liana. In this environment the mouse is not harmful to cereal crops as it is in other places. On the more arid Kusary sloping plain and on the remainder of the Caspian coast, this animal is not encountered.

The distribution of striped field mouse in Ciscaucasia is mostly confined to regions with a dense network of small torrents and springs, such as the developmental zone of piedmont trains. Shrub areas along small rivers and small meadows along turbid brooks are characteristic biotopes.

Consequently, the Caucasian foothills contain several isolated ranges: the Kuban (including the Black Sea coast), the Terek-Sunzha and the Samur (Map 54). The breaches in the Ciscaucasian range areas are created by dry, steppelike divides.

Earlier — in the Pleistocene — the striped field mouse barely penetrated farther south than the lower forests of Khachmas, since its remains were not found in the Pleistocene asphalts of the Apsheron Peninsula. This is further substantiated by its absence from the Alazan-Agrichai valley where conditions are suitable for its habitation.

In humid western Transcaucasia the striped field mouse is distributed along terraces of the Black Sea coast southward to Sukhumi. Here it is frequently observed in glades, clearings, shrubs and orchards.

Shidlovskii's data (1947) (Table 70) are characteristic for striped field mouse distribution in the biotopes on the Black Sea coast.

TABLE 70. Distribution of the striped field mouse according to biotopes in Abkhazia

		Hedges	Vegetable gardens	Orchards	Tea plantations	Corn fields	Banks of reservoirs	Shrubs	Continuous forests	Total
Number of animals caught	(absolute number	1	27	36	12	10	31	135	2	254
	in %) . .	0.4	10.6	14.1	4.7	3.9	12.2	53.2	0.8	100.0

303 These data show that anthropogenic alterations of the topography in the Black Sea littoral zone, especially deforestation, favor the growth of the distribution and population of the rodent. It is possible that the considerable extension of the striped field mouse range south along the Black Sea coast in historic time was promoted by man-made changes in the landscape. However, farther south in Colchis, important to note, there are no occurrences of striped field mouse, although the biotopes are much like those of Abkhazia, a fact probably explained by the excessive humidity.

The peculiar underdevelopment of the field mouse ranges on the Caucasus suggests that the penetration of this species from the north occurred rather late in the Pleistocene. With the postglacial advance, the Caucasian populations of the striped field mouse were apparently cut back by the development of a large belt of dry steppes.

The absence of the animal from the Crimea in the Recent and in the Pleistocene also confirms a late development of the range in the south.

In the Recent epoch, the striped field mouse's distribution on the Caucasus increased in the southwest with forest clearing in places of excessive moisture, and in the dry regions to the north and south with the development of irrigation.

Asia Minor hamster — Mesocricetus auratus Water. (s. lato). The question of the origin of the hamster of genus Mesocricetus on the Caucasus is rather complicated, for the earliest hamster remains — genus Paleocricetus — found on the Caucasus date from the Middle Miocene. In the Lower Pliocene of Ciscaucasia there lived a hamster almost the size of the golden hamster of the eastern Mediterranean area. Thus, the Caucasus could have been as much of a focus of Asia Minor (golden) hamster development as was southwest Asia.

Fragments of hamster remains of the genus Mesocricetus are known from the Middle and Upper Paleolithic of Palestine (Athlit cave; Picard, 1937) and, within the limits of the Caucasus, from the caves of the Rion Basin and Kvirila River (Gvardzhilas, Mgvimevi, Kudaro) and from Pleistocene strata of the Apsheron Peninsula.

It is important to emphasize that, until now, the only hamster remains found in Quaternary deposits of the Russian Plain have been those of the genus Cricetus.

Postglacial cave deposits of Asia Minor hamster remains are quite common on the Armenian Highland, in central Transcaucasia and in central Ciscaucasia.

In recognition of its considerable geographic variability, the Caucasian representatives of the genus Mesocricetus are classified by taxonomists under two or three separate species. Accepting southern southwest Asian origin of the extant Caucasian golden hamster, we can further assume that, in chronological order, Mesocricetus, M. auratus raddei Nehr., and M. auratus nigriculus Nehr. comprise a genetic series of successive subspecies.

The contemporary range of this hamster includes Syria, Asia Minor, the Armenian Highland, Talysh, the northwestern Iranian Plateau, eastern Transcaucasia, central Dagestan and the Ciscaucasian Plain. Surveys of the distribution areas were given by Argiropulo (1935, 1939a), Neuhäuser (1936), Shidlovskii (1940c) and Ellermann (1948). The vertical distribution of Mesocricetus lies within a range of 0-2,400 m. The altitudinal optimum of the Transcaucasian subspecies M. auratus koenigi Sat. is, according to Shidlovskii (1940c), in the range of 1,200-2,000 m (Map 58).

304 On the Armenian Highland within the limits of the U.S.S.R., this hamster is widespread in relatively warm and arid upper river valleys.

It inhabits the festuca-grown upland steppe of the Pambak River valley, the borders of Lake Sevan, and the Saraibulakh and Zangezur ridges. On the cold upland of Dzhavakhetia it can be observed on the steppe meadows near Tabistskhuri Lake.

In the Karabakh uplands the hamster is known from the Gevorkevan vicinity.

In Talysh it has been encountered in an area stretching from the upper reaches of the Vilyash-Chai south to Kel'vyaz, in the upland zone of artemisia—grass-steppe at an altitude of 1,600 to 2,000 m. It was not found, however, in groupings of small goat's thorn and acanthus as in the Armenian Highland but, rather, concentrated in more humid places in the valley bottoms, especially on the margins of sown fields.

The animal's distribution on the ranges of the northern Iranian Plateau is probably discontinuous.

In eastern Transcaucasia the hamster inhabits the Gori depression, occupying regions of earlier steppes or forest clearings. In the Pleistocene and Holocene, it was distributed in Imeretia and in the upper reaches of the Rion. Eastwards, on the Iora and Kartalinia plateaus, the animal inhabits areas grown with the racemose andropogon at altitudes of 550-600 m. It is not found east of the Alazan to Shemakha, but it is possible that relict colonies will be found northeast of Shemakha, for example, in the Kilyazi-Chai and Gil'gin-Chai valleys, and west of Derbent.

The distribution of the Dagestan subspecies, M. auratus raddei Nehr., is limited in inner Dagestan by the valleys of the Argun, the upper Sulak and the Samur. The animal has been traced from the village of Shatili to Evdokimovskoe in the Argun valley. According to Rossikov (1887) it is known from the Andi Koisu River. According to the data from the Orlov expedition, Beme's records (1925), and Dyukov (1927), the hamster is encountered on the whole of the Khunzhakh uplands on the fields surrounding Baitl, Chondotl and other villages.

Here the hamster inhabits the mountain xerophytic steppe and is attracted to fields of grain. Its vertical placement is from 1,600 to 2,300 m (Geptner and Formozov, 1941).

In the Middle Pleistocene these ranges were probably linked with the piedmont areas of the Apsheron.

Perhaps this link was broken in the Upper Pleistocene when Dagestan was divided by water erosion and the formation of a forest zone on its southeastern border.

The present-day range has enlarged somewhat under the influence of agricultural activity.

The distribution of the Ciscaucasian form M. auratus nigriculus Nehr. is very extensive, although always "squeezed" close to the mountains (see Map 58).

Its habitat in northern Ciscaucasia is in the zone of artemisia—festuca-steppes, while on the Stavropol Plateau and in the Kabarda foothills it is found on steppe-meadows and plots planted to corn. The animal is also encountered in the motley-grass of the Terek valley (Ognev, 1924).

In many places this hamster has actively penetrated the mesophytic foothills of Ciscaucasia where the forests have been cut, for instance on the Trans-Kuban, Kabarda and Terek-Sunzha sloping plains. In general, this Ciscaucasian form is more eurytopic than its Transcaucasian parent, although, in the main, it occupies dry places.

305 Its vertical distribution in Ciscaucasia normally extends from sea level to 1,000 m. In central Ciscaucasia, it penetrates the mountains as far as Kislovodsk and Nal'chik, but is not found in dry, longitudinal valleys of the northern slope. It is spread along the valleys of the left tributaries of the Terek. M. auratus nigriculus is distributed only as far as the Chernye Gory canyons.

In the last few decades the settlement of hamsters in the Rostov Region has been reported and in the 1940's they were found northwest of Manych.

Judging from the Asia Minor hamster's contemporary range and from its level of trophic succession, it seems possible that the ancestral species penetrated the Caucasus from the south and southwest during the Tertiary, most probably during a dry phase of the Upper Pliocene.

The path by which the hamster extended its range from the Lesser Caucasus to eastern Ciscaucasia probably passed the foothill steppe zone along the base of the southeastern slope of the Greater Caucasus and farther through the present uplands of Dagestan which at that time were lowlands. Later this route was impeded by loam and pebble sediment on the swamped plains of the piedmont, particularly in the region of presently eroded sections of Adzhinour and of the Kusary sloping plain. The distribution area of the hamster was probably the widest in the Middle Pleistocene during the wide steppe formation on mountain slopes. The subsequent mesophytic trend in landscape and the shifts in altitudinal zones during glaciation created a break and caused the decrease of the hamster range. Another breach in the range occurred with the onset of the postglacial xerothermic period which produced a discontinuous upland mountain relief in southwest Asia.

On the other hand, in the humid mountain regions of Imeretia and South Ossetia the Lower Holocene desiccation of ridges and slopes contributed somewhat to the spreading of the hamster range; there it was only displaced later during another humidification of the climate.

There can be another interpretation of the history of the hamster range development on the Greater Caucasus and in Ciscaucasia, if, while accepting two distinct species for the Dagestan and Ciscaucasian forms, we consider the possibility of their having a common ancestor in a local Tertiary form.

In the Recent epoch, ranges preserved in southern Transcaucasia are relatively stable and are diminished only during cattle grazing, large scale plowing of artificially watered land, or purposeful killing of the animal as a pest through the use of chemical exterminators.

Asia Minor gerbil — Meriones blackleri Thos. Remains of gerbils of the genus Meriones were recorded from Acheulean and Mousterian strata of Palestinian caves (Picard, 1937; Wolf, 1939). In the Caucasus, aside from findings of Gerbillus sp. in Pliocene strata of the Armenian Highland (Bogachev, 1938c), only the remains of the present-day species are known from the superficial layers in caves and shelters of the Araks valley.

The present-day range of Meriones blackleri Thos. includes Asia Minor, Syria, western Iran and a part of Transcaucasia (Ellermann, 1948; Bobrinskii, Kuznetsov, Kuzyakin, 1944; Pogosyan, 1949).

In Transcaucasia Meriones inhabits the middle Araks valley, certain places in the Araks gorge in the Zangezur ridge, the eastern Karabakh foothills, the Mil'skaya steppe, the southern Mugan steppe and the Kirovabad sloping plain. In the wide valley of Akera-Chai, it is found almost as far as Lachin, that is, about 1,500 m above sea level. The population of
306 Meriones blackleri Thos. in the plains of the middle Araks Valley is greater than that of other species; on the stony slopes, however, it is superseded by Meriones persicus Blanf. The animal is not encountered on the left bank of the Kura, although conditions are the same there as on the right bank. On the Kirovabad sloping plain its distribution can be traced to the lower reaches of the Khram. According to data from large-scale catches, it has a greater population than Meriones erythrourus Gray in the foothills of the Lesser Caucasus.

In the Mil'skaya steppe M. blackleri can be seen with M. erythrourus almost everywhere, but in the Karabakh foothills it is encountered only in warm areas with artemisia groupings at altitudes of 350-400 m above sea level. In the northern part of the Mugan steppe, this animal has been largely dislodged by cultivation and irrigation and is seen mainly in artemisia semidesert along the border from Karadonly to Belyasuvar. On the northeastern slopes of Talysh, it has been traced to the Eshakchi outpost at altitudes of about 600-700 m (Map 63).

The animal mainly inhabits alluvial and talus deposits of loessial loam in large fluvial valleys grown with artemisia and ephemeral grasses.

In view of M. blackleri's specific distribution in eastern Transcaucasia and, more particularly, its absence from the Kura-Iora interfluvial area and the Shirvan steppe, we can assume that it settled in the north only relatively recently, i.e., in the Pleistocene or perhaps even in the Holocene. In southern Transcaucasia in the middle Araks valley, M. blackleri may be considered a local species from the Upper Tertiary.

Persian gerbil — Meriones persicus Blanf. Fossil remains of this species from Pleistocene strata have not been validated, but they are known from Holocene cave deposits on the southern slopes of the Armenian Highland and from the middle Araks valley.

The main part of the M. persicus range (Map 62) includes Turkey, Iran, Afghanistan and southern Turkmenia (Neuhäuser, 1936; Geptner, 1940; Ellerman and Morrison-Scott, 1951).

On the Caucasus it is eurychoric over the southern slopes of the Armenian Highland and in the highlands of Talysh. Its population in the Alindzha-Chai Basin, according to large-scale catches, comprised 62.5% of the total Meriones population. It is not encountered on the left bank of the Araks gorge north of Mindzhevan. In the gorges of the southern slopes of the Zangezur ridge, the range reaches an altitude of 1,800 m in astragali—tragacanth formations and stretches as far as Zangelan and Shakhbuz.

On the Saraibulakh ridge, according to Dal' (1904b), Meriones comprised 17% of the rodent constituent of the food of the eagle owl. It is observed in the Zanga valley to an altitude of 1,230 m (Dal', 1948b) and is common on the slopes of the outlying northern ridges of the middle Araks valley among mountain halophytes of the semidesert (Flerov and Gureev, 1934; Argiropulo, 1939b; author's data, 1947).

In the highland steppe of Talysh the species is common in the upper reaches of the Vilyash-Chai and Zuvanda at altitudes of 1,500-1,800 m. Our data collected in the vicinity of the Dyman outpost in 1945 show that its remains constituted 26% of the remains of all rodents found in owl pellets.

In the dry mountain areas of northern Iran and Asia Minor M. persicus is evidently the most numerous and eurychoric. Its usual biotopes are the stony slopes of valleys which are dotted by cushions of thorny astragali,
307 acantholimon and artemisia, and in spring by ephemeral grasses and poppies. In certain places the animal emerges on divides beneath the mountain-grass and steppe zone.

The facility of M. persicus in digging its burrows under stones or shrub roots, its skill in climbing stones, its hairless feet, long tail with panniculus and its long vibrissae — all these features, according to Argiropulo (1939a), are early adaptations to a mountain desert habitat.

This animal is mainly granivorous: during early summer, it feeds mostly on grain of small grasses; in later summer, on grain of mountain saltwort. It is an early indicator species of the southwest Asia mountain desert mammal complex.

M. persicus thrives in agricultural regions. In grain fields and along bordering fences, its population is always increased somewhat. Cattle driving and overgrazing contribute to the spreading of thorny astragali, thus extending the range.

Red-tailed Libyan gerbil — Meriones erythrourus Gray (s. lato). Fossils of this animal are known from Middle Pleistocene strata of the Apsheron Peninsula.

At present, this polymorphous species (for which as many as 23 subspecies have been recorded) is identified with M. libycus Licht. Its vast range includes north Africa, southwest Asia, eastern Transcaucasia and central Asia to Semireche [Dzhety-Su]. Its northern limit on the Caucasus passes the latitude of Shemakha (Ellermann and Morrison-Scott, 1951; Bobrinskii, Kuznetsov, Kuzyakin, 1944).

In Transcaucasia it inhabits all of the Kura-Araks lowland and foothills — from Tiflis on the west to the Caspian coast on the east (Map 61) — and is especially numerous on the Apsheron Peninsula. M. erythrourus has not been observed north to Kilyazi or south to the Kyzyl-Agach Gulf on the Caspian coast.

The species is encountered throughout the central lowland. A dense population is noted among artemisia, saltwort and caper formations in the flat semidesert of the Mil'skaya, Shirvan and Mugan plains. The animal settles more frequently on alluvial ranges and on the margins of minor solonchak depressions overgrown with arboreal saltwort shrubs and Austrian and Sovich wormwood. The maximum population is observed, however, on the sandbank ridges of the Kura, Alazan, Iora and Araks, especially in the tamarisk-thicket zone. Similar high-density populations are encountered on the dunes of the Caspian coast where the sand hillocks are held by tamarisk and ephedra. In such places there are perhaps 40 specimens per hectare. Biotopes created by man, especially vineyards, abandoned irrigation systems, shepherds' camps in the steppes and fallows of several years standing, are of great importance to this animal's settlement.

The animal is crepuscular and nocturnal in summer, crepuscular and diurnal in spring and fall, and diurnal in winter. Meriones erythrourus is mainly granivorous: in spring it feeds on shoots of ephemeral annual plants; in summer, on shoots and grains of goatgrass, ragweed, brome
308 and insects, in particular on non-gregarious locusts; in fall, on new shoots of ephemeral grasses; in winter, on wormwood stalks, seeds of arboreal saltwort and others.

In its search for grain, the animal climbs high on the saltwort shrubs. During snowfalls these animals usually lie in burrows until the thaw, rarely grazing on adjacent shrubs. The abundance of animals on sand hillock ridges in level steppes is explained by the ease of constructing ventilated burrows and the opportunity of winter fattening on artemisia and saltwort. The coincidence sometimes seen of dense rodent populations in cattle camps ("yatagi") in these areas might persuade an unskilled observer that cattle raising is favorable to hibernating populations of Meriones (Gladkina, 1952).

The contemporary range of M. erythrourus and its adaptation to the landscape indicate that the species formed in the southern and southeastern Mediterranean range. It penetrated the Caucasian Isthmus from the south and southeast probably as early as the Pliocene but no later than the Lower Pleistocene, since by the Middle Pleistocene it already inhabited the Apsheron Peninsula.

The animal survived the transgressions of the Caspian Quaternary on the Tertiary hillocks on the northern and western borders of the Kura Bay. In the eastern part of the Kura-Araks lowland, this species is one of several late settlers of the territory after the sea waters retreated from it in the Holocene.

Local agriculture has, until now, been favorable for the development of the species. However, the construction of irrigation works and the expansion of irrigated cotton fields will rapidly drive this animal from vast land areas.

Steppe vole — Microtus socialis Pall. (s. lato). Remains of this genus have been found in Middle Pleistocene strata of the Apsheron Peninsula, in Holocene cave strata of the Saraibulakh Range in Armenia and in many other places on the present-day range, which includes Cyrenaica, the Balkan Peninsula, the southern Ukraine, the Crimean steppes, southwest Asia, central Asia, eastern Ciscaucasia and eastern Transcaucasia (Minin, 1938; Vinogradov and Argiropulo, 1941; Ellermann, 1948).

In Ciscaucasia this vole inhabits the Salsk steppes along the Manych valley, the regions of the lower Malka and Baksan, the slopes of the Terek and Sunzha ranges and steppelike piedmonts of northern Dagestan. The animal penetrated the Terek-Kuma massif of the sandy semidesert along the network of ducts and channels of the Kuma, Kura and Terek.

On the sloping plain of the Kusary, the steppe vole's range is found in warm places to an altitude of 600 m, adjacent to that of the common vole. The animal inhabits only wide plowed fields in lowland forests of the Khachmas plain.

From the western Caspian coast the range extends into eastern Transcaucasia at altitudes of 700-800 m on piedmont ridges (Map 72).

The vole penetrated the lowland forests of the Alazan-Agrichai valley through deforested areas. On the Apsheron Peninsula and in Kabristan, there are small relict colonies in places with a maximum annual precipitation of only 280 mm, relieved, however, by localized, supplementary moistening of the soil and an underlay of impervious layers of Apsheron limestone. The continuous distribution of the animal in the Kura-
309 Araks lowlands begins in a region where the annual precipitation is less than 350 mm. In southeastern Mugan the distribution toward the Lenkoran lowlands is limited by greater soil moisture in winter and 800 mm annual precipitation (Vereshchagin, 1942c, 1946b).*

In the Kura valley the vole was found only as far as the Mtskheti until recently, when it penetrated the Mukhran valley as a consequence of deforestation there. Near the Mtskheti the range is broken by the forested narrow gorge of the Kura, and resumes again in the dry Gori depression at altitudes of 600-800 m. Here, M. socialis goriensis Arg. was isolated as a subspecies, slightly different from the typical species. The vole inhabits the Kirovabad sloping plain up to the existing lower timberbelt, i.e., to 600-700 m, although in some gorges it is encountered even higher. On the deforested northeastern slopes of Karabakh, the steppe vole has spread upward to 800 m in the vicinity of Madagiz, Mardakert, Martuni and other points where its range is adjacent to the lower distribution belt of the pine vole. The vole penetrated high into the mountains through the valleys of the Akera and Okhchi-Chai via the southern slopes of Karabakh. A similar penetration can be observed in gorges of the southern slope of the Armenian Highland.

In the semidesert of the Kura-Araks lowlands the steppe vole forms temporary settlements in caper formations on chestnut soils, and lesser settlements in the artemisia—grass groupings. Summer conditions for the animal in the semidesert zone are rather poor because of lack of moisture

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* K.N. Rossikov's report on the mass daytime migration of voles during August in the Mil'skaya Steppe, noted by Ognev (1950) is, in fact, only a fiction (Vereshchagin, 1946b).

in food and the high temperature of the soil. The vole withstands these conditions by feeding partially on locusts and mollusks and by constructing deep burrows (Vereshchagin, 1946b).

The semidesert population of voles declines catastrophically each year as June approaches because of cessation of reproduction and the sudden death of mature animals brought about by the desiccation of food and the high temperatures. Viable isolated colonies of animals survive in some hollows, in ravines grown with milk thistle (Silybum), in gardens moistened by irrigation, or under caper brush, etc.

In the Mugan steppe, in the area of Belyasuvar and Astrakhan-Bazar, the years of peak breeding witness haphazard nocturnal mass shifts of the steppe vole in the first half of June because of physiologic disturbances aroused by the desiccation of vegetable food and soil overheating (Mamedov, 1950).*

Because vole behavior shows seasonal peculiarities controlled by temperature and insolation, in Azerbaidzhan this animal is more vulnerable to attack by predatory birds and mammals during the winter.

Characteristic "pulsations" in the ranges of this species can be traced over the years near the base of the Apsheron Peninsula. When winters are warm and humid and summers cool for several consecutive years, there is an acceleration in reproductive activity and a significant increase in population. In the semidesert when the fall is humid, large food reserves, consisting of plant shoots and motley-grass—ephemeral grass formations are built up. This makes it possible for the animals to move from the 310 Kabristan ridges through drying rivulet valleys almost to the sea coast, 30-40 km beyond the outer limits of their fixed habitat.

Meanwhile the first hot and dry season again causes mass mortality among the animals and a new withdrawal northwestward from their distribution area. This phenomenon is very significant in explaining the mode and rapidity of migration and the history of the animal range areas resulting from secular climate and landscape variations.

In Talysh the vole may be found at altitudes of 1,500-1,800 m in the grassy mountain steppe, while it is absent in the poor fodder grouping of thorny astragali. A dense vole population developed on the eastern and northern slopes of Talysh near the upper timberline, which has been considerably lowered because of grazing and cutting. The upper parts of the Vilyash-Chai gorge in the Yardymly region and the area of Vassaru-Chai near Lerik which is planted to grain are the real foci of mass vole reproduction. Such foci are the results of human activity. From them, the vole penetrates downwards to the gorge bottoms of the eastern slopes of Talysh only when a forest has been thinned or completely cleared.

In the middle Araks valley the vole is found in Aralik and on some of the tributaries of the Araks, such as Alindzha-Chai, Nakhichevan-Chai and Arpa-Chai. The vole is not observed on the sun-scorched slopes and ridges of the Zangezur Range in the zone of stony-mountain—saltwort-semidesert and tragacanth astragali because of the poor nutritive value of the vegetation. In the central Armenian Highland the vole penetrated into the Araks valley by the left river bank. A steppe vole habitat is located in the upper part of the Pambak River valley, in the grassy mountain-steppe zone,

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* Ognev's report (1950) on the habitat of this vole in the Lenkoran lowlands is based on a confusion in the location of geographic points: the Kelvyaz outpost is in the high Talysh Mountain and not in the Talysh lowlands.

at an altitude of 1,200-1,800 m. This site is cut off from the west by the cold Akhalkalakhi Plateau, and from the north by the afforested spurs of the Bzovdal'skii ridge and the Pambak River gorge. Contrary to Ognev's opinion (1950), the range of this species bears no relationship to that of the Gori subspecies. Such a relationship should be sought to the south in the Leninakan area and Kars Upland where the dry mountain valleys probably have populations morphologically similar to M. socialis schidlovskii. Dal' and Zakharin (1951) indicate that this vole's distribution extends from the upper reaches of the Pambak through the Araks valley up to the latitude of Yerevan.

The population of the steppe vole is greatest during the reproducing season, when the number of burrow openings observed per hectare attains 90,000 on both plowed and unplowed land in the piedmont andropogon-steppe zones of the Adzhinour and Kartalinia plateaus, the eastern foothills of Karabakh and the northwestern slopes of Talysh. In this steppe landscape the contemporary ecological optimum of the species has been reached (Satunin, 1912a; Vereshchagin, 1942c, 1946b).

Viable even in periods of strong inhibition of population, the colonies of this rodent are clearly associated with shrubs of Christ's-thorn which affords them a safe shelter from predatory birds and extreme heat. The juniper—pistachio forests adjacent to the beard-grass steppe — the so-called "arid stunted forest" — is sparsely populated by voles; they are encountered in thinned forest glades of motley-grass where they construct burrows under ephedra shrubs.

The characteristics and the periods of steppe vole reproduction are dependent upon altitude and man-made landscape alterations. In the
311 semidesert zone of the eastern Transcaucasian lowland, its period of reproduction is confined mostly to October-November and to March-April; although if the winter is warm and ephemeral vegetation available, it may extend from October to May. But in the mountain steppe of Talysh and on the Armenian Highland, intensive reproduction is observed in June, because of the later burning-off of the vegetation.

The vole maintains longer sexual activity and vitality on unirrigated cereal croplands in the piedmont (Figure 124) and on irrigated cereal and alfalfa croplands in the semidesert zone of eastern Transcaucasia, than on virgin soil.

Climate is the main factor affecting population variations and area of vole ranges, especially in eastern Transcaucasia. Nevertheless, epizootic factors, predatory mammals and birds also figure significantly in reducing the population of this rodent during peak breeding years. The greatest effect of bird predation on the vole population can be seen on the semidesert and the piedmont steppe from November to April, i.e., during the migration and wintering of the birds (Vereshchagin, 1946b).

Agriculture contributed to the expansion of the range of this species, opening new territories by the felling of lowland forests, and providing for an increased population by supplying a succulent and high calorie diet of cereal crops.

The main morphological features of steppe vole (permeable fur covering, short extremities poorly adapted to rapid and remote migrations, flat skull, elongated diastema indicating its enormous burrow-digging capacity in heavy and medium soils) testify that the species was formed under topographical xerophytic conditions of the eastern Mediterranean.

FIGURE 124. M. socialis in a barley field

Photograph by author, 1939

312 The steppe vole of the Caucasus and eastern Asia never emerges in the desert proper but is dispersed in its eroded interzonal fringe areas, indicating an earlier association of presently separated steppes and semi-desert areas, probably during certain phases of the Pleistocene. The reasons for this association have been discussed elsewhere by us (Vereshchagin, 1942c; 1946b) and by Geptner (1945).

Pidoplichko's opinion (1951) on the recent development of the vole range in the eastern Mediterranean rests on a patently erroneous description of the distribution area.

The initial evolution of a variety of southern gray voles probably took place in the eastern Mediterranean on the relatively dry Pliocene uplands of Asia Minor. One of these forms, the Russian steppe vole, populated the dry coasts of eastern Mediterranean basins in the Lower Pliocene.

The history of the development of the vole's range on the Caucasus follows orogenetic movements, fluctuations in the Caspian Sea level and shifts in landscape zones — both horizontal and vertical — and reveals the lability of the species in adapting to its environment. For instance, isolation of the Gori subspecies was caused by the rise of the northern spurs of the Trialet and the southern spurs of the Kakhetian ridges which partitioned off the Kura valley near the Mtskheti. M. socialis schidlovskii may be considered a special species having an earlier isolation. This isolation was accomplished by the uplift of the Armenian Highland in the Quaternary which spared some xerophytic communities in separated areas. Perhaps vast lava flows overlapping the sections of the ancient plateau in different directions contributed to this isolation (Vereshchagin, 1942c; Shidlovskii, 1945).

The range of the steppe vole on the Isthmus evidently fluctuated repeatedly during the Pleistocene, conforming to the development and reduction of landscapes suitable for habitation during different climatic phases. In our time, forest clearing and slope erosion have facilitated the penetration of the species into the foothills and mountains, thereby greatly expanding its range. This is especially conspicuous on the mountain slopes of Karabakh and Talysh. The vole penetrates the semidesert and desert of eastern Ciscaucasia when channels are dug and new regions are developed for grain growing. New extermination methods have no noticeable reversible effects upon these incursions.

Common vole — Microtus arvalis Pall. The fossil remains of this animal are known from many Pleistocene cave burials and from alluvial deposits in Eastern Europe, from Ireland to the Carpathians and from Italy to Sweden. In the U.S.S.R. the remains of this vole are common in Upper Paleolithic strata of the Crimea (Vinogradov, 1937b) and in Middle and Upper Pleistocene strata of the lower Don and the Urals (Vereshchagin and Gromov, 1952).

On the Caucasus the bones and skulls of this vole were found in Middle Pleistocene strata of the Apsheron Peninsula together with those of the steppe vole (Argiropulo, 1941b; Gromov, 1952).*

In the Recent epoch this vole inhabited the taiga, the forest steppe and even desert areas from the Atlantic Ocean to the Khingan and the upper reaches of the Amur. It has a peculiar distribution on the Caucasus (Map 71).

313 In Ciscaucasia an almost unbroken distribution range runs from the Don steppes through Manych along the Azov shore and includes the lower reaches of the Kuban and the Taman Peninsula.

This vole is widespread in the Stavropol uplands where it lives in mesophytic meadows and deforested areas.

The northeastern limit of the M. arvalis range in the Ciscaucasian steppes approaches the longitude of Budennovsk, coinciding with the margin of semideserts in the lower Kuma area. Eastward it pushes far through the river valley to the Terek-Kumsa sands. Following the courses of the Terek and Sulak rivers as far as the Caspian coast, habitats of this vole occupy ridges and depressions with meadow, tugai and steppe vegetation. On the Ciscaucasian dry steppe, freshwater basins are a requirement for the maintenance of vole habitation (Naumov, 1948). On the Greater Caucasus this vole inhabits only the Trans-Kuban sloping plain in the foothills at an altitude of 900-950 m, and is not encountered in higher forests.

In the mountain meadows of the Greater Caucasus, it is always replaced by the pine vole.

The vole is common on the sloping plain of central Ciscaucasia, but is rarely found, if at all, in the mountains (Ognev, 1950). On the deforested sloping plain of Terek-Sunzha voles are numerous and apparently destructive. Turov (1926c) considered the species to be common only in the forest zone of North Ossetia. According to our observations, the deforested glades and subalpine meadows in the Fiagdon and Gizel'don gorges of the Lesistyi and Skalistyi ridges are heavily populated by this animal. It is common in the Urukh ravine at altitudes of 1,500-1,800 m, and, farther east, has been traced in the Argun and Sulak basins at altitudes from 800 m to 2,700 m (Beme, 1933; Geptner and Formozov, 1941).

It has not been observed in the Dagestan foothills from Khasavyurt to Derbent, or farther southward on the low littoral terrace down to Baku.

It is also absent from the humid regions of the Khachmas lowland which is inhabited by steppe voles, field and house mice. On the Kusary sloping

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* Lower jaws of this vole species were found in the Lower Pleistocene strata of Kudaro I in 1958.

plain, the lower border of the range is at an altitude of 600-650 m in the pasture-forest zone, and only on meadow sections of the Samur valley does it descend to 250-300 m.

If accurate, Beme's mention (1928, p. 143) of animals caught near the Samur estuary is noteworthy.

At the eastern end of the Greater Caucasus this rodent is encountered in grain fields and on subalpine meadows in the Konakhkent and Khizy regions. Its lower range in the Shemakha area extends along an altitude of approximately 800 m, while farther west on subalpine meadows in the upper reaches of the Gerdyman-Chai the species is replaced by the pine vole.

In the deforested areas on the southern slope of the Main Range, the vole penetrated from mountain meadows through glades overgrown with bracken by way of the Demir-Aparan-Chai, Bum-Chai and Mazym-Chai ravines (in the vicinity of Kutkashen, Vartashen and Lagodekhi) up to the base of steep slopes and into the zone of lowland forests of the Alazan-Avtaran valley. On the high mountain meadows of the eastern half of the southern slope of the Greater Caucasus, the species is usually concentrated along the margins of cattle stands heavily covered with manure and overgrown with horse sorrel and orchard grass. It also populates subalpine meadows on the deforested ridges of the southern lateral ranges.

314 The vole is common on meadows of the Kakhetian Range and in intensely deforested South Ossetia down to the reaches and tributaries of the Rion; here it is replaced by the pine vole as on the northern slope.

There is no indication of the species in the dry Gori depression or in humid Colchis, on the Black Sea coast or on the northern slopes of the Adzhar-Imeretian ridges (Satunin, 1913; Shidlovskii, 1947, 1948, 1950).

The common vole is conspicuous on the Trialet ridge and its spurs, e.g., the Mokrye Gory, and on Dzhavakhetia meadows.

The species is eurychoric on the Armenian Highland, where along its lower limits the distribution increases greatly on the south and the east. While this vole is very common on ridges surrounding Lake Sevan (Turov and Turova-Morozova, 1928), it is also found on relatively dry and deforested northern slopes at an altitude lower than Kedabek (1,400 m). And similarly on the Karabakh mountain meadows (e. g., in Dali-Dag, Sary-Yeri and Basargechar) it is widespread and yet descends to 1,200-1,300 m on deforested eastern slopes.

On the southern slope of the Zangezur ridge in the Akulis-Chai Basin, we found it in spring-fed marshland among heavily grazed steppelike spurs and valleys only above 1,800 m. The common vole does not occur in the tragacanth zone, i.e., in the "phrygana" and "gariga" formation or in the artemisia and saltwort semidesert of the middle Araks valley and the Kura-Araks lowland. Contrary to Ognev's opinion (1950, p. 209) and Kuznetsov's maps (Bobrinskii, Kuznetsov and Kuzyakin, 1944), there is no trace of this vole in the Lenkoran lowland or on Mugan. In the high Talysh mountain it is encountered only at altitudes of 2,000-2,100 m on steppe meadows, i.e., near the Kel'vyaz and Kosmalyan outposts. It does not even inhabit those places inhabited by mole in the Talysh forest zone. In general, the present-day range of the common vole in the eastern half of the Caucasian Isthmus diverges somewhat from the distribution of the steppe vole. In northwestern Iran and northeastern Turkey, the common vole is dispersed at altitudes of 2,000-2,500 m, and farther south its range is probably higher. Blanford (1876) recorded this vole under the name of Arvicola mystacinus De Fil. in an area between Shiraz and Eşfahān, at an altitude of approximately 2,800 m.* Goodwin recorded it from the eastern Elburz (1939). It probably inhabits Mt. Savalan and was caught in the region of Lake Urmia by the Caucasian Museum Expedition. In the Georgian Museum collections there are specimens from Kars, Oltu, Great Ararat and other localities in Turkey. The numerous vole populations in the high Eleskirt valley in the upper reaches of the Euphrates can be accounted for by the many swamps and rivulets. In central Turkey some remaining habitats are considered as relicts (Neuhäuser, 1936; Ellermann, 1948).

With higher seasonal and daily temperatures, the factors of soil humidity and mesophytic vegetation assume greater importance for the rodent in the south, and result in an enlarged vertical distribution as the range extends southward. They also account for the division of the range into isolated relict islets adapted to high plateaus and ranges. The animal's range
315 is obviously wedged out on the high mountain ranges of the middle courses of the Tigris and Euphrates.

The absence of the animal from western Caucasia and Transcaucasia is adequately explained by the excessive moisture, while in the forest of the Talysh lowland it can be attributed to dryness of the soil and vegetation.

The feeding habits of the common vole show it to be a typical herbivorous animal. Human intervention during historical time is responsible for the concentrated forage which comprises its present-day diet.

The main natural factor limiting this vole's population in both mountains and plains is unfavorable climate. The influence of quadrupeds and predatory birds on this vole during the summer season on the Caucasus is considerably greater than on the steppe vole.

Based on its contemporary range and ecology, it is assumed that the common vole is a European mesophilous species which developed under conditions of moderate climate and humidity on meadow vegetation.

The explanation of the appearance and total isolation of large, common vole populations on the ranges of southwest Asia and the Caucasus is consonant with this concept if we presuppose an early settlement during a humid epoch when present-day hot desert valleys and slopes were well covered with meadow or, at the least, steppe vegetation.

From an interpretation of the contemporary ecological and distributive characteristics of this vole, it would seem that it could hardly have appeared on the Caucasus before the Middle Pleistocene, and then during a time of considerable climate cooling and development of mesophytic meadow formations in the desert and semidesert zones.

The origin of the local, high-mountain common vole in the mountains of the eastern Mediterranean and its subsequent settlement in the north is substantiated by the Mediterranean origin of northern mesophytic meadow formations. Some botanists now hold the theory of an alpine origin of meadows which were displaced to lower altitudes in the Pleistocene and advanced in a northerly direction (Fedorov, 1952).

Pine vole — Microtus (Pitymys) majori Thos (s. lato). Voles of the subgenus Pitymys are known from Pleistocene deposits of Eurasia

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* A vole closely related to M. guentheri Danf. et Alst. is found on Mt. Talysh and in Iran.

and North America (Wolf, 1939; Simpson, 1945). On the Caucasus remains of a special species of vole M. apscheronicus Arg., probably ancestral to extant Caucasian species, are found in Middle Pleistocene strata of the Apsheron Peninsula.

The distribution of pine vole on the Caucasus includes the Greater Caucasus, the Lesser Caucasus, Asia Minor, Talysh and Elburz (Map 70).

In Ciscaucasia the pine vole can be found from the northern piedmont forest belt up to the talus passes on the Main Range.

On the Trans-Kuban Plain the animal inhabits some locations to an altitude of 250-300 m above sea level, and it is common from Krymsk to Maikop on the first low ridges of relict oak forests and mesophytic meadows. The range does not reach to the broader section of the Kuban River even in the valley of its left tributaries — here it is replaced by the common vole. On the east, the range enlarges and passes south to Cherkessk at an altitude of approximately 600 m. In the forest zone and on the alpine meadows of the northwestern Caucasus, the species is very common, and numerous specimens have been collected from the Caucasian and Teberdinskii reservations.

316 In central Ciscaucasia the animal inhabits the mesophytic ravine areas, and is absent from the greater part of the dry Kabarda sloping plain.

One isolated section of the range lies in oak stands in the Pyatigor'e area (Beshtau, Zheleznaya, Razvalka), and another more to the north in the Stavropol uplands. In this last area the vole inhabits grazed-down meadow glades among relict broadleaf forests, e.g., in the vicinity of Mt. Strizhament.

The breach between this section of the range and the major one in the Caucasian uplands is 50-60 km and is made up of steppelike foothills. There are relict patches of pine vole habitation in forested dry ravines along the Kalaus. On the sloping plains of the Terek and Sunzha the animal inhabits mesophytic meadows which appeared shortly after the forests were cleared.

Contrary to Ognev's opinion (1950), this vole is found neither in the vicinity of Mozdok nor near Grozny, where the climate is too dry for it. In central Dagestan it inhabits meadows at 1,600-2,500 m above sea level.

In western Transcaucasia the pine vole is common everywhere from the Black Sea coast to the mountain talus passes. In humid Colchis it is absent only from periodically flooded alder thickets and reedgrass bogs. The Svanetian alpine meadows are heavily populated with vole along the fringes of birch forest grown with whortleberry and as far as the upper sections of cereal grass—crowfoot carpets which wedge into slate talus. Here it completely replaces the common vole. To the east, the animal is encountered all along the southern slope of the Greater Caucasus near the upper reaches of the Pirsagat rivulet in Azerbaidzhan.

The pine vole is sometimes replaced by the common vole in alpine meadows in the areas of Nukha and Kutkashen. Argiropulo's statement (1939a) that the pine vole does not inhabit the forest zone in the Greater Caucasus is in error; on the contrary, a large pine vole population is often observed on the forest edges and in thinned stands of oak—hornbean.

There is no indication of pine vole in the Alazan-Agrichai valley, in the valleys of the Adzhinour Plateau or on the Kura Lowland. Claims that this animal was found in Geok-Tepe [Geok-Chai] on desert foothills to the north of Evlakh (Shidlovskii, 1938; Ognev, 1950) are erroneous (Vereshchagin, 1949c).

In eastern Taurus and along the ranges of the Lesser Caucasus the animal is spread mostly on the northern slopes and on the high humid plateaus of Dzhavakhetia and Tsalka.

It is very common on deforested slopes of ravines of the Shakhdag Range and in the remaining beech forests of the Terter-Chai ravines in Karabakh where it descended to an altitude of 1,000-1,200 m. In Talysh the pine vole inhabits only the border areas of the upper timberline, and is rare because of the extreme aridity in summer (Vereshchagin, 1949c). The southeasternmost section of the range is the northern slope of the Elburz Range (Ellermann, 1948).

Pine vole is very common on motley-grass meadows near the forest's upper edge. In these areas of ecological optimum, the greatest population of this species can be found.

The pine vole resembles the common vole in feeding habits, but, because of its greater digging capacity, the rhizomic constituents of herbaceous plants feature more prominently in its diet.

317 The population dynamics of this vole are considerably more stable than those of the steppe and common vole. Predatory birds inflict less population loss on the pine vole because of its subterranean way of life and its habitat in tall grasses and forests.

Based upon the degree of fur-cover differentiation (underfur and guard hair), the pine vole is intermediary between the steppe and the common vole.

The pine vole is a typical mesophilous species of the eastern Mediterranean formed on mountain meadows and in broadleaf forests. This species is an excellent indicator species which illustrates the long existence of mesophytic conditions on separate areas of the Caucasus-Asia Minor land mass. The peak in pine vole population coincides with the epoch of greatest cooling during the Pleistocene.

The Stavropol-Caucasus break in range probably occurred at the beginning of the Holocene; the Lesser Caucasus-Asterabad break undoubtedly happened considerably earlier.

Caucasian snow vole — Microtus (Chionomys) gud Sat. (s. lato) (Figure 125). Fossils of this vole were found during the excavation of the Kudaro caves in the reaches of the Rion. The animal is distributed within limits of 1,600 to 2,000 m on the Perevalnyi and Skalistyi ridges but is absent from the frontal chain of the Chernye Gory Mountains (Nasimovich, 1935).

Our observations in the Kuban and Teberda ravines show the vole at 1,500-1,700 m above sea level on the Skalistyi slopes and especially numerous higher in the alpine zone on large rock taluses overgrown with pine, birch and willow, and further on in alpine meadows near taluses and glaciers.

At present this species is not encountered on the Stavropol uplands (Vereshchagin and Gromov, 1953b), but it is found in the trachyte rock taluses on the permafrost section of the Razvalka Mountain in the Pyatigor'e area, at an altitude of 600 m. This population is now isolated from the main range 50-60 km to the north, since the nearest vole habitat is encountered in the canyon of the Berezovka rivulet, south of Kislovodsk (Vereshchagin, 1953a). Higher in the mountains, M. (Chionomys) gud Sat. inhabits the ravines of Malka, Baksan, Chegem and Cherek, especially rock taluses in canyons cut by these rivers in the Skalistyi ridge. It has been observed in certain places in the interior longitudinal valleys at an altitude of 1,200-1,500 m, where there are stone taluses. This vole is rare in the Chernye Gory Mountains near Nalchik.

In the Ardon ravine the heaviest population was observed on the lateral moraine in the pine—birch forest near the end of the Tseya glacier among granite rocks overgrown with fern, whortleberry, sweetberry, honeysuckle and rhododendron.

In the Terek gorges, this vole is widespread on the slope of Mount Fetkhus near Ordzhonikidze (Formozov, 1926).

In central Dagestan numerous voles are encountered in Gunib, in the Bogos Range and in the ravines of the Samur tributaries at altitudes of 1,300, 1,600, 2,100 and 2,500 m (Geptner and Formozov, 1941).

In August 1952, the author observed many of these voles in arid, hot depressions in the upper reaches of the Manas brook among marl taluses near the village of Lavashi at an altitude of approximately 1,000 m. Summer 318 conditions here are pessimum for this animal.

FIGURE 125. Microtus (Chionomys) gud Sat. (s. lato)

From watercolor by K.K. Flerov

On the southern steep slope of the Greater Caucasus in eastern Transcaucasia this vole is found in gorges at 1,300-1,400 m, e.g., in the Gerdyman-Chai ravine and others, but it is common only in the cirques at river sources bordering birch—hornbeam formations at 2,000-2,600 m. It is also encountered on the ridges of the transverse ranges near the upper forest belt of mountain oak at 2,200-2,700 m above sea level. Farther west the vole appears on the Kakhetian ridge above Telavi near the snowline (Shidlovskii, 1951). In relatively dry and deforested South Ossetia, it occurs among the rocks from 2,000 m upward (Ognev, 1950).

In upper Svanetia this animal is very numerous in fir—maple forests. In the arid Ingur valley it lives in sunheated gneiss rocks overgrown with Pontic azaleas, e.g., near the village of Mestia. On steep southwestern slopes in Abkhazia it is common from an altitude of 500 m upward to the glaciers, although Shidlovskii (1950) recorded it for high mountains only in the reaches of the Bzyb River. In all probability, the Surami Range is not actually a habitat for this vole. In Asia Minor it probably inhabits the greater part of eastern Taurus since it was found on Mount Varzambeg south of Rize at an altitude of 3,000 m.(Neuhäuser, 1936). It was recently observed by Shidlovskii in Dzhavakhetia as well.

The southern range of this vole is not as wide as that on the Greater Caucasus.

Taluses of big rocks held by birch and pine forests with undergrowth of whortleberry, honeysuckle, raspberry and Pontic azalea are densely populated by M. (Chionomys).

319 The structure and placement of rocks and stones which ensure dry shelters and food storage are secondary in importance for the well-being of this animal only to the availability of the food itself. The composition of the bedrock is less important, inasmuch as calcareous, gneiss, granite and slate taluses are all found populated.

FIGURE 126. Reserve stocks of hay stored by Microtus (Chionomys)

Photograph by author, 1952

The composition of summer and winter foods of this vole varies greatly according to the habitat. Nasimovich (1935) observed that in the Caucasian Reservation the vole feeds mainly on anemones, ferns, raspberry and Caucasian rhododendron. In the upper part of the Teberda Reservation, Stepanov found that 32 vole stacks contained 47 plant species, of which ferns, raspberry, mountain ash, willow, birch, cereals, strawberry, spruce, pine and foxberry were the most frequently encountered.

According to observations made by Semenov-Tyan-Shanskii and the author in the Tseya ravine, the animals stored mainly twigs of honeysuckle, whortleberry, willow herb, mountain ash, Caucasian rhododendron and stone bramble. They also feed on branches of birch and shrubs, climbing very high on the smooth tree trunks. On the relatively dry meadows of the Doniserdon and Baksan valleys, stacks of hay, stored in fissures in fortress ruins (Figure 126), are composed of veronica, sage, nettle, clover, etc.

The Caucasian vole is adapted to rock reliefs and avoids digging. Among the other voles, it stands out in its astonishing climbing ability, almost the equal of that of the dormouse or the squirrel.

Notwithstanding the fact that great variations in the population of this species have not been noted, in certain years and in certain gorges they are rarely 320 encountered. This may indicate the incidence of local epizootic diseases. This species is not as vulnerable to climatic affects as are other vole species.

Of the predators, only marten, weasel and large owls are dangerous to this vole, although any newly-settled carnivore, like the sable, may prey upon it.

Judging by the large population it supports and the size of the specimens it produces, the subalpine zone of the western part of the Greater Caucasus provides the optimal contemporary ecology for M. (Chionomys) gud.

The formation of rocks during orogeny and glaciation was often more important to the development of this vole's range than the presence of mesophytic vegetation, as can be seen by the densely populated, dry interior valleys and by central Dagestan where the ecology of this species shows features similar to those of Microtus (Chionomys) nivalis Mart. (s. lato). An analysis of the range and habitat brings us to the conclusion that the Caucasian vole is an early local species, associated in its evolution with the development of high-mountain plant formations of the Miocene. The glaciation of the Greater Caucasus in the Pleistocene could not have displaced the populations of these animals to the plain, as thought by some faunists and paleontologists; it only partially lowered their range. Even during the lowering of the snowline to 1,000-1,100 m, a wide habitat for vole existed on the meridian ranges and on the frontal longitudinal ranges. However, the cold and humid climate during the glaciation, which brought about the development of meadow formations in the foothill plains, created the conditions for the penetration of the animals into places below river bank escarpments. The vole probably appeared in the Pyatigor'e area during one of the cold epochs, but it is doubtful that it reached the Stavropol uplands. Future fossil finds in the foremontane regions from the Middle Quaternary may fix this history more precisely.

Nowadays, cattle grazing and the felling of mountain forests diminish the range of the Caucasian vole in the eastern Caucasus, but enlarge it in the western Caucasus.

Asia Minor snow vole — Microtus (Chionomys) nivalis Mart. (s. lato). Remains of this species were recorded from Pleistocene and Holocene strata of many caves in England, France, Germany, Italy, Austria, Sweden, Czechoslovakia and Hungary (Wolf, 1939).

The remains of a special species — M. (Chionomys) machintoni Bate — found in Acheulean to Mesolithic deposits (Bate, 1937) are recorded for the caves of Mount Carmel in Israel. In the U.S.S.R. only remains of Holocene Age are known on the Armenian Highland. The contemporary species is widespread in Mediterranean mountains — from the Pyrenees to the Balkans, in Syria, Palestine and Asia Minor, on the Caucasus and on the western Kopet Dag. In the upper Pleistocene this vole probably inhabited even the Balkan Mountains.

On the Greater Caucasus, the animal is known only from the northern slope of the range: the Fisht, Pshekish, Bolshoi Tkhach, Acheshbok and Pambak peaks, and from the upper Teberda and Cherek river gorges; it is not encountered in the Balkarian Cherek or farther east. The paleontological sites on the Greater Caucasus are located at altitudes of 1,500-2,000 m in the subalpine zone. The habitats here are the same as those of the Caucasian vole (Map 67).

321 On the Lesser Caucasus the Asia Minor vole inhabits the forest and alpine zones on the Trialet ridge, in Dzhavakhetia, on all ridges of the Armenian Highland, in Karabakh and in Talysh.

The vertical distribution increases in a southeasterly direction according to the locations of phytolandscape zones, although there are exceptions. On the Trialet ridge the species has been found at altitudes of 2,000 m near Bakuryan; on the Pambak ridge it is common at altitudes of 1,800-2,500 m; and on the Shakhdag it lives in the Shamkor-Chai ravine between 1,600 and 2,300 m. Southward, it is encountered in the xerophytic mountain steppe, e.g., near Sevan on the Saraibulakh and Daralagez ridges (Turov and Turova-Morozova, 1928; Dal', 1944b, 1949b). Above Yerevan it occurs at a height of 1,200 m in rock taluses covered with shrubs (Flerov and Gureev, 1934).

Along the Akulis-Chai ravine on the southern slope of the Zangezur, in 1947, we found the Asia Minor vole at altitudes from 1,600 to 2,500 m in rock taluses overgrown with spiraea, dog rose, almond, hawthorn and buckthorn in the zone of astragali–traganth.

It was not encountered by the author in the beech forest in the Terter-Chai gorge in Karabakh, but is found higher in the alpine zone near Kelbadzhar.

In Talysh and Kopet-Dag, there is only a relict range. The author found a small vole population in June 1945 on the bald Kelakhan Mountain in the dry Diabar depression at 1,900 m. The animals were encountered here in the taluses of teschenite rocks with a sparse xerophytic cover of saxifrage, oxeye daisy, brome shoots and xerophilic ferns among the mountain-saltwort semidesert (Vereshchagin, 1945b). This vole probably inhabits Savalan and the Elburz Range.

The Asia Minor vole achieves its maximum population in a zone of steppe meadows, e.g., near the Sevan shore. The rocky substrate is required for the well-being of this species. The habit of storing food is not so strongly developed as it is in the Caucasian vole, but the capacity to adjust its habitats to varying conditions is immeasurably greater; it adjusts to a wide range of feeds and of humidity. Whereas in the subalpine zone of the western Caucasus this vole lives side by side with the mole and the earthworm, in Talysh and on the southern slopes of the Armenian Highland it is found in the mountain xerophytic zone living with the tarantula and the scorpion. On the whole, the vole is more adapted to low pressures and rocky substrates and less to succulent foods and low temperatures.

The diminution in the animal's size in its eastern range and its disappearance from the medium-altitude southern slopes of the Armenian Highland indicate that the southeastern sections of the range are already located in a contemporary pessimum region.

Discontinuities in the southeastern areas of this vole's range and the isolation of the mountain habitats in Talysh and Kopet Dag are explained by the increasing aridity in the eastern Mediterranean which followed optimal conditions for the settlement of the species during a pluvial cold epoch.

However separated and various the isolated ranges in the Mediterranean, they indicate that the snow voles of the Pyrenees, Alps, Carpathians and Caucasus are separate species of parallel development from genetically related material.

322 The postglacial rise in temperature and the elevation of phytolandscape zones have reduced the vole range, deepening it and isolating different geographic races of the snow vole.

The limited spread of the snow vole on the Greater Caucasus is partially explained by the insufficient adaptation of this southern species to the marked humidity of the southwestern ridges; it is more difficult to explain its absence from the dry longitudinal valleys of the northern slopes of the eastern ridges and from Dagestan.

Long-tailed snow vole — Microtus (Chionomys) roberti Thos. A unique finding of Quaternary fossils is recorded from the Upper Paleolithic of the Sakazhia cave in western Transcaucasia. The contemporary distribution of this vole includes the northern slopes of eastern Taurus in Asia Minor, the Adzhar-Imeretian Range, the Trialet ridge and the Greater Caucasus (Map 69).

In the northwestern Caucasus this vole is found on the Chernye Gory Mountains from elevations of 800-1,000 m to the alpine zone. It is rare in central Ciscaucasian gorges and is not encountered at all on the Stavropol uplands. It is common in North Ossetia at altitudes of 800-1,000 m.

In Dagestan it inhabits beech forests in the upper reaches of Andi Koisu near the villages of Takhota and Choroda, but it is probably absent from other parts of Dagestan (Geptner and Formozov, 1941), as it still is from the inner longitudinal valleys of the northern Caucasus.

The author found the vole in Azerbaidzhan (Vereshchagin, 1940a) in 1935 in the Katekh-Chai ravine, northwest of Zakataly, at an altitude of 1,450 m, but it is not known farther east.

The vertical distribution of M. (Chionomys) roberti Thos. on the Black Sea slope of the Greater Caucasus is from sea level to the upper forest belt (Shidlovskii, 1947, 1950). In Adzharia the animal inhabits the forest zone from 800 to 1,800 m (Shidlovskii, 1948). It is distributed in all of South Ossetia except the dry Gori depression.

A typical well-populated habitat of this vole is a shady, humid, dead-end gorge. In the western part of the Greater Caucasus and on the Lesser Caucasus, such biotopes are to be found in fir and fir—beech forests with tall broadleaf grasses of burdock, cow-parsnip, nettle and orchard grass covering the bottoms of creek valleys. In Ciscaucasia the population is more numerous in the lower humid area of the Chernye Gory Mountains than in the upper parts of large ravines. In eastern Transcaucasia the opposite is observed.

According to its morphological type, particularly its fur cover, this vole resembles the water vole to a certain degree. The animal often swims in mountain brooks and in general lives in conditions of extreme humidity.

The speciation of this vole is associated with the early mesophytic and even hygrophytic phytolandscapes and biotopes which existed in the mountains bordering the Black Sea depression on the southeast and east in the Miocene. The reduction of the M. (Chionomys) roberti range to the east completely corresponds to the changes in landscape and biotopes in the mountain forest.

The existence of an isolated, actually a relict, population in the upper 323 reaches of the Andi Koisu in Dagestan can be explained by the penetration of the animal from the southern slope during a humid epoch. Tumadzhanov (1940) recorded a similar immigration of the beech into Dagestan in the Holocene.

In all, M. (Chionomys) roberti is an endemic indicator species of the ancient mesophilous faunal complex in the Caucasus.

Common red-backed vole — Clethrionomys glareolus Schreb. Fossils belonging to the genus are known in Europe from the Pleistocene. The main part of this species' range is located in taiga and broadleaf forests of Eurasia. The animal penetrates into the steppe through the forested areas of river valleys. Ecologically this vole is mesophilous and psychrophilic. Only the Pontic subspecies, C glareolus ponticus Thos., is found in the southeastern Mediterranean, inhabiting the northern slopes of Taurus on the southern coast of the Black Sea (Thomas, 1906; Neuhäuser, 1936) and the Adzhar-Imeretian Range (Map 72).

In Adzharia the animal is found in spruce forests along the Supsa River (Shidlovskii, 1940a). This southern section of a wide range, now isolated by the Bosphorus, is a remarkable example of the southern faunistic influence on the Caucasus through the Balkans and Asia Minor.

The common red-backed vole's absence from the western part of the Greater Caucasus indicates that it penetrated the southern Black Sea coast very late, during the period of maximum cooling in the Upper Pleistocene.

Steppe lemming — Lagurus lagurus Pall. Fossils of this Upper Pleistocene species are known from several localities on the Russian Plain — the Don, Volga and Ural valleys. The present range is located in the steppe and semidesert zones from the lower reaches of the Dnieper to the upper reaches of the Yenisei and the borders of northwestern China (Vinogradov and Argiropulo, 1941). The steppe lemming is also widespread on areas adjacent to the Caucasian Isthmus, on the northern coastlands of the Black Sea, the Sea of Azov and the Caspian Sea. On the Isthmus it is found only in the northern Ciscaucasian steppes in the interfluve of the Kuma, Kalaus and Manych, i.e., northwest of the Stavropol Plateau (Sviridenko, 1928). Kistyakovskii (1935) found remains of this animal in bird pellets in the vicinity of Achikulak, Blagodatnoe, Sukhaya, Padina, Petrovskoe and Kambulat (Map 64).

The steppe lemming appears in Ciscaucasia only in peak breeding periods or during migrations provoked by unfavorable conditions. We assume that the steppe lemming penetrated only recently into the Caucasus Isthmus, probably in the Upper Pleistocene or Holocene, from the adjacent steppes of the Russian Plain, drawing the inference from its underdeveloped range in the Ciscaucasian steppes, from its stable connections with the landscape, and from formations of cereal grass—motley grass, feather grass—fescue and steppe—wormwood of the temperate belt of Eurasia. This settlement could have taken place at the time when the Manych strait disappeared.

Promethean vole — Prometheomys schaposchnikovi Sat. (Figure 127). Fossils of this vole carried in by the eagle owl are known from Upper Paleolithic strata in the Gvardzhilas cave in the Kvirila River ravine in eastern Transcaucasia at an approximate altitude of 450-500 m, and from Lower Paleolithic strata of the Kudaro I cave.

The Gvardzhilas cave is located outside the contemporary range of this animal, but to study the shifts in range during the Upper Pleistocene, it is necessary to follow the features of this vole's contemporary distribution on the Rachin ridge and to investigate the radius of the eagle owl's hunting 324 flights in this region.

FIGURE 127. Promethean vole

Watercolor by E.Ya. Zakharov

The present distribution of Promethean vole is confined to the western half of the Greater Caucasus and to the Adzhar-Imeretian Range of the Lesser Caucasus (Map 65). On the Greater Caucasus it is encountered from the Fisht and Oshten peaks to the Kazbek-Krestovyi Pass and Gudaur Dag. It has been traced in the Caucasian Reservation in the Mzymta valley, along the lower Kardyvach Lake, in the meadows where the Kurdzhips and Pshekish rivers rise, in the Kisha and Urushten basins, in the Malaya Laba sources, and near Krasnaya Polyana (Turov, 1926a, 1926b). The animal was caught in Abkhazia at the Avatkhar site at an approximate altitude of 1,500 m. In Svanetia in 1948 the author followed the animal on high-mountain meadows in the upper reaches of the Ingur and the Rion and found it particularly numerous on the Zagar pass of the Lechkhumi ridge at altitudes of 1800-2,800 m. This rodent is not encountered in the dry longitudinal Ingur valley. In South Ossetia the Promethean vole was hunted in the Bolshaya Liakhva upper reaches (Shidlovskii, 1951). The animal was traced on the mountain meadows of the Mamisson pass to the railroad stations Kazbek and Gudaur in the central part of the Greater Range (Turov, 1926a, 1926b). The author found neither the animal nor its tracks in the upper reaches of the Balkar Cherek, Doniserdon and Ardon. We have no data on the presence of this vole in the upper reaches of the Kuban, Baksan and Malka. Thus, the range on the northern slope of the Main Range is broken at least from the Laba basin and Zelenchuk to Ardon. This may be explained to some extent by the destructivity of mountain glaciers.

On the meadows of the Skalistyi ridge in Ossetia, in Kabarda and in the Grozny Region, this rodent was not observed in places perfectly adapted for its habitation. Apparently, the Promethean vole was not distributed north into the dry longitudinal valleys even during the Pleistocene.

Nor has it been observed east of Kazbek on the Perevalnyi Range. In the Zakataly Reservation, which the author has carefully explored, it is absent, as it is from central Dagestan. The rapid thinning out of the rodent 325 population east of the Caucasus can be attributed to the great reduction in area of alpine meadows and to xerophytization as shown by the development of sheep's fescue and matgrass, instead of a motley-grass community.

On the Lesser Caucasus, the Promethean vole has been found only in the upper reaches of the Bakvis-Tskali River, the left tributary of the Supsa, near the Bakhmaro health resort, at an altitude of 1,600 m (Shidlovskii, 1940a, 1947); these subalpine meadows are located west of the Gotimaria (Metis-Tskaro) peak (2,868 m). The range in this area is considerably wider; according to Shidlovskii's data, the vertical distribution lies within limits of 1,500-2,800 m, but the animal can also be found at lower altitudes. The contemporary ecological optimum of this animal is within subalpine and alpine meadow zones with a predominance of lady's mantle and bunch grasses (orchard grass, meadow grass and others). Meadows lying among thickets of Caucasian rhododendron and birch are also densely populated. The rodent does not enter the rhododendron growth where food is not available, but in birch forests and on the upper forest edge grown with tall grass it is as common as it is on open meadows. This vole's habitation of beech forests in the Caucasian Reservation, noted by Turov (1926b), may be, in some cases, the consequence of recently advancing forest formations into the alpine meadow zone. In heavily shaded beech and hornbeam forests the vole is never found because of the lack of grass food.

In many places, the animal inhabits oat, wheat and potato fields or invades their borders, as in the upper reaches of the Ingur.

Its strictly subterranean way of life and its diet of grass roots are reflected in the animal's morphology: flattened skull, extended incisor curve, elongated diastema, rudimentary eyes and shortened extremities. The skull, with a crest extending nearly to the occiput, is very similar to that of the muskrat. In its weakly-differentiated and vertically-disposed fur cover and coloration (often black), the animal is similar to the mole vole.

In general, in a morphological-functional sense, the Promethean vole combines features of the muskrat, water vole and mole vole, but, in contrast to the latter, it lives in mesophytic conditions (see also Vinogradov, 1926; Ognev, 1926b). According to Gambaryan's observations (1952), the Promethean vole, unlike the mole vole, combines terrestrial feeding with root grubbing.

Such adaptations indicate the early origin of the species and its pristine associations with the landscape of the high-mountain mesophytic meadows.

The population fluctuation of the Promethean vole can be attributed to mass death during the spring showers and after frosts when the water freezes in the burrows (Turov, 1926a).

The strict endemism of this species shows the conservation of the ecological conditions on the western Caucasus: the ancient origin and continuous existence of the landforms and the zone of mesophytic subalpine and alpine meadows from the Lower Pliocene at the latest.

The division of the range into two parts — the Caucasian and Lesser Caucasian — may have taken place by postglacial time as a result of the drying-out of the meadows on the Surami crystalline rock massif.

326 This vole is an early Pliocene species endemic to the Lesser and Greater Caucasus with a relict range which has increased somewhat in present time because of the expansion of the high-mountain-meadow zone through forest-felling and animal-grazing.

Water vole — Arvicola terrestris L. (s. lato). Fossils of this vole are known from Pleistocene strata in Europe.

Remains of Arvicola terrestris L. (s. lato) are common on the Russian Plain in Upper Pleistocene and Holocene deposits. South of the Caucasus the remains of this vole have been found in Acheulean strata of Syrian caves. On the Caucasian Isthmus there have been isolated fossil finds in Middle Quaternary strata of eastern Transcaucasia and in the Upper Paleolithic of western Transcaucasia, and numerous finds in Holocene deposits in caves which are day rests for eagle owls.

The contemporary distribution of the species includes the forest, steppe and semidesert zones of Eurasia. South of the Caucasus it can be traced in northern Iran and Asia Minor as far as Palestine.

On the Caucasus the water vole inhabits small areas from the level of the Caspian to an altitude of 2,600-2,800 m, but is not found in broadleaf mountain and coniferous forests, or in rocks and taluses of passes (Map 66). Its greatest population is observed on the floodplain meadows of the lower Don and a somewhat smaller population in the Kuban floodplain.

In the Colchis and Lenkoran lowlands it is very rare, although it is found in damp depressions which flood annually. In the eastern Ciscaucasian semidesert and in Transcaucasia, it is common on lakes and streams overgrown with reed and rush, where it lives in the summer months and builds spherical nests among the thickets, but does not approach the shore area.

The largest population of water vole in the foothills is observed on spring rivers like those on the Terek-Sunzha Plain.

In the interior steppe valleys of the Greater Caucasus northern slopes and in central Dagestan, a peculiar type of vole, ecologically distinguished by its subterranean existence, is found. In these areas this vole inhabits the bottoms of gorges, particularly irrigated farmland. In the alpine zone of the Greater Caucasus it occurs rarely and only in the upper reaches of the Terek and the Aragva.

On the Armenian Highland, in Asia Minor and in Iran, the water vole is common on subalpine meadows on the upper reaches of rivers (e.g., in Karabakh, in the upper reaches of Akstafa and in the lake region of Dzhavakhetia). In the Araks valley many of these voles are found near the spring rivers of the Aralik depression.

It can be seen that this vole is widely distributed and especially attracted to water biotopes.

The ecological optimum of the subterranean populations of these voles is at mean altitudes in the dry area of Caucasian plateaus; that of the hydrophilous populations is in the semidesert zones which lack excessive atmospheric humidity [sic!]. The low population density of the water vole on the Black Sea coast and in the Colchis and Asterabad swamps indicates a certain degree of similarity to the distribution of the common vole. In the Colchis swamps it is the tremendous competition and persecution from the Norway rat that produces this reduction in population, and in Asterabad the drying-up of reservoirs in summer and the compaction of the Lenkoran yellow podzol have the same deleterious effect (Vereshchagin, 1941b, 1949d).

327 Subterranean mountain populations differ from hydrophilic species in elongated diastema, greater curvature radius of the upper incisors, and shorter tail length, and the divergence in the contemporary ranges of the respective species can be observed along a line of secondary remove from the water medium and from these distinctions in features.

In southwest Asia and on the Caucasus the formation of these characteristics is probably related to the uplift of mountain systems during the Quaternary.

Paleoecological data suggest that the water vole of the Caucasus is probably of Upper Pliocene origin. In Transcaucasia the southern, relatively xerophilous populations actually predominate.

The consistency of the species range in the Mediterranean is ensured by both the natural and artificial development of freshwater biotopes and the ecologic plasticity of the animal.

Order **PERISSODACTYLA**

Representatives of the families Equidae and Rhinocerotidae appear in the Quaternary fauna of the Caucasus, but by the Holocene only Equidae remained. The historical origin and disappearance of this family is examined below.

Family **EQUIDAE**

The earliest fossils of the large, true horse, Equus stenonis Cocchi, are known from the Caucasus and adjacent territories from Upper Pliocene deposits. Probably the horse appeared simultaneously with the southern elephant introducing a new phase in the fauna. Later, in the Middle Pleistocene, the "semi-ass" appeared on the Caucasian Isthmus.

The history of true horses can now be traced on the Caucasus very schematically from a number of deposits of various ages.

Quaternary horse — Equus caballus (s. lato). After Equus stenonis, remains of which were found in Akchagyl and Apsheron deposits of the Isthmus, the Taman Upper and Lower Pliocene horse, E. aff. süssenbornensis Wüst., found in conglomerates of the Taman Peninsula and the ancient Caspian terrace shingle near Baku, is the closest to the Quaternary horses (Chapter II and Map 79).

Fossils of Midde Pleistocene horses (which are not recorded in detail) are abundant in Binagady asphalts and are found isolated in clayey beds of the Khazar stage in many localities in the Stavropol area and the Krasnodar Territory. These horses were related to E. caballus chosaricus Grom., found in Middle Pleistocene deposits of the Russian Plain.

Remains of horses from the Il'skaya Paleolithic settlement in Ciscaucasia and from the Paleolithic sites of Imeretia and the Lesser Caucasus uplands are probably related to E. caballus latipes Grom. of the Russian Plain (see Gromova, 1949). South of the Caucasus, remains of Upper Pleistocene horses are known from Paleolithic strata in the Tamtama and Bisotun caves, from talus loams in the Marāgheh vicinity of Iran and, 328 southwest, from Palestinian and Syrian caves. The southern horses were of a lighter build than the northern animals.

Specimens of Pleistocene horse have been taken in the following proportions to other species from sites representing various types of burial: 6.6% from the Il'skaya encampment; 5.2% from the Binagady asphalt; 2.5% from the Sakazhia cave; 16.5% from the Mgvimevi shelters; 50.0% from the Zurtaketi encampment.

Assuming that the forms of horse we have mentioned, which inhabited the Isthmus during the Pleistocene, constitute a unique genetic series, then the origin of the Caucasian Holocene horse should not be sought in migrated forms originating elsewhere.

It is difficult to separate the remains of wild horses which lived on the Caucasus in postglacial time from the remains of domesticated horses.

In the strata of post-Paleolithic encampments, it is quite common to find bones of horse among kitchen middens and skulls and entire skeletons in the deposits. It is very probable that most of these remains belong to tarpans — E. caballus gmelini Ant. — or to their domesticated offspring.

The records of horse remains found on the Caucasus in kitchen middens of encampments and in deposits from the historical age show that this animal had an enormous economic, dietary and ritualistic importance for various tribes and peoples (Table 71).

Numerous remains of horse are known also from Urartu burials of the 10th to 12th centuries A.D. in the Sevan Basin (Lalayan, 1929) and from the cultural strata of the Later Bronze Age and the Middle Ages near Samtavro and near Mingechaur.* The horse (including the wild horse) was among the preferred subjects of Bronze Age drawings and sculpture in Southwest Asia and in the Caucasus.

In the middle of the first millennium B.C., wild horses still inhabited the Caucasus in large numbers. These were thin-legged animals with little

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* Materials from these localities have not been preserved.

ears on small heads similar to the Arab horses. Their slight build and refined form had nothing in common with the body type of tarpans. Marvellous reliefs on the walls of the Assyrian palace in Nineveh (Atlas of Ancient History of Egypt, Southwest Asia, India and China, 1937, Table 156, Figure 2) show hunts in which they were set upon by dogs and brought down by spears. This accumulation of evidence confirms the fact that the tarpan was an aboriginal horse of Europe and the northern half of Asia and not a settler from the south at the end of the Pleistocene (much less during the Holocene) as is held by some paleontologists.

In the monuments of the Koban cultures in Ossetia and Abkhazia the horse was depicted on belt buckles and ax handles as a rather slender and long-tailed animal. Bronze figurines of horses with heavy manes and long tails are among the material obtained by Uvarova (1900) in Ossetia. Without taking into account the stylization of the representations, one sees a similarity in body frame, particularly in the light head of this animal, to the southern type of horse, in marked contradistinction to the tarpan.

(329) TABLE 71. Number of kitchen and ceremonial remains of horse, compared with other animals, in strata of encampments and burials on the Caucasus*

Regions and localities	Dating	Proportion of horse specimens to other specimens (in %)
Ciscaucasia and Russian Plain		
Sarkel fortress (Slav and Khazar strata)	8-13th centuries A.D.	10.3
Settlement near Tsimlyanskaya (Khazar strata)	8-10th centuries A.D.	3.7
Settelement of Zeyukovo near Nal'chik	6-8th centuries A.D.	16.7
Ancient town sites: Isti-Su and Alkhan-Kala in the Sunzha Valley	2-3rd centuries A.D.	7.1
Burials near Ust-Labinskaya	6th century B.C. – 2nd century A.D.	21.2
Site of ancient town of Alkhaste on the Assa	6-5th centuries B.C.	13.0
Site of ancient town of Semibratnoe on the Kuban	5th-1st centuries B.C.	17.0
Ancient Greek towns of the Taman Peninsula: Cepi	5th-1st centuries B.C.	22.5
Ancient Greek towns of the Taman Peninsula: Phanagoria		12.3
Ancient Greek towns of the Taman Peninsula: Taman [Hermonassa]		14.1
Burial on the Manych	1st millennium B.C.	12.5
Tsimlyanskaya on the Don: mud-hut 1	Second half of 2nd millennium B.C.	13.2
Tsimlyanskaya on the Don: mud-hut 2		12.0
Eastern Transcaucasia		
Chukhur-Kabala fortress	12-14th centuries A.D.	16.6
Settlement in the region of Baku fortress	9-12th centuries A.D.	8.1
Settlement near Sumgait	1st millennium B.C.	8.3
Western Transcaucasia		
Akhshtyrskaya cave near Adler	Neolithic and later strata	2.0

* Author's unpublished data.

In large Scythian mounds in Ciscaucasia and south of the Russian Plain, archaeologists often encountered mass ritual burials of horses composed of some tens and even hundreds of specimens (as many as 300).

In Scythian memorials realistic representations of horses are quite common. A drawing of a stallion with a short-standing mane, thick legs,
329 heavy head, small ears and blunt muzzle resembling a tarpan is depicted on a silver dish from the Maikop burial (Farmakovskii, 1914; Figure 128). The well-known horse representations on the silver vase from the Kul-Oba burial probably portray domesticated horses. Outline drawings of horses are also found on the rocks of Kabristan, south of Baku. These were made probably during the time of the ancient Romans or earlier when wild horses lived on the Kura steppes (Vereshchagin and Burchak-Abramovich, 1948).

Pallas, Gmelin and Güldenstaedt reported on tarpan in southern Russia and on the Ciscaucasian steppes at the end of the 18th century . Levchenko (1882), Keppen (1896), Anuchin (1896), Geptner (1934b), Antonius (1938) and others published many articles and notes tracing the history of the disappearance of this animal in the second half of the 19th century. A particularly complete and impartial survey on the investigation of the tarpan was submitted by Keppen, who insisted on the necessity for studying horse
330 skeletons from the southern Russian burials. This investigation has not been carried out however.*

Unlike most investigators, Anuchin did not consider the wild horse of the Eurasian steppes and deserts as a species, but thought it to be a type of horse which belonged to nomads and ran wild. It is obvious that, if this were the case, these horses ran wild on a large scale, and such horses must have closely resembled the original form — the wild horse of the Upper Paleolithic and the Lower Neolithic. There is little data on the tarpans in the Caucasus. Rovinskii (1809, p. 131) wrote: "Wild horses or tarpans are found in flocks in the Kuban steppe, near the Ural mouth and farther."

The author could find no historical data on the presence of wild horses in Transcaucasia. By the Middle Ages, the only survivor of the dense early population of wild horse on the northern plateaus of southwest Asia was the kulan, since the horses had probably been caught and domesticated by Hittites, Assyrians and Urartus long before the Christian era.

The rapid evolution of horses in the Quaternary is usually associated with the subsequent development of steppe topography and coarse grasses, some of which — the grain formations — appeared as early as the Pliocene. The adaptive features and contemporary ecology of wild and
331 domesticated horses corroborate this association. Notwithstanding this typical association, horses could still subsist on the forest steppe and even in the forest zone of Europe because, in large herds, they can actively defend themselves against packs of predators (e.g., wolves), and because they can grab for food under the snow cover. In these areas, they fed in glades and swamps just as the extant domesticated horses of Yakutia do.

The characterization of the Quaternary horse as a stenotopic steppe animal did not do justice to its conformation, which represents a universal form in ungulates. This is substantiated by the success in using domestic horses in widely differing topographies — from the glaciers of Greenland, Antarctica and the Alps to the tropical forests, swamps and deserts of all continents.

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* Skulls and skeletons of horses from earlier diggings in large burials in the Ukraine and Ciscaucasia have not been kept.

(330)

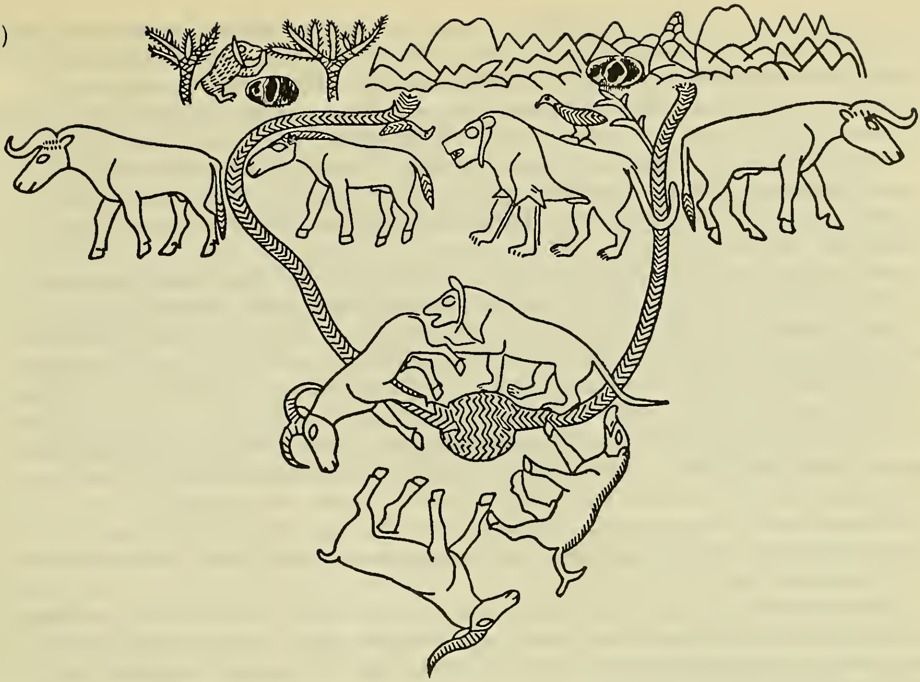

FIGURE 128. Representation of a horse, primitive bulls, lions and other animals on a silver vessel from Maikop hill (Farmakovskii, 1914)

Recently Vetulyani (1952) developed Keppen's theory that, especially in Middle Europe, wild horses were forest animals. As Vetulyani saw it, the tarpan adapted itself to a middle-forest-belt habitat and, in Europe, became a forest animal only during the last stage of its development, i.e., in the historical epoch.

New observations on artiodactyls would indicate that such a change in biotopes resulted from the development of forests in former forest-steppe areas and the hunting down of horses by man.

The intersecting relief and relatively dense population of the Caucasus did not favor such adaptations. The steep slopes, both afforested and deforested, were unsuitable for horses, and the gentle slopes were too exposed.

The date of the disappearance of the tarpan from the Russian Plain has been previously established as the 1870's, but Geptner's recently published data (1934b, p. 482; 1955) on the last tarpan to inhabit the Poltava Region considerably advances this date to 1918-1920.

Tarpan extinction on the Caucasus resulted from their harassment by nomadic horsemen, steppe plowing, human settlement near watering places and, finally, from hunting with firearms (see Keppen, 1896).

Kulan — Equus hemionus Pall. (s. lato). The fossil remains of Equus hemionus Pall. are known from Pleistocene and Holocene strata of Eurasia, particularly in steppe and semidesert zones. In Gromova's opinion (1949) kulan fossils recorded from Western Europe as

E. hemionus fossilis Nehr. may be related to small horses. However, the possibility of an early penetration of kulan into the west from Asia during the postglacial transformation of plains into steppes cannot be excluded. Phalanges and metapodia of semi-asses from upper layers of the Afontova Gora [Krasnoyarsk area] on the Yenisei, from sand dunes near Troitskosavsk [now Kyakhta] on the Selenga, from Irtysh and from Altai caves (Gromov, 1948; Vereshchagin, 1956) are mainly from the Upper Pleistocene and Holocene. Fossils from the Upper Pleistocene of China have also been recorded.

In central Asia remains of kulan are known from Paleolithic deposits in the Bukhtarma cave (Vereshchagin, 1956) and from Bronze Age strata in the Kaunchi-Tepe cave [Tashkent area]. Duerst (1908) recorded the remains of a thin-legged horse, E. caballus pumpellii Duerst, from the earliest Annau strata (3000-1500 B.C.) near Ashkhabad. Gromova (1949) is of the opinion that these animals may be kulans.

Kulan lived south of the Caucasus from the Lower Paleolithic Acheulean up to the present (Bate, 1937). Kulan fossils are also recorded from Paleolithic strata of the Barda-Balka cave in south Kurdistan.

332 On the basis of contemporary data, the wild ass (Figure 129) is undoubtedly a southern species which originated in the Eurasian semidesert and upland steppe.

The vague relationship of the Pleistocene ass, E. hidruntinus Reg., with the wild ass makes it difficult to establish when and by which routes the wild ass emerged on the Caucasian Isthmus. Up to now a direct phylogenetic link between these species was generally denied on the grounds that the wild ass had a more primitive dentition (Stehlin and Graziosi, 1935; Gromova, 1949). If we consider as an analogy related orders of Quaternary elephant, rhinoceros, horse and primitive bison, it is possible to conclude that the wild ass is a direct descendant of the Pleistocene ass. The claim of an autochthonous origin for the wild ass on the Caucasus follows from this conclusion. Remains of Holocene wild ass are known from several localities on the Caucasian Isthmus and in adjacent areas of the Russian Plain (Map 78). The oldest finds are from a settlement of the later half of the second millennium B.C. near Dzhemikent, south of Makhachkala; the latest finds are from 13th-century strata of a settlement in the vicinity of Baku bay.

Historical data on the wild ass on the Caucasus and in adjacent territories are fairly numerous. Xenophon (1896 edition) gives a vivid description of ancient Greek wild ass hunts; these wild asses lived together with ostriches in the wormwood steppes of the upper reaches of the Euphrates. The records of Moisei Khorenskii (1893 edition) state that Armenian kings of the Arsacid Dynasty (1st-2nd century A.D.) hunted onager (wild ass) and boar in the middle Araks valley. These records were recently discussed by Sarkisov (1946a) who mentioned that onagers had been recorded in Armenia in the "Code of Laws of the Armenian-Gregorian Church" in the Geography of Armenia by Ananiah of Shirak (7th century) and by Grigor Narekatsi (11th century).

Under the influence of Satunin's ideas, Sarkisov assumed that the mountain barriers eliminated all penetration routes into Armenia for the onager except one from the "Aral-Caspian lowland." Clearly, mountains are no barrier to this species, since, in historical time, onagers inhabited every intermontane valley that was even slightly accessible, including the uplands of southwest Asia.

Even more convincing are the arguments to substantiate the existence of the wild ass in Armenia in the book of mathematics by Ananiah of Shirak which is discussed by Ter-Pogosyan (1947).

The Armenian historian of the 10th century Moisei Kalankatuiskii (1861 edition) mentioned the wild asses inhabiting the Barda kingdom (in the contemporary Mil'skaya-Karabakh steppe). Nizami Ganjawi (12 century) praises the wild ass hunt in the Kura-Araks lowland. Rashid ad-Din (14th century, 1946 edition) mentioned that among the victims of the grand hunt organized by Gazan Khan in Talysh were wild asses. At the beginning of the 17th century Adam Olearius (1870 edition) recorded an onager hunt by the Iranian shah on onagers or Persian "gurs" in one of the sections of an enormous reservation in the vicinity of Iran's capital, Esfahān.

More recent data on the wild ass developed by Russian naturalists indicates that these animals inhabited only the area beyond the Volga during the time of Pallas.

Levanevskii (1894) gives a good description of the habits of this species in the region of the Kirghiz steppes of the Emba District. From this description it seems that the wild ass was common in the semidesert between Emba and the Urals even in the second half of the last century.
333 It was probably at this time that the wild ass population declined rapidly and the range shifted to the east and southeast. It is difficult to relate this shift and reduction in population only to the extermination of the animal with improved firearms or to an increase in human population. The Nogai and Kazakh retained their main weapons, percussion muskets and flintlocks, from earlier times. The increase of encampments was limited by the fodder capacity of desert and semidesert pastures. It is therefore probable that other causes influenced the dynamics of the animal population.

By the beginning of this century the wild ass was found in the U.S.S.R. only in the semideserts of northeastern Kazakhstan — Bet-Pak-Dala and Semirech'e. These animals disappeared from these areas and from southern Turkmenistan-Badchis in the 1930's. The peculiarities of wild ass distribution in the Iranian uplands and in Arabia are as yet unknown.

Taking into account the stenotopic character of the wild ass and its adaptation to desert-steppe topography, one can fix its appearance on the Caucasian Isthmus at the beginning of the xerothermic period. It may have penetrated northwards into Transcaucasia from the valleys and low ridges of northwestern Iran and into Ciscaucasia directly from the Russian Plain and indirectly from central Asia by way of the northern coastlands of the Caspian.

The broadest range of the wild ass existed in the Bronze Age. It is possible that the extinction of the wild ass in Transcaucasia coincides with the Mongolian invasion in the 13th century, and with the later growth of the Iranian [Persian] kingdom when the animals of the semidesert were destroyed in massive hunts. In northeastern Ciscaucasia wild ass survived until the 19th century.

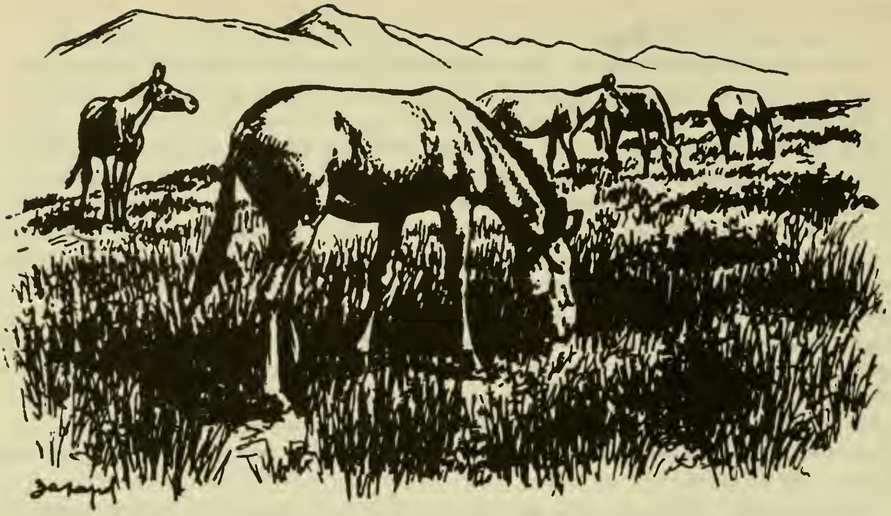

FIGURE 129. Kulans in the Pleistocene semidesert of eastern Transcaucasia

Order ARTIODACTYLA

Representatives of the families Suidae, Camelidae, Cervidae and Bovidae inhabited the Caucasian Isthmus in the Quaternary. Pig, deer and 334 Cavicornia existed there up to the Holocene. Paleontological and zoogeographical data will be examined in order to analyze the history of the range development and the evolution of Holocene species of artiodactyls.

Family SUIDAE

The fossil remains of Suidae, a bunodont nonruminant family, are known in Eurasia from the Lower Oligocene. The genus Sus, including the extinct subgenus Microstonyx, dates from the Lower Pliocene. Most of the fossil remains of Suidae were found in Upper Miocene and Pliocene deposits of the Mediterranean and southeastern Asia.

Boar — Sus scrofa L. (s. lato). Remains of pigs belonging to the polymorphic species S. scrofa occur on the Caucasian Isthmus from the Upper Pliocene. The ancestor of the present-day boar was probably the large Taman boar, S. tamanensis (Vereshchagin, 1951d).

The next stage of evolution is represented by remains of the Apsheron boar, S. apscheronicus Burtsch. et Dzhaf., from Middle Pleistocene loams of eastern Transcaucasia, recorded by Burchak-Abramovich and Dzhafarov (1948).

In the Akhshtyrskaya cave on the Black Sea coast, boar fossils were found in all strata from Mousterian to late Iron Age, their frequency increasing with time. Thus, in Mousterian strata they comprised 0.06%, in Upper Paleolithic 1.2%, and in post-Paleolithic 20.0% of the total number of osseous remains in each strata.

Boar existed in pre- and post-glacial time in Western Europe (Amon, 1938). North of the Caucasus on the Russian Plain, there have been single findings of boar in the Upper Pliocene and Middle Pleistocene deposits of the middle Volga region. During the Pleistocene the boar was probably very rare even in the river valleys of the Russian Plain, penetrating the area sporadically from the south in winters with a low snowfall. The rich fossil collections from the banks of the Don and the Volga contain only one jaw fragment of a Pleistocene boar (found on the Tunguz Peninsula), while from the Ural valley only remains of Holocene boars are found (Vereshchagin and Gromov, 1952). In general, a number of related facts indicate that the migration of boars from the Caucasus and their widespread settlement in the Russian Plain occurred only in the Holocene.

South of the Caucasus, in northern and central Iran, Palestine and Syria, boar fossils have been found in Paleolithic and post-Paleolithic settlement strata, although not frequently because of the predominantly dry topography of these countries.

In examining the contemporary characteristics of central Asian and Caucasian boar — a concentrated succulent vegetal diet taken from the soil or subsoil, short legs, relatively poor fur cover and poor adaptation to low temperatures and deep snow cover — it is evident that the latter features determined the distribution of this animal in the Quaternary. In this respect, Formozov's (1946) opinions on the "chionophobic" character of boars is perfectly reasonable. Under the varied climatic and topographic conditions of a mountain country such as the Caucasus, depth of snow cover,
335 would not, however, have been such a decisive factor and, in fact, would have permitted a satisfactory existence for boar on the Caucasus in the Quaternary.

Settlement strata and burials of the Bronze Age and later cultures on the Caucasus almost always contain remains of boars. They are especially common in the early settlements of the swampy Colchis near Anaklia and in the ancient towns of Kuban. An abundance of boar was characteristic of the Middle Ages. This is particularly true for the Don valley where remains of these animals comprise as much as 6% of all fossils collected in Slav and Khazar strata of Sarkel near Tsimlyanskaya. One can estimate to a certain degree the distribution and population of boar in the Caucasus during the historical epoch from art objects and literature. There are no representations of boars on ornaments and among burial provisions of the Bronze Age on the Caucasus; these are noted only from the later Scythian epoch. Spectacular boar representations (Figure 130) are found in burials of the Kuban area and the Taman Peninsula.

Moisei Khorenskii (1893 edition) mentions the boar hunts of the rulers of the Arsacid dynasty in the Araks valley in the 1st-2nd century A.D., which places them in ancient Roman time. In this description of the reign of Artavazd II and the war with the Romans (Book 2, Chapter 2, page 73) he said: "He indulged in food and drink; he wandered and rambled on bogs, in reed thickets, on steep slopes, hunting onagers and boars..." and further (Book 3, Chapter 55): "Another time we had a boar hunt among the burned reeds."

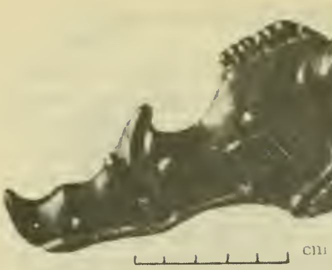

FIGURE 130. Representation of a boar on a bronze plate from the Semibratnoe burial (The Hermitage)

The decrease in the boar population and the restriction of its range was more rapid on the Armenian Highland because no religious prohibition was obtained against boar consumption and because the upland slopes were heavily deforested. Boar remains which can now be found on the shallowed shores of Lake Sevan show how abundant boars were on this upland in the past. Hunting was the chief operative factor in the disappearance of boar from [ancient] Christian Armenia, a fact that is pointed up by the contemporary existence of a large boar population in considerably drier regions of Iran and Turkey. In Georgia the many mountain forests and almost inaccessible swamps maintained a thriving boar population over a long time, and it was only the 19th and 20th centuries that saw the beginning of the rapid extinction of the species.

In Moslem regions, on the other hand, the development of agriculture, especially rice and melon culture, furnished a nutritional base for a stabilized boar population. The Lenkoran lowlands and the Samur forests are examples. In general, the spread of the Islamic population during the Middle Ages on the Caucasus was, perhaps, one of the primary causes of the extinction of the range and the population growth during historical times. Even now, there are more boars in Azerbaidzhan and Dagestan than in other places. One can judge the abundance of boars on the Caucasus in the 18th-19th centuries from the many notations contributed by Caucasian naturalists, students of local lore and travelers.

The rapid decrease in boar population probably commenced in the 1850's
336 after Russian settlement of the Caucasus. This decline was first observed on the lower Don, then on the Kuban and later on the Terek and Sulak.

Boars were already rare in the area of the Don estuary and on the Azov coast by the beginning of the 19th century, and they completely disappeared about 1812.

In the 1870's boars were still found in the forests near Stavropol (Dinnik, 1914a) from which they have completely disappeared in the 20th century.

Before 1900 the boar population on the northwestern Caucasus declined considerably because of the growth of settlements of Armenian hunters who hunted throughout the year.

A small number of boars inhabited the reed thickets of the Kuban as recently as 1932 in the vicinity of the Cossack villages of Grivenskaya and Petrovskaya. A local hunter would usually kill no more than ten of these animals per season.

In the 1930's a small boar population was encountered in the alder-grown bogs of the lower Rion between Poti and Samtredia — an area which had swarmed with these animals over many millennia. In general, western Georgia, Imeretia and Abkhazia supported only a small boar population by 1930.

In 1909 in the Karayazy forest east of Tbilisi, as many as 50 boars were killed during one hunting day. In 1911, 120 boars were killed in a two-day period (Kalinovskii, 1900; Markov, 1931a, 1935). Today it is hardly possible to kill five boars in Karayazy in a day.

In the Kura-Araks Plain the boar population fluctuated throughout the Quaternary period as the Caspian Sea level rose and fell and created breaks in the coastal ridges which resulted in the displacement of wormwood steppes by vast reed—cattail swamps and lakes.

Such a break of the Araks occurred in 1896 when vast floods of Akh-Chala occurred on the Mugan steppe (Shelkovnikov, 1907). Even today such adverse factors as the height of the Kura in flood, the extent to which the steppe lakes fill and the burning-back of reeds largely control fluctuations in boar population.

The booklet "Agriculture and Forest Economy of the Lenkoran District" (1914, pp. 21-22) contains the statement: "Ten years ago the number of wild pigs was so high that they became a real menace but when boar hunting became commercialized, the number of pigs was considerably reduced. Every year Armenians from the Elizavetpol Province came here to hunt wild pigs for their skins to use in the manufacture of shoes. Local Russian hunters kill the swine for their meat. For the last two years, about 5,000 skins were sent to Elizavetpol Province through Lenkoran."

During the 1930's the forests of northeastern Karabakh and the northern slopes of the Lesser Caucasus as far as Georgia did not contain boar. They were, however, encountered in the Akera-Chai valley and on the afforested northern slopes of the Zangezur Range where the local population was replenished by boars migrating through the Araks from the juniper forests of northern Iran.

Before the later 1940's, a vast tugai forest extended 70 km along the Kura River from the outlets of the Iora and the Alazan to Mingechaur; it was destroyed preparatory to the flooding of the Mingechaur Reservoir.
337 The boars which inhabited these tugai forests were either killed or relocated. In the 1950's, after the closing of the Mingechaur Dam, the tugai forests below Evlakh began to dry out rapidly and, as a consequence, disappeared from this area also.

The decline of the boar population in the last decades is visible even in Talysh where the mountain forests are thought to have abounded in boar.

On the whole, the decline of the boar on the Caucasus during historical time is a result of its being hunted, both as a valuable trade animal and as a pest. Anthropogenic changes in the landscape and epizootics were of secondary importance.

The present range of boars on the Caucasus is still important. They are observed all over the northern slopes of the Main Range and in the foothills, even near Kislovodsk and Nal'chik. There are few boars in mountainous Dagestan. The densest population is in the Caucasian Reservation, in the lower reaches of the Terek and the Sulak, in the Alazan-Agrichai lowlands, in parts of the Kura and Araks tugai forests and in Talysh (Map 80). In adjacent territory of Iran, the boar is most numerous on the northern slopes of the Elburz Range (Sarkisov, 1944e).

The vertical distribution of boar on the Caucasus extends from sea level to the alpine zone. The piedmont lowlands are inhabited more continuously; in the mountains distribution depends upon the availability of seasonal forage and the depth of the snow cover. According to the data of Donaurov and Teplov (1938), boars are observed in the following zones of the Caucasian Reservation (percentage/zone/year): broadleaf forest zone — 48%; dark coniferous forest zone — 39%; subalpine zone — 11%; and alpine zone — 2%.

Table 72 is based upon observations of the author's in 1935-36 in the Alazan valley and the Zakataly Reservation; percentages reflect fresh traces of boar (crouching imprints, evidence of digging, and excrements) observed in each zone or biotope.

TABLE 72. Incidence of boar tracks observed on the southern slope of the Greater Caucasus in Azerbaidzhan

Zones and biotopes	Percentage of total traces observed on prescribed 20-km route		
	August 1935	October 1935	January 1936
Lowland forests of Alazan	45	15	52
Foothills with fruit trees	32	35	33
Beech forests of the middle zone	10	32	15
Oak forest edges of the subalpine zone	10	28	—
Alpine meadows	3	—	—

In Talysh and the Lenkoran lowlands, lacking an alpine zone, the distribution of boar is somewhat different: in the mountain semidesert zones, where grain fields and fruit trees are plentiful near the upper forest edge, the boars concentrate in June and July, while in fall and winter they mainly inhabit the lowland and the middle forest zone. The daily activity cycle and
338 distribution of boar are influenced, not only by fodder availability, but by the degree and kind of hunting. In eastern Ciscaucasia and Transcaucasia, boars often couch in the vicinity of the railroad (Dinnik, 1914a), in gardens and among weeds growing in borders of cotton fields (in the Shirvan and Mugan steppes).

Where they are not hunted or disturbed, boars commence to feed at dawn and, in the reed thickets of the Kyzyl-Agach Reservation, they even wander by day. In places where they are constantly harassed, boars may feed only late at night, and before daybreak will travel sometimes as much as 10-15 km from their feeding ground to find couching places.

The animal's preferred biotopes in the eastern half of the Caucasian Isthmus are impassable thickets of tugai, lower forests of Caucasian olive and willow, bramble shrubs and reed thickets. These thickets are the primordial biotope suitable to morphological adaptations of the animal.

Any disruptions in the pattern of their horizontal and vertical migrations in search of food or an escape from deep snows cause the death of contemporary boars. Dinnik has recorded (1914a, pp. 47-48) episodes of mass mortality among boars in the 1880's and between 1902-1908 caused by deep snows, cold and hunger. It seems possible to us that this situation could have been created by their inability to migrate to the warm Kuban Plain.

They could have reached the Kuban valley from the region of deep snow of the mountain forests through stands of forest or tugai. But by the 20th century, their migratory instinct had been suppressed as the result of harassment and habitat modifications, such as human settlement and the deforestation of the piedmont plain.

In the 1940's the total boar yield on the Caucasus was 8,000: Azerbaidzhan — 4,000; northern Caucasus — 2,000; Dagestan — 1,500; Georgia — 300; Armenia — 200 (Vereshchagin, 1947d).

The future of the boar population of the Caucasus essentially depends upon the further development of the agricultural and forest economies.

Boars are pests in fields of corn, barley, wheat, rice and melons and where these crops are grown they will be exterminated or considerably reduced.

In eastern Transcaucasia the development of irrigation flood-control and cotton farming will inevitably reduce the boar population through the reduction of protective cover.

If hunting quotas were established boars could exist in the mountain forests of the Greater Caucasus and Talysh for an indeterminate time.

Family CERVIDAE

Pliocene strata of the Caucasus have been found to contain remains of representatives of the genera Eucladocerus, Procapreolus and Pliocervus, and Cervus, Dama, Megaceros, Alces and Capreolus specimens are known from post-Tertiary deposits. Of these, only Cervus elaphus, Alces and Capreolus have survived to the present.

Red deer — Cervus elaphus L. (s. lato). Fossils of the red deer group (C. elaphus) are known in Europe from the Pliocene. From
339 Mediterranean deposits ten different types of deer are recorded, but only from the Pleistocene. In the Caucasus the remains of these deer have been found from the Upper Pleistocene to the present.

For the most part these belong to the extant C. elaphus maral Ogilby. The location of the fossil remains (Map 83) indicate the wide distribution of this species.

North of the Isthmus C. elaphus was as common a settler of the floodplains and flood valleys in the Pleistocene as the primitive bison and the horse. In the Novocherkassk Museum its remains rank fourth after elephant, primitive bison and tur fossils. In riverbed deposits found on sand banks, bones of C. elaphus account for 3.3% of all the bones accumulated on the lower Don and 0.5 to 5.0% on the lower Kama and middle Volga.

South of the Caucasus on the Iranian Plateau remains of Pleistocene C. elaphus were found in Paleolithic and post-Paleolithic strata of many caves and in diluvium northeast of Maragheh. It is important to mention that in caves in the vicinity of Urmia and Behistun bones of deer account for 57% of the total number of extracted bones. In Mesolithic and Neolithic strata of the Belt cave in the eastern extremity of the Elburz Range there were few deer remains — only 0.8% (Coon, 1951). In the Neolithic strata of the ancient town of Annau in western Turkmenia deer remains are rare (Duerst, 1908). C. elaphus was a common food of Paleolithic hunters in Lebanon, Syria and Palestine. In spite of its frequent occurrence, there can be no doubt that the habitation of deer in southwest Asia was confined to river valleys and wooded slopes from at least the Pliocene.

Fossils of C. elaphus are as numerous in postglacial deposits as they are in Pleistocene deposits. In the Holocene loams of the Stavropol and Pyatogor'e areas, in the Yegorlyk, Kuman and Podkumok river valleys, and in talus fragments of the slopes and banks of Lake Sevan on the Armenian Highland, skulls, teeth and antlers are especially common.

These findings (see Chapter II) indicate that deer was widely distributed over the Ciscaucasian steppes and Transcaucasian plateaus, at least in the spring and fall and at the beginning of winter.

This earlier distribution of deer on the steppes should not be associated with a wide deforestation of these areas as Shelkovnikov (1930), Dal' (1947a) and others thought. In the spring—summer season deer do not require large forests; on the contrary, they migrate from the forests to steppe and meadow areas to escape from bloodsucking insects.

At present deer inhabit the Don, Volga and Ural valleys and adjacent steppe and forest areas. Doubtless the Caucasian population of C. elaphus was always related to the Eastern European population. In the strata of the Middle Ages in the Sarkel fortress near Tsimlyanskaya C. elaphus bones comprised 4.3% of all the fossils investigated.

During the post-Paleolithic C. elaphus was the favorite subject of painters and sculptors of the Caucasus; it was used in the decoration of
340 pottery, on arms and on clothes. Beginning with drawings on rocks in Kabristan (Figure 131), the deer subject is repeated in bronze pendants of Kobanian culture, in the ornamentation of Khodzhala and Sevan bronze belt buckles and especially in gold articles of Scythian-Sarmatian culture of the Trans-Kuban Plain and south Ukraine (Figures 132-133). Deer figured importantly in religious belief and rituals. According to legends of the Abkhazians and Imeretians, deer coming on the Feast of St. George to caves or chapels dedicated to the saint were killed for feasting (Dzhanashiya, 1915). In a number of Ossetian dzuars antlers and sacrificial skulls of deer predominate among the remains of other wild, hoofed mammals. All this indicates that the deer population during the postglacial period did not decrease as rapidly and catastrophically as did that of tur and bison.

Osseous remains of deer found in Quaternary deposits of steppe regions are often cited by naturalists as evidence of either a former steppe way of life or an earlier existence of forests in steppe regions. Recent observations of deer behavior and feeding habits and of the structure of the lower molars clearly indicate that the C. elaphus of Pleistocene and historical time was an inhabitant of the steppes, especially in spring and fall. During these seasons they grazed on the young grasses of the steppes, and at other times of the year inhabited the floodplains and oak forests in ravines. Deer were widely distributed in steppe and forest-steppe at least until the late Middle Ages. Guillaume le Vasseur de Beauplan (1832 edition, p. 92) noted flocks of deer in the Ukrainian steppes at the beginning of the 17th century: "Deer, fallow deer and saiga are encountered in flocks in the Ukrainian steppes." The present existence of deer on the steppe-pastures of the Askaniya-Nova Reservation gives credibility to this earlier report.

341 Shal'kovskii (1885, p. 189) also noted in his account of 18th-century Zaporozh'e that hunters "also caught hares, wolves and deer which, until 1760, inhabited the marvellous forests of the Trans-Dnieper Zaporozh'e."

FIGURE 131. Beyuk-Dag rock south of Baku showing representation of a deer hunt

Photograph by the author, 1946

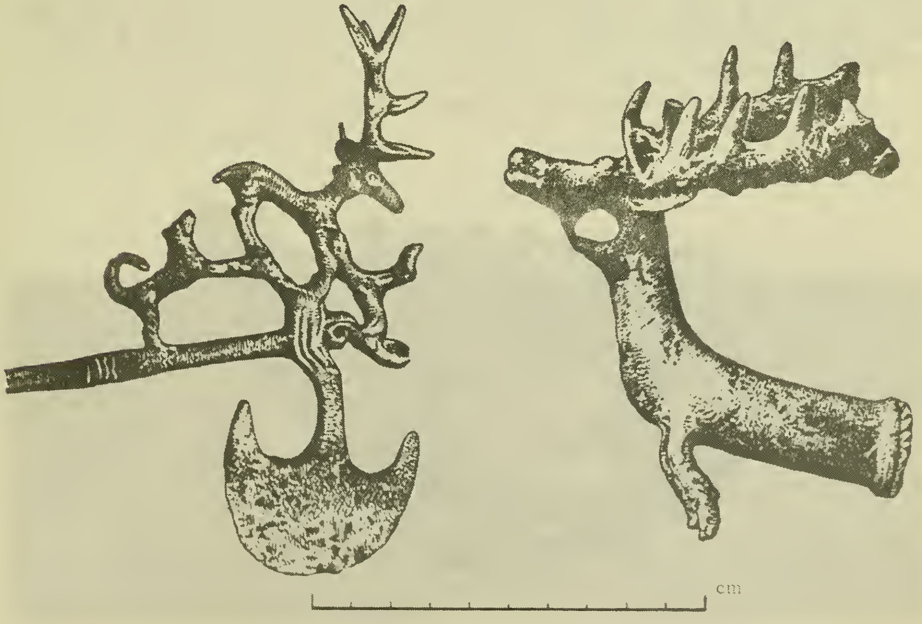

FIGURE 132. Kobanian artifacts from North Ossetia (Uvarova, 1900)

1 — bronze rod representing a deer hunt; 2 — deer head

During historical time a marked decline in the deer population can be traced to the development of cattle herding and agriculture. The greatest decline in the deer population of the East European and Caucasian steppe and forest-steppe zones, however, probably occurred when horses were domesticated and used in stag hunting. During the campaigns of the Scythians, Huns, Kipchaks and later the Mongolians, deer living on the steppes were rapidly decimated. It is possible that stag hunts forced the retreat of deer into the forests and forested foothills where they were out of reach of the mounted hunters. At the beginning of the 15th century, Josaf Barbaro (1836 edition) witnessed a Tartar "pagany" — mounted hunt — for bustards and other animals which formed an encirclement of 120 miles (!) "and [saw] deer and other animals escaping from the Tartars."

The first phase in the depletion of C. elaphus during historical times was the extermination of its steppe population.

The second phase of decline began in the late Middle Ages as a result of agricultural development and the rapid eradication of forests. This forest extermination was accompanied by desiccation and subsequent dwindling
342 of land in the Caucasian foothills and high plateaus.

Historical data on the distribution and yield of deer have been preserved since the 16th century. Georgian and Iranian chronicles and the ancient literature of Georgia, Azerbaidzhan and Iran mention the deer hunts. Thousands of peasant beaters and warriors took part in hunts organized by the Persian Shahs during the late Middle Ages in the forests of Gilan and Karabakh.

The populousness of deer in Mazandaran and Gilan in the 16th century can be reckoned from an end-of-the century account by Adam Olearius (1870 edition, p. 730): the Shah Takhmasp and his retinue killed 2,000 deer and goitered gazelles — "agu" — and he ordered the "building of a tower from their antlers."

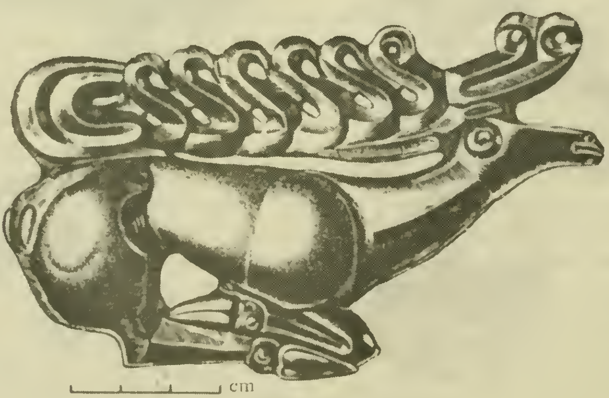

FIGURE 133. Scythian artifact from the Trans-Kuban Plain

Gold-plated reclining deer from a hill near the Cossack village of Kostromskaya

In "The Geography of Georgia" (1904), Prince Vakhusti reports that, at the beginning of the 18th century, the 94th czar, Vakhtang VI, and his entourage killed 180 deer in one day on the Trialet ridge southwest of Tiflis.

The historian Sekhnia Chkhaidze writes in "The History of Georgia" (1945, p. 408): "The Czar Vakhtang Levanovich (1703-1721) invited persons of high rank to a hunt in Trialetia and Shanbiani. The first day 60 deer and countless other animals were killed."

At this time deer still inhabited the reed-grown and forested floodplains of the Don, Kuban, Manych, Kuma, Kura, Terek and Sulak rivers.

The disappearance of deer from Ciscaucasia in the 17th and 18th centuries can be attributed to the settlement of the country by Cossacks and the widespread use of firearms. Dinnik (1914a, p. 97) reports that he found only fragments of antlers as evidence that deer existed there "60-70 years ago," i.e., in the 1850's and 1860's.

In the environs of Krasnodar and on the right bank of the Kuban, where they had been protected, deer still lived up to the early years of this century, when they were finally exterminated during the Civil War.

According to Dinnik (1914a) the northern limit of their range on the northwest Caucasus passed through the Cossack villages of Peredovaya, Kaladzhinskaya, Makhashevskaya and north of Maikop. The largest deer population was observed in the upper reaches of the Belaya, Bolshaya and
343 Malaya Laba rivers where 20-30 deer could be encountered in one day. In winter, deer ranged as far as Novorossiisk and Kabardinka. Later, the distribution area shifted southward. In the early 1930's, the northern range limit lay in the foothills along the line of the villages of Solenyi, Buguzh, Dakhovsk, Samursk, Neftyanaya and Navaginskaya. The range reached its western limits in the upper reaches of the Pshish River (Nasimovich, 1936a). In the 1940's deer could still be seen east of the Caucasian Reservation near the railroad stations of Predgradnaya and Mikoyan-Sakhar.

Rossikov (1887) tells of hunting deer on the piedmont plain north of Nal'chik as late as the 1870's.

FIGURE 134. Illustration of deer hunt in Digoria from "polati" [sleeping ledges or bunks] in the Digorized cave

Photograph by author, 1947

The last of the deer in the piedmonts of North Ossetia were exterminated (Figure 134) by the 1920's (Vereshchagin and Naniev, 1949). They survived for a longer time on the Sunzha tributaries near Gudermes and they are still found in tugai forests along the Sulak and Terek on the Dagestan plain.

In the Dagestan uplands deer were numerous in the gorges of the Avar Koisu. Many antlers have been found in burials in deciduous and coniferous forests near Antsukh [Bogaz Range] and Tlyadal, and in Khevrusetia [eastern Georgia] and Tushetia [Andi Koisu region] (Dinnik, 1914a; Maruashvili, 1955). The deer migrated to Dagestan from the southern slopes of the Greater Caucasus only in the summer to escape from bloodsucking flies, returning again in October or November to winter on the southern slopes. It is the practice of the Dagestanians to hunt them in the passes from Dagestan.

Deer had disappeared from the Samur-Khachmas lowland forests by the beginning of this century and, according to old-time residents of the village of Kusary, they were gone from the higher forests of the Kuban area by the 1880's.

In the Kura lowlands they could still be encountered in the tugai forests and reeds of the middle and lower reaches of the Kura River as late as the end of the last century. Older residents of the ancient village of Shil'yan and of the Shirvan steppe recall deer living along the reed-grown margins of the Lake Shil'yan, and a path through the reeds is still called "maral gel" or "maral elu" (deer path). Deer was already rare in Talysh by the time of Radde, Satunin (1905b) and Dinnik (1914a). According to the Azerbaidzhan Game Inspector, V. V. Vitovich, the last deer in Talysh was
344 killed in 1912.

In Karabakh, deer had disappeared from the Dzegam and Shamkhor ravines by the 1920's. Melik-Shakhnazarov (1898) reported that in the 1890's in Zangezur deer were so abundant that some hunters killed 150-200 head a year. Osipov (1898) tells of deer being common in his time in the vicinity of Chaikent (south of contemporary Kirovabad).

In the 1930's and 1940's some deer still survived in the Karayazy forest on the Kura River where in the 1890's 15-20 specimens had been killed in one day.

In western Georgia, deer were either exterminated or driven into the mountains from the lower Rion, Kodor and Ingur by deforestation at the start of World War I.

The present range of C. elaphus is comprised of four or five isolated tracts (Map 83), the largest of which is located in the northwest and includes the Caucasian and Teberdinskii reservations in the Pshish, Kurdzhips, Belaya, Laba, Malyi Zelenchuk, Bolshoi Zelenchuk and Kuban river basins. In the summer, most of the deer inhabit open places in the fir forests in the interior of the Caucasian Reservation at altitudes of 1,700-2,200 m. Their winter habitats are found in sunny places on the slopes and in the valleys of the lower fir belt and the beech-forest zone with a snow cover of 0.3-0.5 m. After the sharp decrease during the Civil War, the deer population commenced to rise again. A 1934 census (Nasimovich, 1936a) showed a total stock of 900 head. By the 1940's, there were at least 3,000 head of deer in the Caucasian Reservation.

In northeastern Ciscaucasia deer survived in forests and reed-grown areas of the lower Terek from the Cossack village of Chervlennaya to Kizlyar, and on the Sulak from Khasavyurt to the lower river.

These deer live the year around in the tugai stands of the lowlands, because there are no longer any alternative locations open to them for migration: the northern foothills of Dagestan are now deforested and populated.

In western Transcaucasia a small deer population still inhabits the forests on the middle course of the Ingur. In the beech forests of the Borzhomi Reservation (on the eastern spurs of the Adzhar-Imeretia Range), El-Mar (E. L. Markov, 1939) counted almost 900 head of deer in 1934. The summer habitat of the Borzhomi deer had previously been located on the high, cold, deforested plateaus of the Dzhavakhetia and Akhalkalakhi uplands. In eastern Transcaucasia deer are found in the Karayazy forest and on the southern slope of the Main Range from the upper Alazan to the Gerdyman-Chai. The largest deer population has been observed in the Zakataly Reservation in the Belanukh-Chai and Katekh-Chai basins; it was estimated in the 1940's at 1,000 head. To the east, in the Kutkashen and Ismailly districts, deer are numerous both in the mountains and on the plain, and can be encountered near Chukhur-Kabala, Ismailly, Kalandzhak, Rushan-Kend and other villages.

Our own observations made in the 1930's showed the summer habitat of deer to be on the southern slopes of ridges in the upper third of the beech forest zone and in the subalpine zone. If there were no cattle or dogs, they would venture onto the pastures. In the winter they inhabited beech forests in the middle altitudes of ridges with southern exposures.

During winters with a heavy fall of snow deer sometimes appear on the 345 open hilly steppe south of the Shemakha. This habit and the year-round existence of the Sulak population in reeds and tugai explain why deer remains were found together with those of ass and saiga in Pleistocene deposits on the Apsheron Peninsula. Notwithstanding its earlier history and these present variations, the contemporary C. elaphus must be regarded as a mountain-forest species, not accustomed to remote migrations to the plain. The differences between various deer populations in habits and in the directions their migrations take merely testify to the great adaptability of the animal and require a correct reading of its contemporary behavior as a response of its higher nervous system to human influence.

During the 1940's poachers on the Caucasus averaged an annual bag of 200-250 deer (Vereshchagin, 1947d).

The Caucasus is the chief deer preserve in the U.S.S.R. The subsequent fate of the species in this region will depend upon the effectiveness of measures taken for their protection. If poaching is controlled, it will allow renewed breeding in the forests of Karabakh, Talysh and the Kusary sloping plain. In addition, it should be possible to resettle Caucasian deer in the future in the floodplain and watershed forests of the Russian Plain.

Fallow deer — Dama cf. mesopotamica Brooke. Fossil remains of fallow deer similar to the Mediterranean D. dama L. are recorded from Pliocene and Pleistocene deposits in Italy, England and Germany.

A fragment of mandible and a fragment of antler discovered on the Caucasus in Pleistocene alluvium at Adzhi-Eilas near Yerevan are unique and can be reported here as D. mesopotamica only conditionally.

In southern Asia Minor and Palestine fallow deer was the most frequent bag of Paleolithic hunters (Bate, 1937).

FIGURE 135. Bronze head of fallow deer from Semibratnoe Scythian burial (The Hermitage)

Artistic representations of Mediterranean fallow deer heads in bronze (Figure 135) were found in the Semibratnoe Scythian burials on the Taman Peninsula, and also in burials in the southern Ukraine. This is a basis for presuming that the distribution areas of the two species, i.e., Mediterranean and Mesopotamian, encompassed the southern Balkan Peninsula, the Black Sea area, Asia Minor, Iraq and Iran (Map 82). The fallow deer is an inhabitant of broadleaf forests and thickets and of the undergrowth of Mediterranean river valleys. The species is more thermophilic than Cervus elaphus.

By the beginning of the 20th century, the fallow deer was nearly extinct in its natural range; it has since been bred under protected conditions throughout Western Europe and north Africa (Ellermann and Morrison-Scott, 1951).

A successful experiment in breeding fallow deer was carried out on the Caucasus near Borzhomi before the revolution (see Chapter VI).

Through future regulation of hunting, the fallow deer can become a worthwhile element in the piedmont shrub-forest zone of the Caucasus. It can populate the forests of Stavropol, the Dagestan piedmont, eastern Armenia, the Nakhichevan A.S.S.R. and the Nagorno-Karabakh uplands.

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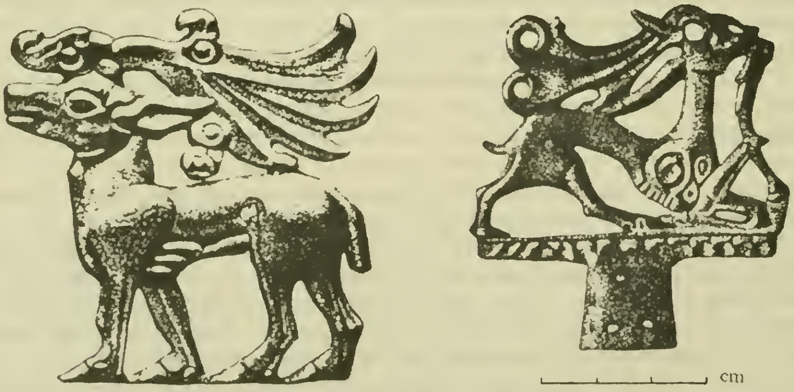

FIGURE 136. Golden plates from Scythian burial with representations similar to giant deer. Berlin Museum (Bachofen-Echt, 1937)

Giant deer — Megaceros euryceros Aldr. Upper Pliocene remains of this deer have been found throughout Eurasia.

In the Pleistocene the distribution area of M. euryceros included the forest-steppe and the steppe zones of Europe and Asia. Its remains are especially common in Khazar strata of the Volga valley, where they are found on the banks and comprise 2–8% of all the bone material. They are also common in Pleistocene strata of Western Europe. On the British Isles fossils have been found in caves, diluvium and peat beds. Some paleontologists, reasoning from 12th-century drawings and the rather fresh remains found in Irish peat beds, view M. euryceros as an inhabitant of Ireland up to the time of the present era (Mitchell and Parkes, 1949). The European continent lacks such recent remains indicating that the species was probably extinct here in the Upper Pleistocene. However, Pidoplichko's report (1951) of a find of M. euryceros remains in the U.S.S.R., which, according to the bone calcination, showed a Recent origin, deserves further attention and verification.

Kitchen middens containing M. euryceros remains, which are common in Paleolithic caves of the Crimea, are completely unknown from the caves of Palestine, Syria and Lebanon. On the Caucasus Isthmus, fossils have been found from the Upper Pliocene — on the Taman Peninsula, through the Mousterian — in Abkhazian caves and camp sites on the Trans-Kuban Plain (Map 82). M. euryceros inhabited Abkhazia in a mountain mesophytic environment.

The species is rarely found in Pleistocene strata of the eastern Transcaucasian steppes, and in the Binagady asphalts only one bone among tens of thousands was identified as M. euryceros. No remains of giant deer have been found in Holocene deposits, even those as large as the Lake Sevan shore and the Sarkel strata of the Middle Ages. It is not depicted in any Caucasian Paleolithic or post-Paleolithic drawings and scuptures. Stylized representations of Cervus elaphus in gold plate taken from Scythian burials on the Trans-Kuban, which somewhat resemble representa-
347 tions of M. euryceros (Figures 136, 137), led Bachofen-Echt (1937) to the erroneous assumption that giant deer existed on the Caucasus in the first millennium B.C.

FIGURE 137. Skull of Megaceros euryceros from the environs of Rostov-on-Don

The usual osseous deposits containing M. euryceros found in flood-plains and peat beds reveal an ecological similarity to the elk. The structure of metapodia and especially of hoof phalanges place the species in a position intermediate between elk and ox. It could probably endure a deep snow cover, but could not undertake long marches in the snow like the elk. It was an inhabitant of the cold forest-steppe and the river valleys of the plains, living in floodplain forests and thickets together with Elasmotherium and Elaphus trogontherii.

Caucasian elk — Alces alces caucasicus N. Ver. Remains of elk of the A. alces L. group are recorded from Pleistocene deposits of the northern Holarctic, but are rarely reported south of the 50th parallel. In the western Mediterranean Pleistocene deposits seldom contain elk, although other species of the Alces genus are sometimes so identified (Wolf, 1938; Pidoplichko, 1951 — map, p. 79, reports all findings as A. alces). Earlier reports on finds of elk remains in the Paleolithic of Palestine, Syria and Lebanon (Blanckenhorn, 1910) were in error (Picard, 1937). The same may be said more emphatically for Egypt. North of the Caucasus remains of Pleistocene elk have been found at Borshevo II, the encampment site near Voronezh, and on scarps of the Volga bank near the village of Osypnoi Bugor beyond Astrakhan. The species does not occur in the Crimean Paleolithic. On the banks of the middle Volga and especially of the lower Kuma, elk remains generally account for 5% of all the large-species bones.

On the Caucasian Isthmus elk remains are recorded for the Upper Pleistocene (Upper Paleolithic) from cave strata in western Transcaucasia from Khosta to Kutaisi.

The Mousterian strata of the Akhshtyrskaya cave, the Il'skaya encampment and the Apsheron Peninsula asphalts revealed no remains of elk. It would be justifiable to conclude that the elk first penetrated the Caucasus from the north in the Upper Pleistocene, although it is equally possible that the development of the ancestral form could have taken place on the Caucasus, or, for that matter, anywhere in the eastern Mediterranean. In either case, it is a matter of established fact that the elk survived the Upper Pleistocene on the Caucasus and became extinct only at the beginning of the 19th century.

The presence of elk on the Caucasus during the Bronze Age can be assumed from bronze buckles and pendants of Kobanian workmanship found in archaeological excavations in North Ossetia (Uvarova, 1900, p. 80,
348 Figure 75; Vereshchagin, 1949a). In the collections of the Moscow State Historical Museum there is a bronze buckle with a design of two elk heads which was excavated near the village of Atage in the Sunzha valley and belongs to the second period of Koban culture (Figure 138). An interesting relief resembling an elk is carved on a stone from Euyuk, a Hittite town which existed in the first half of the second millennium B.C. in northeastern Asia Minor. This suggests the possibility that south of the Caucasus elk inhabited forested tracts in Asia Minor in historical time.

Representations of elk appear in gold and bronze (Figures 138, 139) and on the ornamentation of quivers found in burials on the Trans-Kuban piedmont plain and in the southern Ukraine.

Finally, Keller (1909) reported the find of gold pendants depicting elk in ancient Greek settlements on the northern shore of the Black Sea.

All the elk representations of the Scythian epoch are of great importance, not only in reconstructing the early range of the elk, but also in assigning the origin of gold and bronze artifacts from Scythian burials with ornamental and relief designs of animal subjects. Taking into account that the southern margin of the elk range in the Holocene passed through the Caucasus and the northern Black Sea area, it becomes apparent that most of these Scythian artifacts were in fact produced at their cultural source — in Scythia — rather than, as often assumed by historians and archaeologists, in the southern Balkans, Asia Minor or the Aegean Islands.

FIGURE 138. Bronze buckle with elk head design from the village of Atage on the Sunzha (Moscow State Historical Museum)

FIGURE 139. Bronze plate depicting an elk's head (1:2) from the southern Ukraine

There are references to Caucasian and southern European elk in the literature.

Jean de Luc (1879 edition) in his description of a journey into the Nogai Tartar territory at the beginning of the 17th century tells of seeing elks, in addition to wild horses, deer and other animals. Clarke's reference 349 (1810, p. 386) to two young and very tame "elks" which he saw near Ekaterinodar should certainly be assigned to deer rather than to elk, and Kirikov was wrong to use this citation (1952) as proof of the earlier existence of elk on the Caucasus.

Pallas (1831) reported in his "Zoography" that elk was found on the Caucasus, and Lul'e (1870), in his description of the beliefs and customs of the Circassians, wrote of Mezitkh, their god of the forests, who rode on a boar with golden bristles. At his nod, "deer and elks assembled in the forests, and then young maidens milked the does."

The presence of elk in the contemporary fauna of the Caucasus was later denied, however, by the best zoologists (Dinnik, 1896, 1914a; Satunin, 1903b). Satunin wrote: "Thus he (Pallas) placed even the elk (Alces alces L.) on the Caucasus, although there can be no doubt that this species never inhabited the Caucasus." In our time, Kulagin (1932) and Buturlin (1934) expressed doubts about the occurrence of elk on the Caucasus. Kulagin's reservations, which he bases on Polferov's story, "Eznos", are really only tenuously connected with it. In fact, Polferov mentions encounters with elk and capercaillie somewhere in the taiga zone, and not on the Turkish border as Kulagin surmised.

In the 1930's elk bones were found in archaeological excavations of 8th—12th-century towns near the Cossack village of Tsimlyanskaya on the lower Don. Figure 140 shows a semi-fossilized skull of ancient elk identified by the author in the Stavropol Museum collections in 1944. While investigating Ossetian dzuars in the Urukh Basin in 1947, we found seven elk skulls (Figure 141). These findings establish that the elk inhabited the foothills of the northern Caucasus contemporaneously with the primitive bison, both becoming extinct at the beginning of the 18th century (Vereshchagin and Semenov-Tyan-Shanskii, 1948; Vereshchagin, 1949a, 1949b, 1955; Vereshchagin and Ganiev, 1949).

FIGURE 140. Semi-fossilized skull of elk in the Stavropol Museum

Photograph by author, 1945

Ritual collections containing remains of elks, similar to those of Digoria, are probably to be found in other gorges of the northern slopes of the Greater Caucasus, particularly on the Balkar-Cherek.

350 Even during the time when the Ossetian dzuars of Digoria flourished and skulls and horns were being accumulated in them in quantity, elk was already rare by comparison with deer and even bison. The seven skulls of elk found in our investigation of 16 dzuars were in a 10% ratio to bison skulls and 0.8% to deer skulls. The extinction of the species was brought about through direct extermination and through the general destruction of forests on the Terek-Sunzha plain. It is possible that the last of the elks survived until the beginning of the 19th century.

During the 1950-1951 excavation of the Sarkel fortress on the lower Don carried out by The Hermitage (Artamonov, 1952), kitchen middens were found to contain many remains of elk, together with remains of deer, boar, saiga, bear and beaver. The elk remains comprised 0.3-0.8% of all the bones of domesticated and wild animals found during the excavations.*

Elk remains were also found recently, together with those of reindeer, in the Roman strata of Olvia (Pidoplichko and Topachevskii, 1953).

A. A. Sadovskii has reported (through a verbal communication) his observation in 1937 of a mandible of elk among a large quantity of wild ungulate bones, including deer and roe deer, which had been uncovered during the excavation of the ancient burial of Naokhvami in Mingrelia. The relict alder swamps in the lower reaches of the Rion with thickets of osier and buckbean are even today an ideal elk habitat.

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* K.B. Yur'ev, G.V. Khrabrov and others investigated 200,000 bone fragments under my direction in Sarkel in 1952-1953.

FIGURE 141. Skull of elk from the Digorized cave

Photograph by author, 1948

The recent existence of elk in the Trans-Kuban was confirmed by the find of a horn (Figure 142) in the pebbles of the Urup River near the Cossack village of Otradnaya. The horn is preserved in the Krasnodar Museum; although wind-eroded on the surface, the inside shows it to be quite recent.

If the elk settled on the Caucasus from the north during the Upper Pleistocene, it can be assumed that the principal penetration route of the species passed southward through the valleys of the Don and the Volga. However, the possibility of an immigration route from the southwest through the Balkans and Asia Minor cannot be excluded. The distribution of elk on the Caucasus was probably limited by the foothills (Map 84). Their chosen biotopes (Figure 143) were along spring and swamp 351 rivers of the Trans-Kuban and Terek-Sunzha plains, on the littoral terraces of Abkhazia and in the lowlands of Colchis. As opposed to C. elaphus, the elk did not adapt to the Caucasian Range and to the mountain-forest environment.

When the lumber and hunting industries of the country are regulated, it will be possible to resettle elk on the Trans-Kuban sloping plain in the valleys of the Afips, Psekups, Laba and Zelenchuk rivers. It is also possible that the species might be successfully settled in young mountain forests of pine, aspen and willow in the Teberda and Caucasian reservations.

Roe deer — Capreolus capreolus L. and C. capreolus pygargus Pall. The genus Capreolus is of Middle Pliocene origin (Simpson, 1945). The ancestor of the contemporary genus is probably Procapreolus which is known from the Lower Pliocene of Europe and Asia. Flerov (1952, pp. 98-99) considers that the contemporary roe deer is the descendent of Mio-Pliocene Cervulinae.

The infrequently found remains of small European roe deer derive from various types of Quaternary deposits in Europe and Asia, almost all of them within the limits of the contemporary range (Wolf, 1938; Pidoplichko, 1951). For the Caucasus, roe deer remains are recorded from Upper Quaternary travertines of Mount Mashuk and from Transcaucasian cave strata, Acheulean to Recent, at Kudaro II, Akhshtyrskaya and Gvardzhilas caves and others. A large form of C. pygargus has been recorded from further south for Palestine, Syria and Lebanon from Acheulean to Neolithic cave strata (Picard, 1937; Bate, 1937).

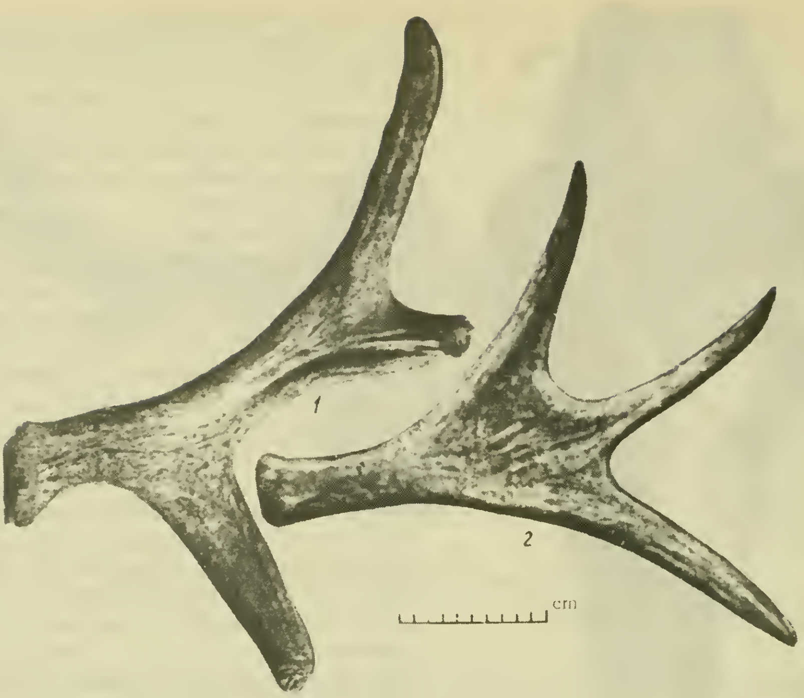

FIGURE 142. Horns of elks:

1 – from the strata of the Sarkel fortress on the Don; 2 – from the pebbles of the Urup River

On the Russian Plain remains of a large roe deer were found in Upper
352 Paleolithic strata of Kostenki on the Don and in Upper Quaternary alluvium of the middle Volga region (Khryashchevka). To the west, in the Ukraine and the Crimea, only remains of smaller specimens were discovered in Paleolithic strata. Roe deer remains are numerous in Holocene deposits of the Caucasus, e.g., in Copper—Bronze-Age strata of camp sites near Anaklia, in post-Paleolithic strata of the Akhshtyrskaya cave, etc. (Map 85).

During the excavations of the Sarkel fortress on the Don remains of the large Siberian roe deer were found in 8th—13th-century strata. The North Ossetian dzuars, e.g., the Digorized cave, contain preserved skulls and horns of small roe deer of C. capreolus type hunted in Urukh between the 15th and 20th centuries.

Roe deer is seldom depicted on artifacts left by the ancient Caucasian tribes. One of the rare examples is a silver bucket from a Bronze Age burial on the Trialet ridge which bears a contour representation of a roe deer wounded in the chest by arrows (Kuftin, 1941).

The range of roe deer on the Caucasus in the Recent has continued to be widespread, and today the species is better preserved than other ungulates. A larger form, similar to the Siberian, inhabits the northern Caucasus (Dinnik, 1914a), and a small form is found in Transcaucasia. The roe deer does not occur in the reedlands of the lower Don and Kuban. It is certain that, as late as the Middle Ages, the Caucasian range of the large roe deer was connected with the range of the large Siberian roe deer along the Don valley. The presence of the large roe deer in Ciscaucasia can probably be explained by a relatively recent postglacial migration from the north.

FIGURE 143. Caucasian elk

The ultimate disappearance of roe deer from the island forests near Stavropol took place in the 1920's. There are few of these animals remaining in the broadleaf forests of the Trans-Kuban sloping plain between 353 Khadyzhensk and Maikop. But on the northwestern spurs of the Greater Caucasus, they are still populous in beech—hornbeam forests (e.g., near the Goryachi Klyuch and Krymskaya).

TABLE 73. Distribution of roe deer in the Zakataly Reservation based on number of tracks encountered daily in summer and winter

Date	Southern spurs; beech—hornbeam and aspen forests with glades; 700-1,800 m	Deep gullies in ravines; beech forests; 1,200-1,600 m	Upper forest belt and subalpine meadows; 2,000-2,400 m
22-26 August 1935	8	2	1
21-26 November 1935 (snow: 15-30 cm)	16	3	—
1 January 1936 (snow: 30-50 cm and more)	7	1	—

In Kabardino-Balkaria and North Ossetia, roe deer inhabit the forests of the Chernye Gory, the canyons of the Skalistyi ridge and the sparse forests on the northern slopes of the Terek Range. They are not found in the Sunzha valley, but have been observed in the tugai along the Terek and Sulak between the Cossack villages of Chervlenaya and Kizlyar. The forests of the piedmont spurs of the Grozny Region contain a roe deer population, but the area near Makhachkala does not, and the many wolves in the reedlands of the lower Sulak and Terek preclude the habitation of roe deer there. Neither are they numerous in the forests of the Kusary sloping plain. On the whole, the distribution of roe deer on the northern slopes of the Caucasus reaches its summer limits at altitudes of 1,500-2,000 m. In the winters when the snowfall reaches disastrous proportions the animals descend to the piedmont plains, sometimes even venturing into the villages of the Maikop area (Olenich-Gnenenko, 1955).

In western Transcaucasia, the population of roe deer is sparse in the lower forest belt because of the dense network of villages; it is heavier in the middle third of the forest zone. The snowfall in the upper Svanetian gorges, e.g., on the Ingur, is too heavy to support the existence of roe deer there.

A small population inhabits the Colchis alder swamps near the Chaladidi station and on the middle course of the Pichora River, where Poti hunters kill as many as 50 animals yearly. Roe deer is common on the northern slopes of the Adzhar-Guri Range and the Trialet ridge. On the southwest, its range extends to Asia Minor. In Palestine roe deer was still common in the last century in the Carmel Mountains where the last specimen was killed in 1912 (Bodenheimer, 1935).

In east Transcaucasia it is found on the southern slopes of the Main Range inhabiting mainly the lower third of the forest belt where there are thickets of Cornelian cherry, hawthorn and hornbeam, or the glades of beech—hornbeam forests overgrown with giant fern and blackberry.

In 1935 we made the following observations of fresh roe deer tracks on rivulet shoals and in the snow in the Zakataly Reservation as they were distributed altitudinally along the Tala-Chai and the Katekh-Chai. (Table 73).

354 On the Alazan-Avtaran lowlands the habitat of roe deer is confined to the oak—Caucasian-wing-nut forests, and the population is greater in winter than in summer. The species does not inhabit the tugai, reedlands and oases of the Kura-Araks lowlands.

On the Lesser Caucasus roe deer can be found wherever there are large stands of deciduous forest. In summer it inhabits subalpine tall-grass meadows near relict forest islands at altitudes of 1,800 and 2,000 m in the gorges of the upper Debed and Akstafa rivers.

In Karabakh many roe deer are to be found in the Terter-Chai beech forests. They are not encountered on the southern slopes of the Armenian Highland.

In Talysh and in the forests of the El'brus Range, the few deer live in isolated colonies in well-defined areas of some of the gorges. Only single tracks could be observed in the Vassaru-Chai and Vilyash-Chai ravines in our investigations during June and July of 1945.

Broadly stated, roe deer is frequently found on the Caucasus, but never in the numbers in which it is found in the piedmonts of northeastern Tien-Shan or the Maritime Territory.

In the Iranian uplands, roe deer are sparsely settled in relict forest islands. According to Blanford (1876) roe deer inhabited only the forests of Asterabad. The southern margin of the species range probably lies in the passes of northern Mesopotamia.

Although the principal range of roe deer is now located in northern Eurasia, it can certainly be regarded as an Upper Pliocene species of the Caucasus whose closest ancestors are to be found in the Lower Pliocene of Transcaucasia and throughout the Mediterranean.

The roe deer is adapted to a forest habitat and a diet comprised mainly of leaves; it has the capacity for very swift movement and high jumps in shrubs and tall grass; it does not endure deep snow.

The rapid decline of the roe deer population and range on the Caucasus occurred in the last century as a result of unrestricted hunting and deforestation (see Chapter VI).

The present yield of roe deer is estimated as follows: northern Caucasus — 4,600; Azerbaidzhan — 1,500; Georgia — 700; Armenia — 300; Dagestan — 200 (Vereshchagin, 1947d).

The development of agricultural shelterbelts in the Ciscaucasian plain will undoubtedly create ample opportunities for the breeding of roe deer in a cultivated landscape.

Family **BOVIDAE**

The Quaternary fauna of the Caucasian Isthmus includes representatives of the sub-families Bovinae, Antilopinae and Caprinae. Seven genera occur in the Holocene fauna: Gazella, Saiga, Rupicapra, Capra, Ovis, Bos and Bison.

Goitered gazelle — Gazella subgutturosa Güld. Fossil remains of a number of Gazella species are known from the Upper Miocene-Lower Pliocene. The genus is generally regarded as a Miocene species. Fragments of horn stems and teeth of gazelles, which show some similarity to the Mediterranean Pliocene G. deperdita Gerv., have been found on the Caucasus in Sarmatian deposits near Georgievsk, in Middle Pliocene sandstones south of Baku and in Lower Quaternary strata of the Taman Peninsula.

355 In addition, a fragment of horn core which resembles goitered gazelle horn was found in postglacial loams in the upper reaches of the Kalaus, southwest of Stavropol (Ryabinin, 1918).

Remains which are true to goitered gazelle type were reported for Pleistocene strata of the Tamtama and Bisotun caves in central Iran (Coon's excavations, 1951), for Mesolithic strata of caves near Dzhebel and Krasnovodsk (Okladnikov's excavations, 1949) and for Anau strata near Ashkhabad (Duerst, 1908).

Picard (1937) and Bate (1937) have recorded remains of gazelle similar to G. gazella Pall., G. dorcas L. and G. subgutturosa from Paleolithic cave strata (Acheulean to Upper Neolithic) of Lebanon, Syria and Palestine. No fossil remains of goitered gazelle have been found in Pleistocene deposits of the Russian Plain nor in the Middle and Upper Pleistocene of eastern Transcaucasia. Validated finds of goitered gazelle remains on the Caucasus are recorded only from Holocene strata of the historical age in Ciscaucasia and Transcaucasia (Map 87).

Goitered gazelle remains are particularly numerous in the strata of ancient Baku in which they account for 14.5% of all the bones found. Their ratio to sheep and goat bones is 3.9:10.

Most of the present range of goitered gazelle lies within northwestern Iran and Afghanistan and the deserts of central Asia.

The absence of goitered gazelle in the Binagady fauna of the Middle Pleistocene and the frequency of its occurrence in Holocene strata of the eastern part of the Isthmus lead to the conclusion that the species appeared relatively late in postglacial time replacing the saiga in Azerbaidzhan. It probably penetrated directly from the south through the ranges of northwestern Iran which border the Mugan steppe on the south. This extension of the range would have been possible in the dry, warm phase of the Holocene. There is also the possibility that the species was imported to the Kura lowlands by ancient nomadic tribes which spent the summer in the northern Iran uplands and the winter on the Mugan steppe.

Cattle herders on the Mil'skaya and Mugan steppes capture young goitered gazelles which are easily tamed and tether them close to their tents. In Syria, Palestine and Lebanon and throughout the Near and Middle East newborn gazelles were caught each year by the thousands for domestication or for their meat. Usamah ibn Munkidh (1922-23 edition, p. 204) described the hunting of gazelles: "When young gazelles are born, the hunters go on foot and take the young which were born that night, the previous night or two or three nights before. In one day, 3,000 young were caught near the Dzhabar fortress." Young adult gazelles were sent as gifts to chiefs and princes, sometimes over very long distances.

The pursuit of goitered gazelles by Median, Albanian, Persian, Arabian and Mongolian horsemen was probably one of the causes of the separation of the species range on the plateaus and its penetration into isolated valleys. Even now when gazelles are hunted on horseback or in automobiles over long distances, it can be observed that they will seek refuge in solonchak, tugai and reed thickets or escape into creek valleys or onto the slopes of clayey ridges. From these places they emerge one or days later onto the
356 open plain because they are frequently vulnerable to attack by wolves in the thickets and mountains.

Ancient writings give evidence on the large population and area of distribution of goitered gazelle in eastern and southern Transcaucasia in the Middle Ages. Nizami Ganjawi (13th century A. D.) frequently employed the goitered gazelle as a poetic metaphor.

Olearius (1870 edition) mentions herds of goitered gazelles which he observed in 1633 near Dzhevat [near present-day Sabirabad] on the Mugan Steppe and commented on the abundance of these animals on the adjacent Iranian Plateau. In the 18th century goitered gazelle existed on Svyatoi Island (now Artem Island) which they had reached either through importation by Arabs for breeding purposes or in a migration from the Apsheron Peninsula during some postglacial drop in the Caspian Sea level. They were observed there in 1720-1724 by Soimonov who wrote (1763, p. 110): "However, the island is inhabited by many wild goats which reproduce there and it is not known what their food is if not mosses growing on stones." ..."December 3 (1724)... whereas on Svyatoi Island Don Cossacks with their general killed some wild goats."

Academician Dorn (1875) noted that Svyatoi Island was called by the Arabs "the island of steppe sheep." Goitered gazelles were observed in the Araks valley in the middle of the last century by Nordman (1840) and Chopin (1852). They were exterminated in this area only in the second half of the century through game drives.

The species is adapted to a habitat on level semidesert with a solid footing (for details, see Vereshchagin, 1937). The animal's great speed (up to 50-55 km/hr) permits easy escape from wolves and even cheetahs, except on a boggy soil. It is not found, therefore, on newly plowed or especially on irrigated soils. Goitered gazelle does inhabit barley and wheat fields on the Adzhinour Plateau, but only those that are not irrigated and whose soil is more or less compacted.

While the goitered gazelle is more numerous on level steppes, it is also encountered in the Tertiary hills of Dzheiran-Chel, Boz-Dag, Turut-Sarudzha and Kabristan — areas of rugged relief with mountain xerophytes. Deep frosts and heavy snowfalls bring mass mortality to goitered gazelle inhabiting the Kura lowlands (Vereshchagin and Dyunin, 1949). In general, the goitered gazelle is a chinophobe because it cannot reach food under the snow nor move rapidly over a deep snow cover. This characteristic also confirms its recent migration to Transcaucasia from the south.

Fluctuations in the Caspian Sea level, breaches of the coastal ridges and the flooding of the Kura and Araks rivers, as well as changes in the nomadic and settled populations of eastern Transcaucasia and in their agricultural techniques, have produced far-reaching changes in the range and population of goitered gazelle in this area in historical time.

In the 1920's, the distribution area of goitered gazelle coincided with the saltwort solonchak-semidesert and andropogon steppes, and reached nearly to Tiflis on the west.

The sharp population decline and the shrinkage of range in eastern Transcaucasia began in the 1920's and accelerated in the 1930's when the
357 development of motor and air transport made it possible for poachers to work mass destruction on the species. It was driven from the Apsheron Peninsula early in the century and from the Shirak steppe in the 1920's.

In the 1930's hunting with cars and trucks developed to such an extent that the goitered gazelle was nearly exterminated in the northern part of the Shirvan steppe. Just in the area around the Kara-Su railroad station poachers bagged more than 500 goitered gazelles annually. Poachers from the cotton sovkhozes of the Mil'skaya steppe bagged from 500 to 600 gazelles each year with the use of automobiles, and this steppe yielded the same number to herdsmen wintering there. In 1937 goitered gazelle could be encountered in eight isolated areas of semidesert and poorly-developed tracts of the Kura steppes and the ridges of Adzhinour and Kabristan comprising approximately 8,219 km². Its population was in the 5,000-6,000 range (Vereshchagin, 1939a) (Map 87). During the years that followed, the range and the number of animals decreased rapidly as poaching techniques were motorized and as semidesert land was developed for cotton growing.

In the 1940's the species was displaced from the territory north of the Sumgait River. In Kabristan it was confined to deep semidesert ridges by the development of the oil industry. Small herds of goitered gazelle could sometimes be encountered in 1935-1937 on the Gezdek Plateau and near Mount Kergez 10 km southwest of Baku. By the 1940's only single specimens could be observed and those no closer than 25-30 km from Baku in the Kara Dag and Shakhi-Kai region.

With the irrigation and plowing of the Kura-Araks lowlands the goitered gazelle will become extinct in eastern Transcaucasia unless a steppe preserve is established and effective measures taken for the protection of this animal.

Saiga — Saiga tatarica L. Saiga remains are recorded for Pleistocene and Holocene strata from the British Isles in the west to the Novosibirskie Islands in the north and Alaska in the east (Nehring, 1890; Cherskii, 1891; V.I. Gromov, 1948; Pidoplichko, 1951). The stability of the adaptive features of the saiga from the Middle Pleistocene to the present points toward a Pliocene or even Miocene origin for the genus. The lack of findings of closely related forms in Pliocene strata of the Palaearctic is rather mysterious, but, in view of the adaptation of the contemporary species, it can be assumed to have developed in steppe and savannah environments.

Although the Pleistocene fauna of the northern shores of the Mediterranean generally resembles that of the middle belt of Europe, saiga remains have not been found in southern France, Italy and Greece (Wolf, 1938, 1939). The most southerly finds of Pleistocene saiga remains have been in the Crimean steppes and on the Caucasian Isthmus. On the Russian Plain saiga bones present massive and certain evidence of Middle and Upper Pleistocene deposits.

On the Caucasian Isthmus fossil remains of saiga have been reported from Ciscaucasia and eastern Transcaucasia (Map 86).

There has probably been no penetration of saiga to the south of Transcaucasia. Nor has it been found in western Transcaucasia which also has long been a woodless area of rugged relief.

The appearance of the species on the Caucasus can be dated at least Middle Pleistocene.

358 The saiga remains of at least 70 specimens found in the Binagady bituminous strata of the Apsheron Peninsula are convincing evidence that the penetration route of European-Asian steppe forms from the north followed the western coast of the Caspian Sea. In the pre-Khazar stage of the ancient Caspian regression, the ecological barrier which the Khachmas lowland forests of the Kusary sloping plain now present to steppe species probably did not exist. The winter migrations of saiga recorded by Glitsch (1865) raise questions on the stability of saiga habitats in eastern Transcaucasia. Is it possible that these were only seasonal migrations taken during cold winters? The answer is supplied in a study of the age groups of animals which perished in the bitumen, based on 60 mandibles with preserved molars:

1. Young — June-July; milk molars worn down; first true molar erupted: 33.3%.
2. Young — August-September; first true molar erupted and worn down: 21.7%.
3. Semi-adult — November; second true molar erupted; milk teeth replaced by permanent teeth: 5.0%.
4. Adults and aged specimens — worn-down true molars: 40%.

This data shows beyond doubt that saiga reproduced on the Apsheron and inhabited eastern Transcaucasia at least in summer, in fall and at the start of winter. This habitation continued until some time later, and was probably terminated only by the Khvalynsk transgression which greatly constricted the developing steppe belt of the piedmont.

Saiga inhabited the Trans-Kuban piedmont plain and the Taman Peninsula of Ciscaucasia in the Upper Pleistocene together with primitive bison and giant deer. But whether these habitations represented only winter migrations from the Kuban valley and through the Kerch Strait from Crimea is difficult to judge from the existing data. The fact that such migrations were possible is confirmed by the run of saiga on the Aral Sea islands (Berg, 1905).

In postglacial time the saiga range was still enormous, extending from the Carpathians to Mongolia. Saiga inhabited the Ciscaucasian plain during the Holocene from the Azov to the Caspian coast. From this area and particularly from adjacent areas of the Russian Plain multiple findings of Holocene remains of saiga have been taken. They have been found in cultural strata in the following proportions (ratio to total number of bones extracted at each site expressed in percentages): 1) Cossack village of Tsimlyanskaya, Bronze Age, 15th-10th centuries B.C. — 5% in one excavation area, 12% in another; 2) the farmstead of Krasnyi Yar near Tsimlyanskaya, Late Bronze Age — 4.2%; 3) the village of Lugovoe in the Assa valley, Scythian strata — one horn among a great number of remains of domestic animals; 4) Cossack village of Tsimlyanskaya, Khazar strata, 8th-10th centuries A.D. — 14.8%; 5) Sarkel fortress near Tsimlyanskaya, 9th-11th centuries A.D., from 1934 excavations — 6.5%, and from 1950 excavations — 3.3%.

The saiga is not depicted in drawings, sculptures or folklore of the Caucasian peoples, except for a representation of antelope on a vase from the Maikop burial (Figure 128) and unrealistic recent drawings that are almost contemporary reported from Chokrak sandstones near Kapchugai in Dagestan by Markovin (1953).

359 In the Ukraine saiga was common in the later Middle Ages (Beauplan, 1823 edition). Litvin (1890 edition, p. 48) recorded saiga and roe deer in the province of Kiev of the Lithuanian Grand Duchy as follows: "Wild goats run across from the steppes into the forests in winter and from the forests to the steppes in summer in such large numbers that each peasant kills up to 2,000 of them each year." This was approximately the year 1550.

In the last century the southern range limit of the species in Transcaucasia lay along the Ust'-Urt, the Aral and the northern Kyzyl-Kum.

During the 19th century and at the beginning of the 20th, the decline in saiga population on all surviving ranges proceeded very rapidly as the result of direct extermination (Glitsch, 1865; Dinnik, 1914a; and others). The plowing of land was also a contributing factor. At the time of Rossikov (1887) saiga still inhabited the lower reaches of the Malka, and in the 1890's could still be encountered near Stavropol: Dinnik (1914a) reports their being killed near the Sengileevskoe Lake and the village of Staro-Mar'evka. At his time saiga were common near Arzgir, Raguli and Turkmenskaya Stavka [Letnyaya Stavka, Stavropol Territory] but had become extinct in the vicinity of Bol'shaya Kugul'ta, Dzhalga, Burukshum and Takhta. By the beginning of the 20th century they were no longer to be found in the western Manych area (Bogachev, 1918). At this time numerous armed detachments on the steppes contributed to the disastrous decrease in saiga population. They survived only in certain parts of the Chernye Zemli, in the lower reaches of the Kuma, Volga, Ural and Emba rivers, in northern Kazakhstan and in Mongolia. They completely disappeared from the Terek-Kuma semidesert. In the 1930's migrating herds were seldom seen near Arzgir and Terekli-Mekteb. The establishment of hunting limits, the confiscation of rifled arms and the gradual depopulation of the semidesert have brought about a restoration of the saiga population.

According to Adol'f (1950, 1952) a total of less than 3,500 saigas inhabited the interfluve of the lower Kuma and Volga in 1939, whereas in 1950 herds of more than 1,500 specimens each were encountered; the total number of these animals living on the right bank of the Volga was several tens of thousands at this time.

After World War II saiga again became common on the Terek-Kuma steppes (Babenyshev, 1948).

In the severe winter of 1948-49 thousands of saiga died on the Astrakhan and Ciscaucasian steppes from cold and hunger. In the spring of 1950 carcasses of saigas were found on the steppes of the eastern slopes of Yergeni in groups of five to eight (Kolesnikov, 1950). As snowfalls start large numbers of saiga rush to the south, toward the Terek and Sulak, and isolated groups reach the Dagestan foothills. Lavrovskii (1950) reported the gathering of tens of thousands of saiga north of the Chernye Zemli on tracts of fully-developed tall weeds.

During blizzards, storms and deep cold in severe winters, saiga, like goitered gazelle, retreat into the tugai and reeds. Their appearance in the tugai along the Terek and Sulak is, therefore, not astonishing. When saiga undertake long migrations, going hundreds of kilometers northwards in search of moisture to quench their thirst during cold winters without snow, they are liable to die if they are suddenly caught by a snowstorm. As a result of such a migration, large numbers of saiga grazed in the corn and wheat fields of the Grozny Region in 1951.

The present range and habits of saiga characterize it as a steppe animal which was driven into the desert by man. During the Pleistocene and Holocene it very probably lived in the forest-steppe and, in any case, 360 inhabited thickets and reedlands of the floodplain, much like some African antelopes. Long migrations from forest to steppe and back, even in winters of unusually light snowfall, are confirmed by Litvin's cited report. In general, it may be said that the present stenotopic features of the species are only superficial and, to a considerable degree, forced. The prospects for the continued existence of saiga in Ciscaucasia are poor; plowing and irrigation of vast steppe and desert areas will each year restrict further the areas suitable for the habitation of saiga.

FIGURE 144. Representation of a chamois on a silver bucket from burials in the Trialet ridge (Kuftin, 1941)

In 1950, 15 saigas were settled on Bulla Island, south of Baku: they could probably successfully inhabit any part of the semidesert of eastern Transcaucasia.

Chamois — Rupicapra rupicapra caucasica Lyd. Fossil remains of chamois have frequently been found in Pleistocene and Holocene cave strata in Belgium, France, Germany and Italy, e.g., the Colomby grotto which is very rich in animal remains. The finds are almost always in mountain or piedmont areas.

Only isolated occurrences of chamois have been found in Paleolithic cave settlements in western Transcaucasia, but the North Ossetian dzuars contain Middle Holocene remains. None has been found in either Pleistocene or Holocene strata in the vast piedmont plain region of the Caucasus, nor have they been encountered in Pleistocene deposits of Iran, Syria, Palestine and Lebanon. The contemporary distribution lies in the Pyrenees, the Cantabrian Mountains, the French, Swiss and Italian Alps, the Apennines, the Carpathians, the Balkan Mountains, Asia Minor and the Caucasus (Couturier, 1938).

Thus both paleontological data and present zoogeography characterize the chamois as a mountain species occurring in the alpine fold systems lying to the north of the western Mediterranean and to the southeast of the eastern Mediterranean.

Contour representations of chamois, depicting the animal with its chest pierced by arrows, appear on a silver bucket from Early Bronze Age burials on the Trialet (Figure 144). Since the chamois does not endure captivity well and could not have been transported far from its natural habitat by ancient tribes, this find indicates to archaeologists that the bucket was fabricated either in the Armenian Highland or in Asia Minor. The contemporary range of the chamois on the Caucasus is widespread (Map 88). On the Main Range, the distribution area can be traced from the west from the Goitkh Pass and Mount Semeshko (1,032 m) in the upper reaches of the Pshish (Dinnik, 1896, 1914a; Nasimovich, 1949b), with some occurrences observed (1955) in northwest Tuapse in the rocks of the Dzhubgi district,
361 to the east on both sides of the Caucasus as far as Mount Baba-Dag in Azerbaidzhan. On the western Caucasus the chamois range is from 250-300 m to 3,000 m above sea level. At the end of the last century and the beginning of the present one the species was very numerous in the reaches of the Belaya, Urushten and Malaya Laba rivers; as many as 400 chamois could be observed daily and sometimes herds of 90 head were encountered (Dinnik, 1914a). Between 1926 and 1937, at least 4,000 chamois inhabited the Caucasian Reservation (Nasimovich, 1949b) and Zharkov reports as many as 12,000 (1940a). Winter concentrations are likely to occur on slopes with either a western or an eastern exposure. The animal is most frequently found in the middle altitudes of the subalpine zone — from 1,500 to 1,700 m.

In the central part of the northern Caucasian mountains, there are chamois habitations on the slopes of the Elburz and in pine forests of the ranges which border the upper Baksan, Chegem and Cherek rivers. The species is not found in the furthest chain of the Skalistyi, appearing only in Digoria and Ossetia. In Dagestan chamois live among rocks in an area of subalpine tall grasses and beech—hornbeam forests with a very humid environment on the ridges of the Chernye Gory to the middle course of the Argun. Their habitat in Urukh and the upper reaches of the Ardon is characterized by rocky areas grown with pine forests and stretches to Nogkau and Tseya. Chamois cannot be observed in central Dagestan which is deforested, and is found only in small numbers on the eastern slope of Mount Shakhdag.

On the southern slopes of the Main Range the species is common in Abkhazia and Svanetia, and it has found habitats on the very steep slopes of the upper Kodor, Ingur and Rion gorges in fir, spruce and maple forests, and particularly in the upper reaches of the Tskhenis-Tskhali, which are very rich in chamois. There are few to be found in South Ossetia or Kakhetia, but, further to the east, they are numerous in the beech and birch forests of the Katekh-Chai and Shin-Chai gorges and in the basin of the upper Turyan-Chai in Azerbaidzhan.

Herds of 50-70 chamois can be observed in the Zakataly Reservation in August. In the 1930's the census of chamois in this reservation was approximately 1,000 head (Markov and Mlokosevich, 1935). The usual habitats of this animal are the edges of birch forests and very steep sod slopes grown with matgrass and fescue in those parts of the subalpine meadow-steppe with bedrock of black slate. On rocky slopes near Kurban-Efend in the Ismailly region chamois live even in the summer at altitudes from 800-900 m. In winter, the bulk of the population inhabits beech forests in the range of 800-1,200 m.

The population and distribution of chamois is considerably less on the Lesser Caucasus. They are still found along the middle course of the Chorokh in the Artvin area and, further to the west, on the eastern Taurus, e. g., the Trebizond vicinity. There are no data on the habitat of chamois on the northern slopes of the Adzhar-Imeretia Range. At one time chamois was common in the beech forests and rocks of the Kura left bank in the Borzhomi area. In 1890 five chamois were penned in on a 130-ha-tract in the Borzhomi Reservation (Shil'der, 1892). On the Trialet ridge, the species can be observed in the Belyi Klyuch area, although it has been exterminated in other places. There were probably no chamois in the past and are none now on the deforested plateaus of Dzhavakhetia.

As late as 1873, Bogdanov and still later Kalishevskii (1904) noted their presence on Alagez. Neither Burchak-Abramovich in 1944 nor Dal' in 1950 found any chamois there. In the last century the species inhabited the northeast margin of the Armenian Highland, and in the 1860's
362 could be encountered along the Dzegam-Chai and Shamkhor-Chai rivers as far as the village of Barsun (Radde, 1899, p. 74). Folklorist Osipov (1898) mentions the presence of chamois in the mountainous areas around the village of Chaikend. By the 1930's it was no longer observable in Karabakh and on Shakhdag, although Sarkisov (1944g) maintains that it disappeared from the Murov-Dag only in 1930. Generally speaking, Sarkisov's data on chamois distribution on the northern slopes of Shakhdag, on the Lori uplands and in northeastern Karabakh (1944g) require verification.

The disappearance of chamois from Karabakh and Asia Minor cannot be explained only by human activity, because on the Murov-Dag and other ranges there are forests sufficiently deep for the survival of wild goat.

There are no indications of chamois now or in the past in Talysh and on the Elburz, although they could certainly exist there. South of the Armenian Highland, chamois probably exists in relict forest areas. A horn of chamois from the mountains of the southern coast of Lake Van is preserved in the Zoological Institute of the Academy of Sciences.

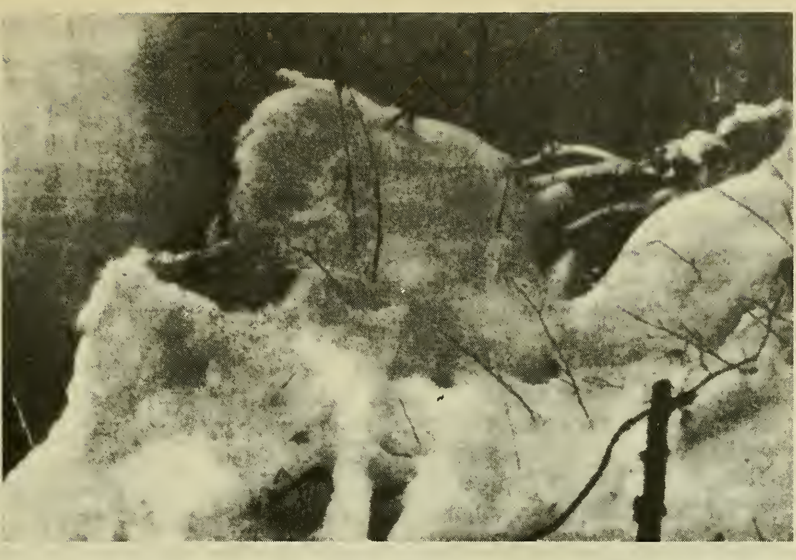

FIGURE 145. Chamois lying on a scarp in the Katekh-Chai ravine

Photograph by author, 1935

Chamois is less well adapted to the intersecting relief of the mountains than is the goat. Its skeleton is lighter and its hooves are smaller. It avoids the rocky places frequented by Caucasian goats (although some naturalists think otherwise). Its principal enemies are big cats (panthers and lynx). It can survive in stable rocky areas which are inhabited by wolf and bear, because it is swifter of movement; it is even frequently found grazing side by side with bears. The seasonal and daily migrations of chamois are less pronounced than are those of goats. They do not migrate in winter to Dagestan where the snow cover is poor, and in summer they do not leave the forests for the glaciers, because they probably
363 endure the attacks of bloodsucking diptera better than goats. Their attachment to biotopes of forest and mesophytic meadow is more stable than that of goats (Figure 145). On the whole, the chamois is a species adapted to the mesophytic areas of the mountains rising around the Mediterranean. It probably did not descend to the plain during the Quaternary because, being a specialized mountain species but without the speed of the roe deer or goitered gazelle, it could not move from range to range across the plain at that time without being destroyed by predators, particularly by wolves.

The absence of chamois remains in plain burials and the data on its contemporary distribution and adaptations both indicate that the Caucasian and Alpine chamois derived independently from common ancestors which existed in the Tertiary on the folded uplands of the Sarmatian sea coasts.

There is, thus, no room for discussion of a chamois migration in the Quaternary to the European Alps from the mountains of Asia Minor and the Caucasus or, conversely, from Europe eastwards through the Balkans and Asia Minor. The Caucasian chamois should be regarded not as a subspecies of the alpine chamois but as an independent species. A comparison of the two shows the Caucasian chamois to have distinctive morphological features, including a different voice — a long, hissing sound noted even by Dinnik (1896).

The absence of chamois from Talysh and El'brus and the rapid decline of its population and shrinkage of its range in the 19th and 20th centuries on the Lesser Caucasus indicate that the contemporary ecological optimum of the species and probably the focus of its origin lie in the ranges surrounding the Black Sea to the south and east.

The organization of a rational forest and hunting economy requires the renewed breeding of chamois in Karabakh — in the upper reaches of the Dzegam, in Shamkhor and in Talysh

West Caucasian and east Caucasian goat — Capra caucasica Güld. and C. cylindricornis Blyth. Fossil remains of representatives of the subfamily Caprini have been found in Eurasia from the beginning of the Lower Pliocene, but on the Caucasus the only goat remains that have been found are from the Pleistocene and Holocene. The Pleistocene localities are all situated in western and central Transcaucasia on the margins of the contemporary range, often a distance of 50-60 km in a straight line from the present habitats of the species (Map 89). The explanation lies partly in the effects of the glaciations which forced the goats to lower altitudes, but even more in its widespread distribution in the Pleistocene (see Chapter II).

To the south remains of local southern forms of C. sinaitica Erenb. have been found in the Paleolithic of Lebanon, Syria and Palestine and are recorded under the names of C. beden Wagn., C. ibex L. and C. cf. nubiana Cuv. (Picard, 1937). Remains of Pleistocene goats are also reported from many mountain and foothill settlements in Western Europe — from Ireland and Belgium to Bulgaria. These remains, sometimes consisting of entire skulls, which are generally related to some species of the contemporary European goat — C. ibex L., C. aegagrus L., C. pyrenaica Schinz. — and to fossil species — Ibex priscus Wold., I. cebennarum Gerv. and others, have been found in Pleistocene as well as in Holocene strata (Woldrich, 1893; Wolf, 1938). A large goat, Capra sp., inhabited the mountains of the Crimea in the Paleolithic (Gromova and Gromov, 1937).

364 Carvings of Caucasian goats, especially of the east Caucasian type, were often produced in the Bronze Age; figures of goats appear on warders, pendants and seals (Figure 146).

The contour representations on silver vessels from the Maikop burial show a similarity to west Caucasian goat (Figure 128).

There are no paleontological or archaeological data on an earlier habitation of the Lesser Caucasus and the Taurus by Caucasian goat.

Nevertheless, it seems very probable that such a habitation occurred, particularly if one compares Caucasian goat with species endemic to the area: Caucasian birch mouse, Promethean vole, pine vole, snow vole and the Caucasian black grouse. The feasibility of Caucasian goat existence on the Lesser Caucasus is demonstrated in the present day by the experience of the Borzhomi Reservation (Shil'der, 1892).

The contemporary range of Caucasian goat includes almost all of the Greater Caucasus for 9 longitudinal degrees (between 39°45' and 48°30'E). The chief habitat is on the slopes of the Main Range, but

FIGURE 146. Kobanian pole top of bronze representing east Caucasian goat — from North Ossetia (Uvarova, 1900)

they are also encountered on parallel ridges to the north and south and on spurs with southern exposures.

In this vast area two contemporary species developed: the western — C. caucasica (C. caucasica severtzovi) and the eastern — C. cylindricornis, which differs from the western chiefly in the structure of the male horns (see Chapter IV).

The distribution of the west Caucasian goat (Figure 147) now begins to the west of Mount Chugush (Nasimovich, 1949a), although in the 1880's they could be found 30 km westward on the peaks of Fisht and Oshten (Dinnik, 1914a). In the Caucasian Reservation goats inhabit the Vodorazdel'nyi Range and its northern spurs. On the mountains of Bolshoi Pambak, Dzhuga, Akhtsarkhva and Yatyrgvarty, the habitats are somewhat separated in summer (Nasimovich, 1949a). At the start of this century, goats were often encountered on the Skalistyi ridge and on Mount Achesbok. Temporary habitations by single specimens have been noted during the last fifty years on the summits of Dudugush, Chura and Khatsavita.

The west Caucasian goat is also dispersed along the Vodorazdel'nyi Range and its northern and southern spurs from the upper reaches of Belaya and Mzymta to the upper reaches of the Balkar Cherek. Very few specimens are now found in the upper reaches of Teberda and Kodor, but in the Teberda Reservation, groups of 10-15 can be observed near the glaciers.

Goats have completely disappeared from the upper reaches of the Ingur. To the east, they inhabit the southern slopes of Tetnuld in the upper reaches of the Mulkhra and single specimens are seen beyond the village of Ushkul'. The species is rare on the summits of Shoda and Laila, which are isolated from the Vodorazdel'nyi Range. There are numerous goats on the northern slopes of the southern ridges of El'brus. At the beginning of the 20th century,
365 they lived on Mount Kinzhal, and at the beginning of the 19th century they were even found in the Pyatigor'e area on Mount Beshtau (Vietinghoff, 1812). Beyond the villages of Tegenekli and Verkhnii Baksan groups of 20-25 goats were observed in the 1950's.

The species is also common in the Bezingi Cherek gorge, where in the 1940's during the fall shepherds killed as many as 40 head. And it is even more common in the upper reaches of the Balkar Cherek on the slopes of Dykh-Tau. There in the course of a day in August 1948 the author encountered three females with young and two young males in the Dykhsu gorge, and observed numerous tracks and signs of goat-grazing near the glaciers.

It is very rare in the upper reaches of the Urukh.

366 The present distribution of east Caucasian goat lies to the east of limits drawn by the Ingur and Tskhenis-Tskhali headwaters on the southern slopes and the Baksan and Malka headwaters on the northern slopes. The skull of a female specimen from Teberda is preserved in the Zoological Institute of the Academy of Sciences. The Georgian Museum contains in its

collections a skull of a male from Teberda with horns of a type showing a transition from C. cylindricornis to C. caucasica, and a skull of an 11-year-old male from Baksan showing a transition from C. caucasica to C. cylindricornis. Thirteen skulls taken from the northern spurs of El'brus and Mount Kinzhal and now in the Zoological Institute collection also belong to the east Caucasian form. V. G. Khachvani, a Svan of Ushkul', near the Ingur source, owns a stuffed specimen, male, 5½ years old and typical of the east Caucasian form, which was killed near the summit of Shkhara in December 1947. From the same village Radde, in the last century, brought the horns of an aged goat of a transitional (hybrid?) type between west and east Caucasian.

(365)

FIGURE 147. West Caucasian goats in winter

Watercolor by E.Ya. Zakharov

In 1949 Nasimovich (1950) discovered in the Psygansu ravine five skulls of east Caucasian goat and one skull of west Caucasian goat which had been discarded by hunters. In finds in the upper reaches of the Bezingi Cherek, four skulls had horns of the west and central Caucasian type, and one had horns of the east Caucasian type. Two skulls found in the Balkar Cherek region both belonged to the eastern type. Of Dinnik's ten finds of skulls in 1887 in the Cherkess village of Kundyum two proved to be of the western form and eight of the eastern (Dinnik, 1890b). All 46 skulls taken from the Urukh and Ursdon gorges in the villages of Styr-Digor and Nogkau, which were examined by the author, belonged to the east Caucasian species.

The Rekom dzuar in the Tseya gorge of the Ardon Basin contained 298 pairs of horns, of which 292 belonged to the eastern type and only six to the western.

From this location the range of the east Caucasian goat is continuous along the Vodorazdel'nyi Range (Map 89).

According to data collected by the author and V.I. Naniev in North Ossetia in 1948, the east Caucasian goat can be observed on all the northern slopes of the Bokovoi and Main ranges and occasionally in the upper reaches of the Urukh, Ardon, Fiagdon and Gizel'don rivers. Herds of up to 100 head are encountered in the upper reaches of the Arkhon River and occasionally in the neighborhood of the villages of Dunta, Arkhon and Aksai.

The species is now rare in the Grozny region and in central Dagestan. It was probably rare on the Gunib and Khunzakh plateaus even at the time of the Caucasian wars in the mid-19th century. Although now completely extinct in the middle reaches of Kara-Koisu, it undoubtedly could be found everywhere in that region in the last century. East Caucasian goat is rarely seen in the Samur and Lakskii areas, but is common in the Avar Koisu Basin on the Bogos Range, from which Geptner and Formosov (1941) report herds of 20 head in the 1920's. It is also numerous in the rocky upper reaches of Kara-Chai and Kusar-Chai on Shalbu-Dag and Shakh-Dag.

There are now few goats on the southern slopes in the upper reaches of the Aragva and Alazan, and they are completely absent from the Telavi Range, even though they inhabited this area until quite recently. In the 1930's some 200-300 head were counted in the Lagodekhi Reservation (Markov, 1940). Following some epizootic outbreak, their numbers were greatly reduced along the Belokan-Chai and Mazym-Chai (Vereshchagin, 1938a).

The Katekh-Chai ravine is the habitat, both in summer and in winter, for a particularly heavy population; herds of 200 and more head can be observed there. The census in the 1930's in the Zakataly Reservation was 3,500-4,000 head (Markov and Mlokosevich, 1935; Vereshchagin, 1938a). The species is frequently found in cirques in the Shin-Chai and Demir-Aparan-Chai gorges, and is especially numerous on the southern border of Dagestan in the upper reaches of the Samur (Figure 148) and in the vicinity of the three high peaks of Bazar-Dyuzi, Baba-Dag and Shakh-Dag —
367 a fact noted even in 1896 by Satunin (Radde, 1899). In the 1930's the author observed there many herds of 30-40 goats, and occasionally aggregations of 250 or more. The extreme eastern margin of the east Caucasian goat range passes near Mount Aivasel 25 km east of Mount Baba-Dag. Today groups of 15-20 goats can be observed near Konakhent in the upper reaches of the Gil'gin-Chai.

FIGURE 148. Khalakhi Lake in the upper reaches of the Samur. The surrounding rocks are a favorite habitat of east Caucasian goat

Photograph by author, 1937

The eastern Caucasian goat (Figure 149) ranges between wide altitudinal limits. This animal can be found in summer at altitudes up to 1,200-1,300 m in ravines of the Zakataly Reservation which are nearly inaccessible from the south. It frequents mineral springs and passes in valley bottoms at altitudes of 800-1,000 m. To the east above Vartashen and Ismailly its summer habitat is on the treeless slopes of the southern ranges at altitudes of 1,400-1,500 m. In winter the lower limit on snow-covered slopes drops 200-250 m, but remains the same as in summer in the valley bottoms. After slaking their thirst at the mineral springs, the adult goats either stay near the riverbed at altitudes of 1,400-1,500 m or climb up to altitudes of 2,800-3,000 m where they rest near snowdrifts, thus completing a daily vertical migration of 1,500-2,000 m. In August the goats often use passes at altitudes of 3,400-3,500 m.

On the southern slopes the goat population of the upper reaches of the Alazan to the upper reaches of the Pirsagat divides in summer, because the entire alpine meadow belt is occupied by cattle herders with herds of sheep and cows guarded by dogs. One group of goats spends the entire summer in the forest, resting on taluses and rock overhangs; the other is to be found in the passes above the meadow zone on rocks and taluses.

368 The west Caucasian goat of the Recent is now a mesophilous species, but its adaptation to the humid forest and to alpine meadows is probably a later, secondary phenomenon.

The contemporary population of Caucasian goat is greater in the eastern, drier parts of the Caucasus; its preferred pasturage is in meadow-steppe rather than rich alpine meadows. It is characteristic of the goats of the forest populations to take long rests on rocky scarps, taluses and in sunny forest clearings — a habit which may revert to the ancient ways of their ancestors whose mountainous habitats were treeless and more arid.

The pattern of Caucasian goat behavior as it relates to firn-snow and glaciers is more clearly seen in summer than in winter. The animals generally frequent the firn in August and rest in the sun enjoying the coolness and the absence of flies (Vereshchagin, 1949a). They avoid frozen slopes and glaciers, and will look for footing on uncovered stones after a fresh snowfall. It is rare that they will attempt a crossing over a large glacier area. During the author's crossing of the huge glaciers near Mount Laborda east of Mount Shoda in August 1948 no goat tracks were observed on the glaciers. According to observations of hunters (M. G. Ivkin and others), large herds of goats migrate each year in November-December from Lagodekhi and Belokany to Dagestan, always using the snow-free crests of ridges.

The general outline of the Caucasian goat ranges has changed little during the last 150 years. Presumably during the Caucasian wars in the mid-19th century there were more goats killed than there are now. The population declined with the establishment of Russian settlements in the Ciscaucasian piedmonts and the introduction into the mountains of the four-barrelled Berdan rifle and the triple-barrelled rifle at the start of this century.

The decline was progressive during the first half of the 20th century throughout most of the goat ranges. One exception was the hunting preserve of the Grand Duke in the Kuban Basin where the animals were well-guarded. The protected environment of the Caucasian and Zakataly reservations brought about an increase in the goat population in these areas beginning with the 1930's.

Goats fled from harassment in Fisht and Oshten in the 1880's, and disappeared from Mount Achishko near Krasnaya Polyana in 1908 (Nasimovich, 1949a). Villagers of Ushkul' killed 200-250 goats in the area of the Ingur sources over a 35–40-year period in the last century. Their sons, using improved weapons, killed no more than 15-20 in the same time span in the first half of this century.

By the beginning of the 20th century, goats had been routed from the furthest ridges of the Skalistyi in the central part of the northern Caucasus, particularly from Kinzhal and Barmamyt (Dinnik, 1914a). Dronov collected thirteen skulls in the upper reaches of the Malka as late as the 1880's. They have probably been extinct in Pyatigor'e in the Beshtau region since the beginning of the last century.

Judging from skulls found in the dzuars of Lesgor and Digorized, the east Caucasian goat inhabited Digoria early in this century on the Skalistyi ridge which cuts off the longitudinal valley of the Doniserdon from the north. Since no fresh skulls have been found in these sanctuaries, the species must have disappeared by the 1930's-1940's.

The approximate annual yield of Caucasian goat in the 1930's was probably no less than 4,000 head (Figure 150).

369 Caucasian goats, then, are not to be considered as on their way to extinction, even though there is no control over hunting in the mountains. The existence of three reservations — Caucasian, Teberda and Zakataly-Lagodekhi — is a guarantee of a continuing, thriving population.

The development of cattle breeding, accompanied by the extermination of wolves and panthers, had both a positive and a negative effect on the Caucasian goat population. In the early stages of cattle herding, wolves preyed on the domestic cattle in the mountains in the summer and followed 370 the herds to the plains in winter, thus diminishing the danger to the goat population. However, as cattle breeding was further developed and pastures were enlarged, cattle diseases such as scab, foot-and-mouth disease and others spread to the goat population (Dinnik, 1914a; Vereshchagin, 1938a; Nasimovich, 1941).

FIGURE 149. East Caucasian goats in summer

Watercolor by E.Ya. Zakharov

The facility with which Caucasian goats can be crossed with domestic species, domesticated and acclimatized to the plains, leads to an anticipation of further development of both species through controlled expansion. They will probably be bred in the Karabakh uplands, on the Shakhdag, and on the Trialet and the Adzhar-Imeretia ridges, as well as in Talysh and El'brus.

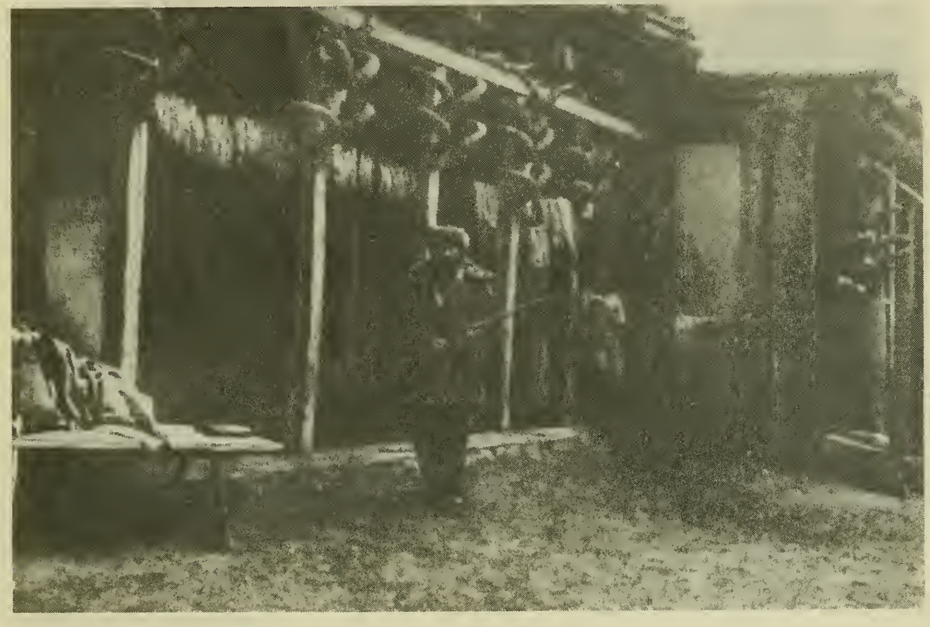

FIGURE 150. Horns of Caucasian goats mounted on a veranda of an Ossetian house in the Urukh gorge

Photograph by author, 1947

The economic effects to be obtained from the hybridization of Caucasian goats with domestic goats could be considerable (Vereshchagin, 1938a).

Taking into account the endemicity and morphological isolation of Caucasian goats from other representatives of the genus (see Chapter IV), the species should be regarded as local in origin, springing from Caucasian Tertiary ancestors.

Bezoar goat — Capra aegagrus Erxl. Fossil remains of this species are recorded for Pleistocene and Holocene cave strata in Italy, Lebanon, Syria and Palestine (Picard, 1937; Wolf, 1938). They have been found in the Caucasus only in postglacial strata in caves in the Araks gorge (Polyakov, 1882) and on the Saraibulakh ridge, in Bronze Age strata of the Teishebaini fortress ruins near Yerevan (Dal', 1940b, 1952), and in dzuars in Tushetia and Khevsuretia.

371 Bronze Age drawings on limestone rocks in southeast Kabristan west [? south] of Baku show a similarity to Bezoar goat (Figure 151), and may indicate a recent habitat for this species on the lower ridges of Kabristan near the Caspian Sea. The collections of the historical museums of Moscow, Makhachkala and Grozny contain exquisite bronze figurines of Bezoar goat

from Dagestan (Figure 152) which are associated with the cultures of the Kobanian and Kayakent-Khoro-Chai period (first half of the 1st century B. C.).

FIGURE 151. Representations of goats on rocks of Beyuk-Dash south of Baku

Photograph by author, 1945

The contemporary distribution of Bezoar goat extends beyond the Caucasus to the mountains of southwest and central Asia, from Crete to western India through Turkey, Iran and Afghanistan. There are three isolated ranges on the Caucasian Isthmus: the eastern part of the Greater Caucasus and the central and the eastern parts of the Lesser Caucasus. The upper reaches of the Alazan, the Argun and the Gerdyman-Chai, which is to say the arid, treeless part of the country, form the limits of the range on the Greater Caucasus (Map 90). In the 1920's the species inhabited the Lakskii area of Dagestan, and, according to Dinnik (1914a), could be encountered 30 km from Gunib at the start of the century.

The Bezoar goat of Dagestan is rarely seen in the forested, humid slopes of the Main Range between Lagodekhi and Shemakha and in the passes of the divide — perhaps once in two or three decades.

It is common in the upper Avar Koisu area, in the vicinity of the villages of Tlyadal, Kidero, Chorod and Takhota, where it inhabits pine and beech forests. Along the upper Terek and Aragva it is not now observable and, 372 to judge from the complete absence of skulls of the species in Ossetian dzuars, it was probably never an inhabitant of this area.

The range on the Lesser Caucasus is more extensive: it includes on the southwest the fir forests of the upper Chorokh, certain parts of the

Adzhar-Imeretia Range, the western spurs of the Trialet in the Borzhomi District and the southeastern part of the Armenian Highland. The species is common on the Shakhdag and in the Kedabek and Kalakent areas, e.g., in the upper reaches of the Shamkhor near the Kashkar summit (3,379 m), on Mount Kyapyaz, beyond Lake Gek-Gel and below the peak of the Murov-Dag (3,740 m).

In 1940 a small number of these goats inhabited the taluses in beech forests on the southeastern slope of Mount Kechel-Dag at the eastern extremity of the Shakhdag ridge. The guard at the sawmill there killed seven or eight goats each year.

Mount Kirs (2,743 m) above Stepanakert was the easternmost summit inhabited by Bezoar goats in the 1930's.

The habitat of this animal in the central and southern Armenian Highland lies in rocky mountains from the Azat River valley to the Zangezur, Megri and Bargushet ridges. North of the upland the range is limited by the southern slopes of the Gegam and Vardeniss ridges (Dal', 1951b). The Bezoar goat is frequently observed on the Urts and Aiotzdzor [Daralagez] ridges and on the rocky massifs close by. In 1950 Dal' (1951b) counted 124 goats in five aggregations on 33.5 km^2 on the Urts ridge.

FIGURE 152. Bronze figurine of Bezoar goat (Makhachkala Museum)

In the 1870's goats could still be encountered near Elenovka on the Sevan; Polyakov collected one skull from this region.

In the Nakhichevan A.S.S.R. in 1947 the summits of Alindzha-Dag and Ilyanlu-Dag in the vicinity of the villages of Abrakunis, Boyanur and Khanagya provided a habitat isolated by the upland semidesert. During the historical era, goats were repeatedly routed from these heights by ancient Armenian tribes which used the summits as natural fortresses. Bezoar goats are more adaptable than the Caucasian type; they often cross vast desert areas easily and, therefore, have a great migratory potential.

On the Zangezur ridge and its southern spurs the goat population spreads eastwards as far as the Araks gorge. It is particularly numerous in the Negram Mountains between Dzhulfa and Ordubad at altitudes of 1,000-1,200 m. In the Araks gorge it is distributed on the southeastern slopes of the Megri ridge as far as Okhchi-Chai. In 1947 a small goat population inhabited desert rocks near Akluis and Ordubad.

There are references in the 14th-century writings of Rashid ad-Din to the Bezoar goat as an inhabitant of Talysh, where it could still be encountered in the high mountains, e.g., on the Kyz-Yurdy summit, (Radde, 1899, p. 75) in the mid-19th century; later it was no longer observed there.

373 To the south the range of this goat extends into the dry uplands of Asia Minor and Iran. Collection specimens were taken from Erzurum, Van, Kars, Ararat, Tabriz, Sabalān and Damāvand at the end of the last century

and the beginning of the present one. In the U.S.S.R., the Bezoar goat also inhabits the Kopet-Dagh and the Bolshie Balkhany. According to Sarkisov (1944e) it can be observed in Iran throughout the mountains of Azerbaidzhan, Kurdistan, Kermanshah and Luristan, and to the south in the provinces of Yazd and Shiraz, in Makran, Baluchistan and as far as the Sulaiman Range.

The most usual habitat of the species is an arid, rocky mountain biotope with buckthorn, hawthorn, juniper and other xerophytes. The vertical distribution of the contemporary Bezoar goat on the Caucasian is from 900 to 3,500 m, but it manages very well at altitudes lower than that, even down to sea level.

The adaptation of the present range to the eastern Mediterranean area and the life pattern of the Bezoar goat indicate a protracted evolution of the species in a dry, hot rocky mountain environment at relatively low altitudes. The penetration of this goat into the Greater Caucasus probably proceeded northwards from southwest Asia in one of the xerothermic periods of the Pliocene or Pleistocene, similarly to that of hamsters of the genus Mesocricetus. The Surami Range and the steppe-like piedmont of eastern Ciscaucasia would have provided a likely route. The subsequent isolation in the arid eastern part of the Greater Caucasus can be explained by the glaciation of the ranges and the development of a wide mesophytic zone of forest and meadows to the west. The occurrence of the species in Dagestan at a later time, e.g., Lower Holocene, is less probable.

Anthropogenic influences on this goat only came into play in the last decades with the development of cattle herding and the introduction of long-range guns into the mountains. The decrease in the range is particularly apparent today on the southeastern Armenian Highland.

In an ideal hunting economy on the Caucasus, the species would have an unlimited future. Its range could be extended by controlled settlement along the longitudinal valleys of the central Caucasus, e.g., in the Malka, Baksan, Cherek, Urukh and Fiagdon ravines where there are places on the cuesta scarps of the Skalistyi which provide favorable conditions for its habitation.

Sheep: Argali — Ovis cf. ammon L. — and **Armenian mouflon** — Ovis gmelini Blyth. Argali remains are reported from Western Europe for the Pliocene to the Upper Pleistocene, and mouflon remains for the Pleistocene to the present.

On the Caucasus occurrences of large sheep of the argali type (Figure 153) are very rare and have only been found in Middle and Upper Pleistocene strata of the Transcaucasian mountains and plains. Finds of mouflon remains are even more rare and have been made only in the Paleolithic of the Lesser Caucasus and the Mesolithic of Dagestan.

The localities closest to the Caucasus from which finds of Pleistocene argali have been recorded are caves in the Crimea (Acheulean and Aurignacian strata). Bones of mouflon-type sheep, O. cf. argaloides Nehr., were found in Acheulean-Mousterian strata of the Kiik-Koba cave and in Aurignacian strata of the Adzhi-Koba cave (Gromova, 1935a; Gromova and Gromov, 1937). In spite of the suitability of the topography of Palestine, Lebanon and Syria, remains of sheep from Paleolithic and Neolithic cave strata in these regions are unknown (Picard, 1937).

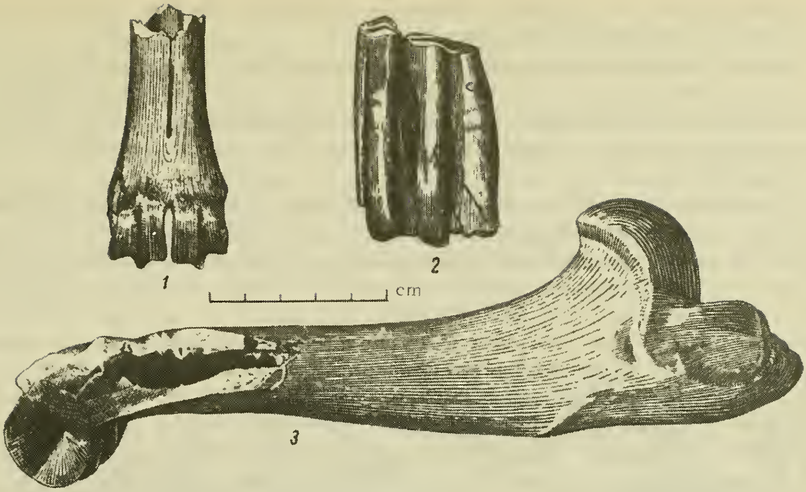

FIGURE 153. Remains of argali

1, 3 — metacarpal and humeral bones from Middle Pleistocene asphalts near Baku; 2 — M_3 from Upper Pleistocene diluvium near Marāgheh

A tooth of a large argali was found in Quaternary loams of northwest Iran near Maragheh, and remains of Ovis sp. were found in caves in the vicinity of Urmia and Asterabad (Coon, 1951).

There are no occurrences of argali remains in Holocene strata of the Caucasus.

Aside from the Mesolithic of Dagestan, bones of a small post-Pleistocene sheep, O. cf. gmelini, have been found only within the limits of the contemporary range of this species: in the ruins of the Karmir-Blur fortress near Yerevan (7th-5th centuries B.C.) and in cave strata of the Saraibulakh ridge (Dal', 1941, 1952) (Map 91).

Depictions of sheep are scant in the ancient literature and representative art of the Caucasian peoples. The earliest are to be found in sculptures. A mouflon head carved on a belt buckle from the Trialet burials in southern Georgia has been related to the second millennium B.C. (Kuftin, 1941). Bronze pendants in the form of sheep with argali-like horns are quite common in Kobanian burial and settlement sites. These representations give an impression, however, of domestic rather than wild animals, as they do not have the force or vivid quality of untamed animals (Figure 154). Argali probably disappeared from the Caucasus in the Holocene, not even surviving in central Dagestan where environmental conditions were most favorable.

Gold articles have been found in Scythian burials of western Ciscaucasia, Kellermess and other localities which bear traceries and relief representations of small-horned sheep of the mouflon type. Similar representations on so-called "Sassanid metal" from Transcaucasia date from 220-657 A.D. Silver plates in the Hermitage collection show a mounted hunt of Chosroes I and Shapur II in pursuit of fleeing sheep (Orbeli and
375 Trever, 1935). The area in which the plates were produced — the Iranian-Anatolian Plateau — corresponds to the contemporary rage of southwest Asian sheep.

The present range limit of mouflon-like sheep in the U.S.S.R. is reached in southern Transcaucasia (Map 91).

Horns and pelts of this species collected from Yerevan, Nakhichevan, Negram, Dzhulfa, Darry-Dag and the village of Puzian in Zangezur are preserved in the Georgian Museum. The nearest Iran localities to produce specimens are Kotur-Dagh, the vicinity of Khoi and the island of Koyun-Dagh on Lake Urmia.

The collections of the Zoological Institute of the Academy of Sciences contain horns found by Academician Brosse in Alagez in 1849 and a skull from the same mountain near the village of Mastart found by Pfizenmair in 1911. There are also skulls and pelts collected throughout Armenia; from the Nakhichevan A.S.S.R. (the environs of the village of Shakhbuz, Dzhamaldin, Arazia), and from Turkey (Mount Ararat, the environs of Bayazid, the village of Gurdzhi-Bulakh, Pir-Reshid Mountain 60-80 km from Van Lake). The collections of Mil'kovich (1910), Brandt (1879), von Vik (1914), Khanykov (1851) and Vvedenskii (1908) contain horns, skulls and pelts from Kara-Dag to the south of Ordubad, the Zorskie Mountains, Lake Urmia, Mount Sabalan and the environs of Tabriz.

The distribution of sheep in southern Transcaucasia has diminished rapidly since the last century. Chopin (1852) comments on the presence of sheep in Alagaz, but contemporary authors — Sarkisov (1941, 1944a, 1944b) and Dal' (1945, 1949b) — note that the distribution area ends east of the Zanga River on the Saraibulakh and Daralagez ridges.

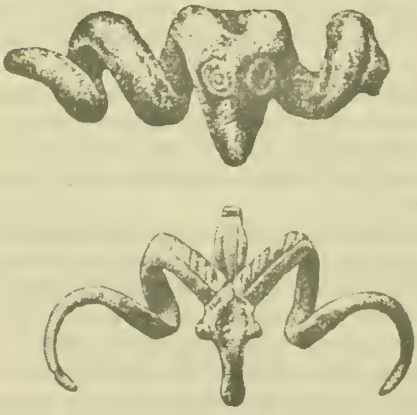

FIGURE 154. Bronze heads of argali-like sheep from Kobanian burials of North Ossetia Uvarova, 1900)

In 1947 the species was rare in the environs of Abrakunis, Dzhulfa, Negram and Ordubad and on the Darry-Dag and Ilyanlu-Dag mountains, and only a small number inhabited the Zangezur ridge, particularly the vicinity of the villages of Bichenakh and Shakhbuz.

The contemporary range of mouflon in Transcaucasia is associated with the upland steppes where groupings of dense xerophytic grasses and sibbaldia predominate, with formations on mountain slopes of thorny astragali in the middle zone, and with salt—wormwood groupings in the Araks valley. The summer habitat of the species is in the high mountains and their descents into the warmer valleys are made mainly in winter.

It can be supposed from the general distribution of sheep in Eurasia (Nasonov, 1923) that argali and mouflon are newcomers to the Caucasian Isthmus. Their range expanded from a southern focus after the development of a xerophytic landscape.

The distinctiveness of argali-like sheep and mouflon-like sheep cannot be considered as mere geographic variations of a single species, since the divergence between the two can be traced as far as the Middle Pleistocene (Vereshchagin, 1953c).

The immediate future of wild sheep on the Caucasus, like that of other ungulates, will depend mainly upon the effectiveness of hunting regulations.

376 The argali-like sheep should be settled in central Dagestan in Gunib, Botlikh and Khunzakh.

Primitive and Caucasian bison — Bison sp., B. cf. schoetensacki Freud., B. priscus Boj., B. bonasus caucasicus Sat. Bison remains occur in Eurasia from the Upper Pliocene, the earliest finds — horn stems of the small bison Bison sp., B. cf. schoetensacki — being in Upper Pliocene Apsheron clays in Kabristan (eastern Transcaucasia) and in conglomerates on the Taman Peninsula (Burchak-Abramovich, 1949; Vereshchagin, 1957a).

FIGURE 155. Caucasian bison

Middle Pleistocene remains of a larger bison — B. priscus longicornis — and Upper Pleistocene remains of a smaller one — B. priscus deminutus — have been found in many localities in Ciscaucasia and western Transcaucasia. Most of the finds were made in lacustrine-fluvial and cave strata (Map 92).

The form was rare in the Pleistocene of eastern Transcaucasia and of the Armenian and Iranian uplands, even being replaced by primitive tur. Its absence from the Binagady complex is especially puzzling. To the southwest, however, it occurs quite commonly in caves of Lebanon, Syria and Palestine in strata from the Acheulean to the Neolithic (Picard, 1937).

The trend toward a smaller size in the bison of Eurasia which can be observed at the end of the Pleistocene was reinforced and fixed by the harassment of man and the aridity of the landscape. There is no reason to attribute this phenomenon to "deterioration" of the climate in the Upper

Pleistocene, as zoologists and paleontologists have often done. The cooling of the climate and the development of meadow formations caused an increase in the size of bison in the Middle Pleistocene. The contemporary Caucasian
377 bison (Figure 155) is undoubtedly a direct descendant of the local Pliocene-Pleistocene bison.

At the same time that the bison size diminished in the Upper Pleistocene and postglacial periods, the populations became isolated in river valleys, on high plateaus and in broadleaf forests on the mountain slopes. The Caucasian bison has not retained the steppe habits of its Pleistocene ancestors and American relatives. It has become an inhabitant of the mesophytic forest-steppe and the mountain forest zone. Its remains have been observed in certain localities of western Transcaucasia and the Lesser Caucasus.

In the Middle Ages the Caucasian bison population was probably linked to the bison population of Eastern Europe by way of the wooded valley of the Don.

The different fates of the Eurasian bison and the American bison in the Holocene were caused by different anthropogenic effects (Vereshchagin, 1956). The survival by large bison and turs of the destructive mounted assaults of hordes of Khazars, Polovtsians, Kipchaks and Mongols would have been strange indeed. They did survive, however, into the 16th century in Great Lithuania and Mazovia (Vizhener, 1890 edit.) where they were hunted with spears ("metabulo"), and into the 18th century in western Siberia (Bell, 1776). Pidoplichko's assertion (1951) that the European bison of the Pleistocene was a permanent inhabitant of the steppe is not well founded.

It is strange that among ancient Caucasian artifacts scuptural and graphic representations of bison are almost unknown; only some unrealistic figurines of bulls that somewhat resemble bison have been found among bronze trinkets of the Kobanians. References to Caucasian bison in literature date from the Middle Ages.

Rashid ad-Din (1946 edition) writes that when Abaga-Khan was wintering in Arran in 1275-1276, he and five farsang (Parsees) from Shahrud hunted the "mountain buffalo" in the forest. In describing a hunt of the Ghazan-Khan in Talysh in 1301-1302 (pp. 188-189), this chronicler reported: "After this the warriors organized a round-up and chased the game — mountain buffalo, dzhurs, wild goats and asses, jackals, foxes, wolves and bears and all kinds of wild animals and beasts of prey — inside the fence until they all were gathered in that enclosure." The author probably referred to roe deer ("dzhuyurs") as "dzhurs," and to Bezoar goats or goitered gazelles as "wild goats."

It is noteworthy that tales of wild bulls in Talysh and the El'brus Mountains were repeated up to the 19th century (Ménétries, 1832). Brandt's critical survey (1867) added nothing new on this subject. It is possible that the extinction of bison in the forests of El'brus and Talysh occurred at approximately the same time as it did in the forests of the central Caucasus, i.e., in the 18th-19th centuries.

The earliest literary reference to bison in Circassia is probably that of Jean de Luc (1625, 1879 edition) and Arcangelo Lamberti's (1954) is the first allusion to the species in Abkhazia.

It was known in Moscow that the bison existed in Kabarda, Ossetia and Ingushetia long before the publications of Academicians Lovich, Güldenstaedt and others who are considered the earliest discoverers of bison on the Caucasus (Bashkirov, 1940).

Page 7994 of the 10th volume of "The Complete Collection of Statutes of the Russian Empire, 1649" gives this directive:

"Written Order from the Cabinet of Her Majesty the Empress Anne Holstein [daughter of Ivan V] to the Astrakhan Obercommandant — on the yearly catching of various living animals to be sent to the Court and to the Izmailovo menagerie... It is known to us that there are in Kabarda wild bulls and kdosy [bison] which they call dombai, for the sake of which you
378 shall do your best and not spare money from the Treasury in order that the local princes shall command the catching of five or ten such bulls and young cows and send them to the Kizlyar fortress. There they should be lured with bread, and when they are habituated to it, you shall send them to Moscow together with the other animals. Write this to the Gori Shah and to the commandant of the Kizlyar fortress and to the Elmurza of Cherkassia, asking them to do their utmost for the capture and dispatch of these bulls and cows."

FIGURE 156. Bison skulls in the Digorized cave

Photograph by author, 1947

It is possible that bison still inhabited North Ossetia at the time of Güldenstaedt's journeys in 1770-1774.

Dinnik (1890a) was able to find old men of the village of Zadalesk who told him how their fathers and grandfathers killed the bison-dombais with iron bullets. There is an inscription carved on one of the skulls of the Digorized cave which reads "1833" and may signify the date when one of the last bison was killed (No. 10, North Ossetia Pedagogic Institute) (Figure 156).

By the middle of the 19th century bison survived only in the mountains and forests of the northeastern Caucasus, from which they gradually disappeared in several stages. The range limit in the north was probably the longitudinal course of the Kuban, including the mouth of the Malyi-Zelenchuk, and in the west the Pshish River. A comparative reading of recorded folklore led Bashkirov (1940) to assume that bison very possibly
379 inhabited the upper reaches of the Shakhe, Sochi, Mzymta, Psou, Bzyba, Kodor and Ingur.

In the 1870's there remained a total of more than 2,000 head of bison.

Little by little, the Caucasian wars and the settlement of Cossacks in the foothills drove the bison to the upper Belaya-Laba interfluve. The decline in population and the shrinkage of the range continued without interruption as cattle breeding and hunting expanded and deforestation proceeded.

By the 1890's the Caucasian bison population was estimated at 500-700 head (Satunin, 1898), and by 1918 Kulagin's census was only 442.

FIGURE 157. Bison (male) in a fir forest

Photography by D. F. Filatov, 1909

The establishment in the 1890's of the Grand Duke's hunting preserve in a 522-dessiatina tract [1 dessiatina — 2.7 acres] of the Kuban and the control of poaching in this area halted the decline to a certain extent.

Filatov's investigations (1910, 1912) revealed a further contraction of the bison range; this map shows a distribution area only in the upper Belaya-Bolshava Laba interfluve. He placed the bison population at that time at several hundred, mostly inhabitants of fir forests (Figure 157).

After the 1917 Revolution, the Kuban hunting preserve was overrun by cattle herders, lumbermen, army deserters and hunters armed with triple-barrelled rifles who destroyed nearly all the Caucasian bison in that area.

380 In 1919 an epizootic, probably endemic to domestic cattle grazing in the mountains, broke out among the bison and killed virtually all the rest.

Only 50 animals survived in 1920, at least 20 of them in the Dishi-Khamyshki district, and these too were subsequently driven off by poachers.

The establishment of the Caucasian Reservation in 1924 could not save the bison because of the number of small arms among the local population and the difficulties of protecting the animal in the mountains.

Several bison killings are recorded for the years 1921-1926: near the Cossack village of Lineinaya, 50 km west of Maikop (1921), near Mount Gefo (1923), and in the upper reaches of Kodor on Alous and Mastakan (1925-1926). The latter report from Mount Alous describes the killing of three bison, probably the only survivors, by Imeretian herdsmen, and is the last one on record (Bashkirov, 1940).

With the year 1940, the history of the hybrid Caucasian-American bison begins on the Caucasus (see Chapter VI). These bison possess a greater vital capacity and can live in the mountain forests throughout the northern Caucasus and Transcaucasia.

Primitive bull* — Bos trochoceros Meyer, B. mastan-zadei Burtsch., B. primigenius Boj., B. minutus Malsb. It is customary for a history of the genus Bos to commence with the deposits in northern India in which many Pliocene and Pleistocene fossils of extinct species of Bovidae have been preserved.

Like bison, the genus displayed on the Caucasus a successive series of related forms, which, however, were not as clearly defined as the bison species. In addition, some species represented lateral phylogenetic branches.

The history of the primitive European-type Bos — a branch of B. primigenius — begins on the Caucasian Isthmus with the Middle Pleistocene.

The most ancient find is the skull of a giant B. trochoceros in Middle Pleistocene sands of Adzhi-Eilas south of Yerevan (Avakyan, 1946). Later, Upper Pleistocene finds are recorded for the Apsheron Peninsula bitumens (Bogachev, 1925b; Burchak-Abramovich, 1951d, 1952d), for the Armenian Highland and for Ciscaucasia (Map 93). There the history of Bos on the Caucasus seems to be broken, although burials of the second millennium B.C. (Hittite ? culture) on the Trialet ridge near Tsalka and Kirovokan revealed skulls, metapodia and phalanges of bulls of a size close to the Holocene wild bull.

Related forms on the Caucasus are those of the Middle Pleistocene B. mastan-zadei from the Apsheron bitumens (Burchak-Abramovich, 1952d), and of the Holocene B. cf. minutus, a small postglacial bull from the sands of the Sevan coast (Dal', 1950a). These are isolated localities. The Caucasian B. mastan-zadei did not become an inhabitant of forests and did not migrate to the mountains — an interesting point of

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* [The Russian text uses "tur" here, but to avoid confusion between bull and goat (since, in English, "tur" can also mean Caucasian wild goat) we have substituted "primitive bull" in the translation as the common name for the genus Bos where it is apparent that the reference is to one of the primitive species of Bos.]

difference from the bison. The distinguishing ecological characteristics of these Quaternary species can be observed in the distribution of their remains in Eastern Europe and on the Caucasus.

For instance, to the north of the Caucasian Isthmus, remains of primitive bull are well authenticated from alluvial and diluvial deposits of the Russian Plain river valleys.

The Bos population was less than that of bison throughout its range. The lower percentage of remains of Bos is particularly apparent to the
381 southeast. Table 74 shows the breakdown between authenticated bison and bull skulls collected mainly from river banks and now in museum collections.

TABLE 74. Distribution of finds of bison and bull skulls on the Russian Plain (data from museum collections)

Museums	Bison		Bull	
	no.	%	no.	%
Kazan	23	85.1	4	14.9
Ural	13	76.5	4	23.5
Kuibyshev	11	84.5	2	15.4
Saratov	36	81.8	8	18.2
Astrakhan	67	95.7	3	4.3
Novocherkassk	38	74.5	13	25.5
Stavropol	6	85.7	1	14.3

This distribution confirms to some extent Pidoplichko's statement (1951) that primitive bulls inhabited more humid landscapes and biotopes than did bison.

In Europe, the bull was mainly an animal of the mesophytic forest particularly toward the end of its existence. On the Caucasus and in southwest Asia this was not the case: it inhabited humid valleys and meadows of open plateaus and, of course, was easily exterminated. Recent experience with cattle breeding in the plains of central Asia shows a parallel: the spring ephemeral growth of the desert and semidesert suffices for pasturage for only a short time; later, from June onward, grazing is concentrated in meadow-swamp formations on the shores of lakes that are not stream-fed (e.g., the Chushka-Kul lakes near the city of Turkestan) and in the river valleys. Similar feeding habits can be observed in the coarse-grass steppe: as the dense, scrubby grasses become coarser, the cattle migrate from the steppe to the ravines, gulleys and humid floodplains.

Attracted as the genus is to meadow formations, the primitive bull probably found its optimum biotope in the southern regions — southwest Asia and the Caucasus — at the time of cooling and humidification of the climate.

The habitation of the Apsheron Bos on the Pleistocene semidesert — the eastern Transcaucasian steppes — was probably seasonal, that is, confined to the period of winter-spring ephemeral growth and not including the summer. Primitive bulls did not inhabit the forested and swampy

Transcaucasus, but, to the south, they were common on the wooded and steppe-like plateaus of southwest Asia.

Remains of Bos primigenius found in Mesolithic strata of the Belt cave near Asterabad Bay should probably be correlated with descendants of B. mastan-zadei, a more xerophilous form than European Bos. (The same correlation holds for goitered gazelle remains — Coon, 1951.) B. nomadicus Falc., remains of which are recorded for Lower Neolithic strata from the site of the ancient town of Annau near Ashkhabad (Duerst, 1908), was probably a descendant of the Middle Pleistocene Apsheron Bos.

Two forms of Bos, one large and one small, probably existed on the Armenian Highland at the end of the Pleistocene. Judging by the finds of 382 bones of bulls in the Neolithic strata of Urartu, it can be assumed that both forms were domesticated.

There is no documentation of the existence of Bos on the Caucasus in our time.

Remains of Bos have been found, extraordinarily enough, in kitchen middens of ancient towns on the Russian Plain. However, to interpret this find to mean that the wild Bos was a dangerous enemy of prehistoric man (Gromova, 1931, p. 362) and that man began "to avoid the hunting of this dangerous prey" when domesticated animals were available is very naive. We have Shumerian and Assyrian bas-reliefs showing scenes of hunting to contradict this interpretation.

The explanation lies rather in the sharp decline in the population of this animal in the Neolithic and in the habits of the European Bos which made it difficult to hunt. The bison which lived in the forest and was no less dangerous was hunted throughout the Holocene. In the Middle Ages Bos were encountered only in isolated localities and were often specially protected (Vizhener, 1890 edition).

The Bronze Age and, particularly, the Scythian epoch on the Caucasus have furnished us with representations of bulls: a silver vessel from the Maikop burial (second millennium B.C.) bears a contour drawing — two bronze figures are designed in the form of bulls, and flat gold plates show a bull in profile (Figure 158).

It is likely that contour drawings of bulls and cows on rocks (Figure 159) in Kabristan south of Baku, probably belonging to Roman time, depict domesticated animals (Vereshchagin and Burchak-Abramovich, 1948). A bronze figure of a powerful bull, similar to the primitive species, was found in a Kobanian burial in Ossetia. In the collection of the Historical Museum of the Academy of Sciences of the Azerbaidzhan S.S.R. are many signets and rings with relief representations of bulls which date from the first millennium B.C. and were found in the vicinity of Mingechaur. There is a marvellous representation of a bellowing bull on a gold signet from the Chertomlyk burial in the southern Ukraine.

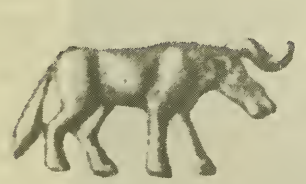

FIGURE 158. Gold plate depicting a primitive bull from the Maikop burial (actual size)

To the south and southwest of the Caucasus, Mesopotamia, Syria and Egypt produced the wonderful bas-reliefs of the ancient Egyptian, Sumerian, Babylonian, Assyrian and Hittite cultures, many of them depicting bulls and bull-hunts, from the second and early first millennia [B.C.] when wild bulls were common in southwest Asia and northeastern Africa. Usamah ibn Munkidh hunted bulls in Syria as late as the 12th century.

We could find no reference to the existence or disappearance of Bos in the histories of the Caucasus. Consequently, we can only infer its history on the Ciscaucasian steppes and on the plateaus of the Lesser Caucasus from references to it elsewhere: the ancient Russian chronicles, "The Lay of the Host of Igor," epic ballads ("byliny") and "The Instructions" of Vladimir Monomakh (see Dolgikh, 1905, Gromova, 1931, Kolesnik, 1936).

It is very probable that Bos became extinct on the forest-steppe of Ciscaucasia and on the Lesser Caucasus some time earlier than it did in Europe.

383 The difficulties of evaluating paleontological, zoogeographical and ecological data to determine species origin and fauna formation are significantly revealed in this survey of the appearance, development and contemporary status of certain Quaternary mammals of the Caucasus.

These difficulties are all the greater in elucidating the origins of eurytopic ubiquitous species (such as European hedgehog, fox and wolf) and several other mass species of the Quaternary (such as deer and bison) which have nearly stable distribution areas. Nevertheless, it is apparent that the local nucleus of the Caucasian mammalian fauna of the Tertiary formed in the Pliocene or even in the Upper Miocene, whereas for the most part the ancestral forms of Quaternary species do not occur in the strata of these periods.

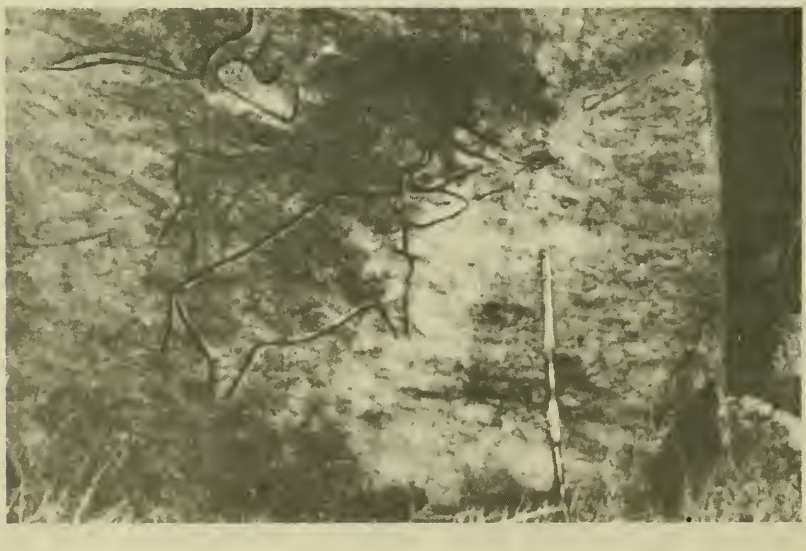

FIGURE 159. Representation of bulls on the rocks of Beyuk-Dash south of Baku

Photograph by author, 1945

The development of the ranges of many Caucasian mammals was demonstrably dependent upon the formation of Quaternary topography.

The characteristics of the ranges depend to a lesser extent upon the species development of morphological-physiological adaptations and the interrelationships of biocenoses.

The history of the development and disappearance of herbivore ranges even suggests that the processes proceeded autonomously within each species, each independent of the other; the harassment of predators exerted a secondary influence on herbivore distribution.

Three principal types of ranges characteristic for Caucasian mammals can be distinguished from species distribution and ecological interrelationships:

384 1. Caucasian forest and alpine type, associated with Tertiary mesophytic forest and mountain-meadow landscapes. Examples: the ranges of moles, Promethean vole, pine vole and chamois.

2. Southwest Asian mountain-desert and mountain-steppe type, associated with Tertiary xerophytic landscapes which developed on the Caucasian landmass in the arid, hot Cezonoic period. Examples: the ranges of Persian and red-tailed gerbil, Asia Minor hamster, steppe vole and wild goat.

3. European-Asian steppe type, associated with steppe landscapes which developed on the Ciscaucasian plains in the Pleistocene. Examples: the ranges of corsac fox, little suslik and saiga.

The secondary phase of mammalian development proceeded during the Quaternary from the bases of these three ranges and resulted from the settlement in the Pleistocene and Holocene of European, central Asian and southern Asian species on the Caucasus. The range of central Asian desert species is the most isolated and alien to the Caucasus (see Chapter V).

Data drawn from the Recent and based on paleontological studies of the distribution areas and on observations of the ecology of the species under discussion provide a broad chronological scheme of the origins of Caucasian Quaternary mammals. Three different age (stratigraphic) groups can be isolated in this fauna: Tertiary (Pliocene), Pleistocene and Holocene.

The assemblage of local Tertiary forms (or their ancestors) which undoubtedly still existed on the Caucasus in the Pliocene was composed of: Insectivora, Chiroptera, Carnivora, Rodentia, Proboscidea, Perissodactyla and Artiodactyla — these formed a part of the base of the Holocene fauna. The assemblage is heterogeneous in both ecology and origin and is subdivided into mesophilous and xerophilous classifications.

The species of the first — mesophilous — subgroup are local; they appeared in mesophytic eastern Mediterranean landscapes, i.e., mountain and lowland broadleaf forests and alpine meadows. They are the Caucasian mole, trogontherium beaver, European beaver, black rat, Promethean vole, Caucasian snow vole, long-tailed snow vole, roe deer and Caucasian goat.

The species in this group are eurytopic and ubiquitous. Pleistocene deposits contain remains of related forms: white-toothed shrew, fox, wolf, bear, deer, tur and bison. From this group the principal survivors are the ubiquitous species, the mountain-forest species and those other species which could adapt to the mountain-forest.

The second — xerophilous — subgroup is composed of thermophilous species, endemic to arid, hot habitats of the eastern Mediterranean, known in zoogeographical literature as Iran-Asia Minor and Mediterranean species. Most of the species migrated to the Caucasian Isthmus from the south and their principal ranges lie in the southern and southeastern Caucasus and extend to the south of the Caucasus. The others survived on the Caucasus from the Pliocene, e.g., the Georgian macaca.

Typical of this subgroup are the stone marten, Asia Minor suslik, common hamster, Persian gerbil, steppe vole and wild goat. Some of these forms can be found now in xerophytic locations on the Greater Caucasus 385 and its foothills, and some only on the southern borders of Transcaucasia. It is very probable that this subgroup comprises relatively eurytopic animals, which, however, tend to be more xerophilous and southern in their adaptations. Examples are the long-eared hedgehog, tiger polecat and migratory hamster; the range of the latter passes through the eastern half of the Caucasian Isthmus, extending from the mountain steppes and semideserts of northern Iran to the steppes of the Russian Plain (see Maps 1, 26, 60). The ranges of some species in this subgroup were developed on the Caucasus in the Pleistocene, in some cases to a greater extent than in the Holocene, e.g., the common hamster and other southwest Asian forms. In other cases, the ranges developed in a northerly direction, i.e., on the plains of Transcaucasia and even in Ciscaucasia in the Upper Pleistocene and as recently as the Holocene, e.g., Asia Minor gerbil, kulan and goitered gazelle.

European-Asian hydrophilous and forest species formed the fauna of the Isthmus. The emergence of European forest-type animals on the Caucasus from Western Europe was feasible in the Tertiary, the Pleistocene and all epochs when the broadleaf forests of Europe and the Caucasus were connected through Asia Minor and the Balkans or through the Russian Plain. The formation of parallel species, especially in mountain forms like lynx, Caucasian snow vole, roe deer and chamois, was also possible.

Those species which penetrated the Isthmus from the north, southwest and southeast belong to the younger — Pleistocene — genetic group. The reasons for their settlement lie in the ancient formation of the landmass of the northern Caucasian Isthmus, in the development of forest and meadow-steppe landscapes during the time of climate-cooling, in the development of steppe and semidesert landscapes in the Ciscaucasian plains during the time of climate-warming. It is very probable that there were two migratory routes to and from the Caucasus open to forest species in the Pleistocene — a northern one along the Don floodplain, and a southwestern one along the northern coast of Asia Minor.

By either of these ways, the elk and the typical European brown bear could have penetrated the Caucasus. Only the northern route would have been feasible for the striped field mouse, the large Asian roe deer and other species; pine marten and European wildcat are more likely and common red-backed vole is certain to have followed the southwestern route. The time of their emergence on the Caucasus probably varied for each of these species — common hamster penetrating a little earlier, European brown bear and Asian roe deer a little later.

The Pleistocene assemblage also included steppe elements: corsac fox, little suslik, saiga and other species which emerged on the Caucasus in the Lower Pleistocene, and steppe lemming which emerged later. In the Pleistocene, the northern steppe influence reached even into eastern Transcaucasia.

The development of southern southwest Asian species was difficult in the Pleistocene because of the progressive cooling.

The so-called interglacial epochs, warm, dry periods, can be traced on the Isthmus from the distribution areas of Turan desert species and, to some extent, of southwest Asian species.

The latest genetic group to emerge on the Isthmus in the Holocene was composed of southern, thermophilous species which migrated to the Caucasus during the postglacial warming and dessication of landscapes. 386 It is comprised of jackal, striped hyena, lion, tiger, jungle cat, kulan, goitered gazelle and probably some Insectivora and Chiroptera. Some of these species became extinct on the Caucasus as the result of human activity.

The Norway rat and the European races of house mouse can be counted as casual species, which were brought by ocean and river vessels of the ancient Greeks, Slavs, Khazars and Varangians, and later by railroad and automobile.

A study of the characteristics of former and contemporary ranges of Caucasian mammals shows the effects of a great natural dynamic on the populations and on the range patterns of isolated species during the Quaternary. It also reveals the significant relationship between the anthropogenic influences of the historical epoch and the populations and ranges of many species.

The discontinuities in the ranges of stenotopic and relatively stenotopic mammals of the Caucasus can be explained in the majority of cases by the alternation of dry and humid epochs during the Cenozoic and the orogeny and glaciation of the mountain ranges.

The most characteristic are the high-mountain breaches in the ranges of Caucasian endemics — Caucasian snow vole, Promethean vole and chamois — in the region of the Surami Range; their age is probably Lower Holocene. Discontinuities in the ranges of mesophilous and forest species, e.g., mole, pine vole and roe deer, are peculiar to central Ciscaucasia and eastern Transcaucasia; some date from the Pleistocene and some from the post-Glacial. Among the xerophilous species, breaks can be observed in the ranges of common hamster, steppe vole and wild goat.

An analysis of discontinuities like these, particularly those occurring in the ranges of rodents, reveals the patterns of two xerothermic epochs on the Caucasus — one in very ancient and the other in Recent time. The effects of a cold, humid epoch between these two can also be traced.

Chapters IV and V are devoted to a general analysis of the distribution of all Holocene animals, based on zoogeographical maps, and to an attempt to evaluate with some precision the degree and kind of faunistic influences of the adjacent territories through a study of the stratigraphic and geographic variabilities.

387 *Chapter IV*

STRATIGRAPHIC AND GEOGRAPHIC VARIATION IN CAUCASIAN QUATERNARY MAMMALS*

The study of the phylogeny of Caucasian Quaternary mammals presents many problems.

The fossil remains from most localities are fragmentary, and suffer from post mortem crushing, making biometric studies very difficult. Skull material and skins of Recent small animals have been collected in different years and seasons by many workers using a variety of preservation. For these reasons conclusions on the spatial distribution and evolution of animal species are not always reliable and convincing. For example, the annual and seasonal changes in growth rate and weight among rodent populations with short life cycles (e.g., moles and voles) may be more pronounced than variation which is related to local environmental changes.

Insectivores and murids preserved in spirit and by dry method are of little use for detailed systematic study, as pointed out by Shidlovskii (1953a, b, 1954a, b). Data on geographic variation in fur-bearing animals is mostly based on information from the fur-trading stations and must be accepted with reservations, as a study of this type must take into account individual, sex and age variability within the populations.

It is felt that comparative study of the morphology and systematics of the mammals of the Caucasus and the Russian Plain may contribute to an understanding of the development of the fauna, and therefore a summary
388 of data on some orders is presented below. Most of the work on the evolution of the species through time has been based on better material, more amenable to biometric study.

Order INSECTIVORA

The number of fossil insectivores in the Caucasus is negligible. The Middle Pleistocene hedgehogs (Hemiechinus aff. auritus and Erinaceus aff. europaeus) from the bitumens at Binagady on the Apsheron Peninsula are practically indistinguishable from the Recent forms in size and structure of the mandibles and teeth.

The geographic variation of the common hedgehog in the Caucasus is reflected in the darker spines and abdominal fur in gray woodland and wooded lowland populations. Dark varieties — Erinaceus europaeus concolor, E. europaeus ponticus — occur on the Black Sea

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* Because it seems to us more correct to refer to evolutionary and geographic changes in living organisms as variation we reserve the more commonly used term variability to denote individual and age changes.

coast of the Caucasus and in Asia Minor, the Eastern European E. europaeus rumanicus is found in Ciscaucasia, and the light-colored E. europaeus transcaucasicus in the semideserts of Transcaucasia.

The variation in the Recent long-eared hedgehog is slight over the Caucasian Isthmus. The populations of the small forms, Hemiechinus auritus calligoni and H. auritus brachyotis, occur in the semideserts of eastern Ciscaucasia and in the middle Araks valley.

Detailed information on the stratigraphic variation of the Caucasian moles (genus Talpa) is not available. The Recent mole populations can be subdivided into distinct geographic varieties, particularly in the areas which became isolated long ago.

The biggest Caucasian moles (Talpa caucasica ognevi) inhabit the southern slopes of the western half of the Greater Caucasus and the Trialet ridge (Ognev, 1926a, 1928; Stroganov, 1948)*. The moles decrease in size to the south and southeast. Populations of the smallest varieties, T. orientalis transcaucasica and T. orientalis talyschensis, occur in the ridges of the Armenian Highlands and in the forests of Talysh. These populations are isolated from the main area of distribution of the species; however, N.K. Deparma has recently found a relatively small population of moles in the southeastern Caucasus, even smaller than the Talysh population.

The size of the skulls and metatarsals of the Caucasian moles is given in Table 75.

(385) TABLE 75. Geographic variation in size (mm) of Caucasian moles*

Measurements	West of Greater and Lesser Caucasus Talpa caucasica ognevi 8 specimens	Greater Caucasus Talpa caucasica caucasica 240 specimens	Lesser Caucasus Talpa orientalis orientalis 170 specimens	Lesser Caucasus Talpa orientalis transcaucasica 62 specimens	Talysh Talpa orientalis talyschensis 3 specimens
Condylobasal length of skull	35.9 35.1-37.2	33.9 33.1-35.7	30.1 29.8-32.6	32.4 31.3-33.0	29.6 29.5-29.8
Length of upper tooth row	14.5 14.0-15.0	13.4 12.5-13.8	12.2 11.9-12.7	11.2 10.5-11.7	11.1 11.0-11.2
Length of foot	19.6 19.0-20.0	18.3 17.5-19.2	16.9 16.0-17.9	16.5 14.2-17.5	15.5 15.0-16.0

Note. Mean value of observed ranges in the numerator, limits in the denominator.

* Measurements by Stroganov (1948), Dal' (1944a), Vereshchagin (1945b) (Talysh).

This size decrease to the southeast may be attributed to the prolonged isolation of moles on mountain ranges under conditions of increasing

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* In 1948 S.U. Stroganov tentatively identified 8 specimens of moles from the region of Kutaisi and Borzhomi as the Italian mole T. romana ognevi. Subject to the final clarification of affinities of the Caucasian and west Mediterranean moles, we regard this form as a subspecies of T. caucasica; T. europaea transcaucasica, described by Dal' (1944a) from the Pambak ridge, is tentatively referred to T. orientalis.

draught, increasing annual temperatures and depletion of food resources, i.e., land invertebrates.

The speciation of the Caucasian shrews can be understood in the light of the fact that these mesophilous forms, like the moles, were isolated for a long period in the forest-mountain massifs.

389 Recent shrews of the genus Sorex on the Caucasian Isthmus (e.g., Sorex minutus) also decrease in size from west to southeast. The Caucasian population of the common shrew is at present regarded as a subspecies of the European shrew, S. araneus satunini (Ognev, 1928). This shrew is distinguished by a short, wide nasal region and shorter mandible, etc.

There are, however, certain larger local species of shrews which have evolved in the Caucasus, for example, the darker-colored and long-tailed S. raddei, closely related to the European S. araneus.

European water shrews in the Caucasus (genus Neomys) are morphologically and ecologically more specialized than land shrews, but their genetic relationships are not well known. The forms described — Neomys leptodactylus, N. schelkovnikovi, N. balcaricus and N. dagestanicus — are regarded here as subspecies of the European N. fodiens. The first two of the above are characterized by narrow paws, as pointed out by Satunin (1915a), whereas the Dagestan subspecies is characterized by a poorly-developed tail, pale coloration, etc., characters typical of animals inhabiting lands with progressive desiccation (Spain, the Crimea).

The structure of the skull and teeth of the white-toothed shrews of the Middle Pleistocene from the Binagady burial (Crocidula russula, C. leucodon) does not differ significantly from the contemporary forms inhabiting eastern Transcaucasia. Southern white-toothed shrews are much more widely distributed over the Caucasian Isthmus than other species; particularly abundant is C. russula güldenstaedti which inhabits both the dry and the humid zones.

Geographic color variation is well seen in the Recent species and is directly related to the aquatic biotopes in the hot semidesert and humid shady forests of Colchis and Asterabad. According to Shidlovskii (1953b), the long-tailed shrews of Transcaucasia are smaller and darker in the humid forests of the coastal plains of the Black and Caspian seas than in the
390 center of the country and in the dry areas of eastern Transcaucasia (Table 76).

Clearly, if the isolation of the Caspian shrew can be proved, then any similarity in color will be the result of convergence due to the ecological similarity in the areas of Colchis and Asterabad.

Order CHIROPTERA

With a few exceptions, fossil Chiroptera are known in the Caucasus only from the Holocene beds. Thus there is no basis for discussion of the phylogenetic changes in this order. According to the data available in the literature (Bobrinskii, Kuznetsov, Kuzyakin, 1944; Kuzyakin, 1950), the geographic variation in some Caucasian Rhinolophidae is expressed in the development of lighter coloration from northwest to southeast and in the increase in body size with increasing altitude above sea level (R. hipposideros, R. ferrum equinum).

The widely distributed genera Myotis and Vespertilio are sometimes intermediate between the European-Siberian and central Asian populations (e.g., Myotis mystacinus), while other species (e.g., Vespertilio serotinus) are closer to the European forms.

TABLE 76. Geographic variation in dimensions (in mm) and coloration of long-tailed shrew in Transcaucasia*

Dimensions and color	Western Transcaucasia, Colchis Crocidura russula monacha 150 specimens	Central Transcaucasia, Kura valley Crocidura russula güldenstaedti 170 specimens	Eastern Transcaucasia, Talysh Crocidura russula caspica 40 specimens
Body length	$\frac{70.6}{60\text{-}89}$	$\frac{74.1}{60\text{-}91}$	$\frac{70.6}{63\text{-}80}$
Foot length	$\frac{12.7}{11.0\text{-}15.0}$	$\frac{13.0}{11.0\text{-}15.0}$	$\frac{13.1}{12.0\text{-}13.6}$
Condylobasal length of skull	$\frac{18.1}{16.7\text{-}19.4}$	$\frac{18.7}{17.5\text{-}19.8}$	$\frac{19.3}{18.6\text{-}20.2}$
Length of upper tooth row	$\frac{8.1}{7.6\text{-}8.8}$	$\frac{8.2}{7.3\text{-}8.9}$	$\frac{8.9}{8.3\text{-}9.4}$
Color	Whole body dark chestnut brown, tail very dark all over	Upper part of body gray-brown, lower part grayish white; tail uniformly dark	Whole body dark chestnut brown, tail uniformly dark

Note. Mean value of observed ranges in the numerator, limits in the denominator.

[*] According to Shidlovskii (1953b), whose measurements are given in the above table, C. russula caspica must be identified as a distinct species, C. caspica. This, however, needs further study, since the long-tailed shrew is a highly variable species, both ecologically and morphologically.

391 In order to reach reliable conclusions on the geographic variation in the Caucasian bats, good southwest Asian data must be studied, as the ranges of distribution of most of the species extend from the Caucasus far to the south and southwest.

Order CARNIVORA

The paucity of carnivore remains in Quaternary burials causes difficulties in the study of the morphological evolution of this order. The only exception is the Binagady locality, where there are particularly numerous canid remains.

The Middle Pleistocene Caucasian wolves are characterized by a smaller brain cavity, narrower nasal cavities, a narrower cheek region, shorter upper tooth row and smaller intertemporal width (Figure 160). It is of interest to note that no differences were recorded in the shape and structure of the teeth themselves. The decrease in the length of the upper tooth row was due both to closer spacing of the teeth and to the gradual disappearance of M^3. In 33 wolf skulls from Binagady, M^3 was present in only 2 (i.e., 6%). Out of 222 skulls of Recent wolves from the U.S.S.R., M^3 was found in only 0.9%. Changes in the limb bones are reflected in the gradual narrowing of the scapulae with time (Vereshchagin, 1951b).

The present geographic variation of the wolves on the Isthmus has been poorly studied; however, it is known that the wolves of the Transcaucasian plains are somewhat smaller than those of Ciscaucasia, while the Armenian Highland forms are larger. According to Dal' (1951a), the Armenian Canis lupus hajastanicus is no smaller in size than the Kuban wolf, and is distinguishable from it by its long, soft fur; its back is bright whitish gray and yellowish with a black tint. The fur traders in the Caucasus distinguish the "steppe", relatively light-colored wolves of the open plains, and the darker varieties from the "forest". Wolves of bright iron-rust color occur in Kabarda. This is a fairly rare example of an aberrant variety. Three skins of this variety are in the collections of the ZIN Museum.

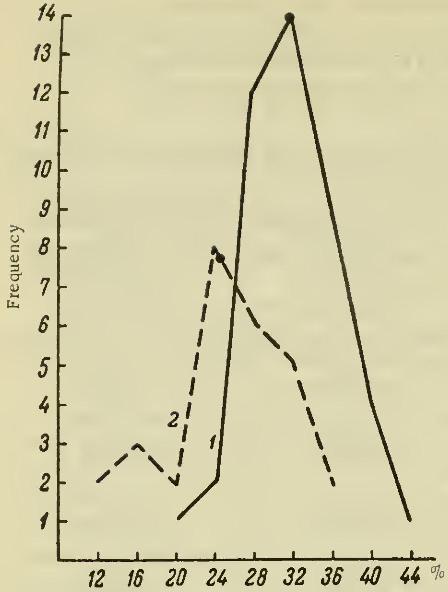


FIGURE 160. Variation in the temporal index (ratio of the intertemporal width to the length of the brain case expressed as a %) of Middle Pleistocene wolves from the Caucasus

1 — Recent Canis lupus cubanensis; 2 — Fossil C. lupus binagadenis, eastern Transcaucasia, Binagady. Dots indicate mean values

The probable Middle Pleistocene ancestor of the Recent fox, Vulpes khomenkoi from the fossiliferous beds in eastern Transcaucasia, is characterized by small molars and short canines, like those of the Arctic fox (Bogachev, 1938c; Vereshchagin, 1951b). Towards the end of Middle Pleistocene times (Khazar stage) the fox evolved into the modern form and the subsequent changes in the structure of the skull have been negligible. 392 The cranial features of the Middle Pleistocene foxes of eastern Transcaucasia (Binagady), however, are quite variable. This variation is characteristic both of the Recent fox of the Kura Lowlands (Vulpes vulpes alpherakyi) and the foxes of the highlands — V. vulpes kurdistanica, V. vulpes alticola. The basic structure and size of their teeth, however, does not differ from the former species, as shown in the graphs (Figure 161).

The skull size and fur of the Recent Caucasian foxes display a marked geographic variation. The general pattern of variation has been traced on individual skulls and pelts by Ognev (1931), who published a distribution map of the described subspecies of Caucasian foxes: Vulpes vulpes stepensis, V. vulpes karagan, V. vulpes caucasica, V. vulpes alticola, V. vulpes kurdistanica, V. vulpes alpherakyi.

The distribution of the Caucasian foxes, based on the differences in the fur coloration (material studied at fur-trading posts), has been accurately described by Kuznetsov (Bobrinskii, Kuznetsov, and Kuzyakin, 1944).

The first distribution map of local variation (in such features as fur color and other associated characters) and size variation in the Caucasian foxes was published by us (Vereshchagin, 1947d).

Pelts obtained in the course of hundreds of years are subdivided into six races by the local fur traders: Ukrainian, Don, Kuban, North Caucasian, Yerevan and Transcaucasian.

Our study of the pelts of more than 13,000 specimens of foxes at the Rostov and Tbilisi fur stations may be briefly summarized as follows.

393 **Ukrainian.** This race is subdivided into north and central Ukrainian. These are big foxes with relatively stiff guard hair, rusty white on the back and straw on the sides. The belly is mostly rust in color and the upper surface of the paws is black. This variety occurs, though rarely, in the Ciscaucasian plains. Populations of these foxes occur in pockets among the typical north Caucasian foxes, from the northwestern Manych region to the Kabarda plains. According to the fur traders, the presence of this variety in the 1940's in Ciscaucasia was noticed only after World War II.

Don. Fairly large light-colored foxes, rusty white, with red shoulders and belly. The guard hair is shorter than in the Ukrainian race. The most commonly occurring colors are probably related to age and sex: rust, light rust, rust gray; more rare are dark rust and gray rust specimens.

These foxes lived round the coast of the Sea of Azov, the lower reaches of the Don, and the Sal'sk steppes. In the east their range extends to the Yegorlyk, in the south, to the Yeya.

(392)

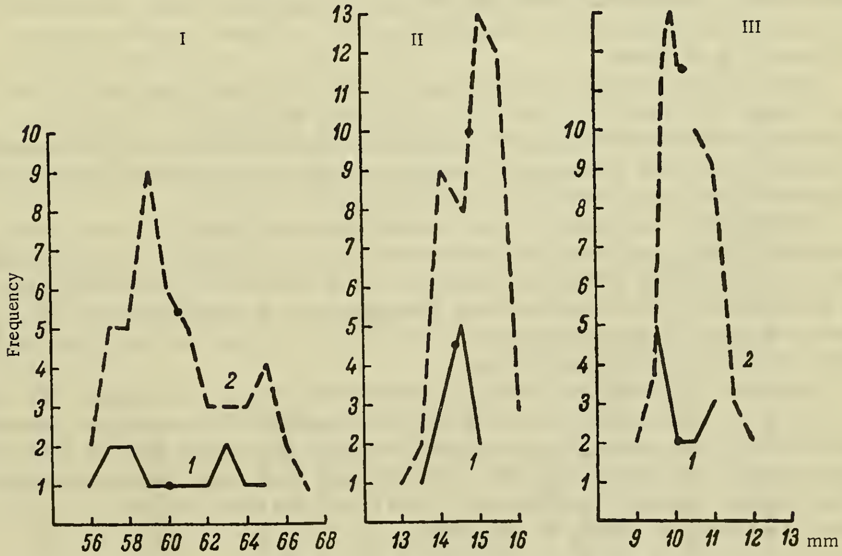


FIGURE 161. Variation in tooth size of Transcaucasian Middle Pleistocene foxes

I — length of lower molar row; II — length of crown of M_1; III — length of crowns of M_2+M_3; 1 — Recent Vulpes vulpes alpherakyi; 2 — fossil V. vulpes aff. alpherakyi; eastern Transcaucasia, Binagady. Dots indicate the mean values

Kuban. These foxes are somewhat larger in size than the Don race. The characteristic bright rust and even reddish color on the face, back and, particularly, neck and shoulders produces a noticeable "cross" pattern. The guard hair on the back is shorter than that of the Ukrainian race. Individuals of very rich rust color are most common, while rust gray individuals are less abundant, and even more rare are the light rust forms.

The range of this race is on the steppes of the Kuban region, on the Trans-Kuban inclined plain from the Kerch Strait in the west to the Kuban-Kuma water divide in the east.

North Caucasian. These are foxes of a somewhat smaller size than those of the Kuban race. The fur is coarse; on the back the guard hair often forms "curls" — patches of standing coarse hair. The belly is black to dark gray. These foxes occur in two varieties, the red and the paler red-gray forms, the latter becoming more abundant to the southeast. The foxes identified as V. vulpes caucasica belong to this variety.

The distribution of this race is from central and eastern Ciscaucasia, from the Trans-Kuban Plain to the Caspian coast, and from the lower Kuma and Terek to the Samur. Pelts of such foxes also come from eastern Transcaucaia and show great similarity in coloration and other features with the eastern Ciscaucasian form.

Transcaucasian. This race is represented by the small foxes of the eastern Transcaucasian plains. They are subdivided into three varieties: Transcaucasian red, Transcaucasian red-gray, and Transcaucasian gray. Their fur is relatively coarse and short, often with considerable admixture of black hair on the rump and shoulders. The foxes are characterized by a yellowish rusty "band" of variable width, which runs along the length of the back. The band is particularly conspicuous in the paler colored young specimens; as a rule, young individuals are gray in color. The small fox of eastern Transcaucasia, described as V. vulpes alpherakyi, belongs to this race.

Foxes of the Transcaucasian race inhabit the lower reaches of the Terek and Sulak, the western coast of the Caspian, the plains of eastern
394 Transcaucasia and the middle Araks valley. In the forties, the Transcaucasian Vulpes vulpes karagan, disseminated in the fox population of eastern Transcaucasia, was identified as belonging to this race.

By the state standards of the forties, this is a small fox with soft uniformly dark gray and even somewhat dark brown fur. The limbs below the elbow and knee joints are black or black-brown. This variety has little in common with the central Asian karagan fox, as the former is an aberrant form, a dark-colored variety of V. alpherakyi, like the black-brown varieties of the arctic fox.

Yerevan. A large fox, though smaller than the Ciscaucasian fox, with a weakly ossified skull. It is clearly distinguishable from other Caucasian varieties by its extremely thick and soft fur. The guard hair is very long and silky to the touch, and the color varies from light yellow to a dirty rust brown. Foxes identified as V. vulpes alticola and V. vulpes kurdistanica belong to this race.

TABLE 77. Distribution of pelts (in %) of different fox races in regions of the Caucasus*

Sites of skin collection	Ukrainian	Don	Kuban	North Caucasian red	North Caucasian red-gray	Transcaucasian red	Transcaucasian red-gray	Transcaucasian gray	Karagan	Yerevan	Cross fox; gray	Mongrel	Number of skins studied
Sal'sk steppes, Veselyi village	20	75	5	—	—	—	—	—	—	—	—	—	301
Kuban steppes, Slavyanskaya	6.2	—	47.4	46.0	—	—	—	—	—	—	—	—	352
Trans-Kuban Plain, Novo-Labinskaya	23	—	72	5	—	—	—	—	—	—	—	—	310
Manych steppes, Arzgir	2.3	3.5	0.3	88.5	—	—	—	5.2	—	—	—	—	1,250
Terek-Kuma steppes, Mozdok . .	0.2	—	2.5	97.0	0.5	—	—	—	—	—	—	—	1,199
Foothills of Dagestan, Buinaksk	—	—	—	57.5	3.5	9.0	3.5	32.5	—	—	—	—	872
Caspian Coast, Derbent	—	—	—	10	53	—	—	17	—	20	—	—	566
Colchis Plain, Lanchkhuty	—	—	—	—	—	—	—	—	—	21	—	79	19
Central Transcaucasia, Staliniri	—	—	—	—	—	—	—	—	—	33	—	57	76
Central Transcaucasia, Tbilisi. . .	—	—	—	2	1.5	15.3	24	18	2.5	34.2	2	—	3,704
Mugan Steppe, Sabirabad	—	—	—	—	24	—	8.5	65.5	2	—	—	—	685
Armenian Highland, Yerevan . . .	—	—	—	0.2	11.6	5.6	—	10.0	—	72.5	—	—	3,738
Araks valley, Nakhichevan.	—	—	—	26	10	13	—	23	—	28	—	—	127

* Data in this and following tables were collected by the author in 1945 at the Rostov fur station.

(396) TABLE 78. Geographic variation in size (cm) of fresh fox pelts from the Caucasian Isthmus and the Ukraine

Races and fur station	Length from nose to tail base	Middle width	Area of pelt (cm^2)	Length of tail without fur	Number of skins measured
Central Ukrainian, Stalino	$\frac{85}{79-90}$	$\frac{24}{23-25}$	4106	$\frac{44}{42-47}$	31
Don, Novocherkassk	$\frac{76}{73-86}$	$\frac{22}{21-26}$	3384	$\frac{42}{39-45}$	34
Kuban, Slavyanskaya	$\frac{79}{71-94}$	$\frac{22}{19-25}$	3424	$\frac{44}{37-45}$	30
North Caucasian, Blagodarnoe	$\frac{76}{70-86}$	$\frac{21}{19-24}$	3380	$\frac{41}{35-43}$	28
Mongrel, Batumi	$\frac{77}{70-88}$	$\frac{14}{14-17}$	2174	$\frac{39}{37-43}$	28
Mongrel, Tsalka	$\frac{76}{70-84}$	$\frac{15}{15-17}$	2312	$\frac{40}{40-44}$	34
Transcaucasian, Yevlakh	$\frac{68}{66-80}$	$\frac{16}{16-22}$	2208	$\frac{38}{38-44}$	36
Transcaucasian, Baku	$\frac{66}{54-76}$	$\frac{15}{13-22}$	2020	$\frac{34}{24-45}$	65
Yerevan, Tsalka	$\frac{75}{70-84}$	$\frac{15}{13-18}$	2302	$\frac{42}{35-45}$	23
Yerevan, Yerevan	$\frac{77}{70-90}$	$\frac{20}{17-21}$	3048	$\frac{43}{40-48}$	29

Note. Mean value in the numerator, observed range in the denominator.

These species inhabit the Armenian highlands, and probably the ranges of northwestern Iran and eastern Turkey in the south. Similar though not identical skins come from the highlands of the Greater Caucasus, particularly from south Ossetia and central Dagestan.

It should be mentioned that the age variation of the animals could not be taken into account in the construction of the distribution map of the fox races (Figure 162) and the diagram of the distribution of different color types (Figure 163). The distribution and relative proportions of the different races are given in Table 77.

397 Unusual coloring is observed occasionally in certain strains of Caucasian foxes, e.g., the "sivodushka", which has dark blue-gray to black fur on the belly and blackish brown fur on the back. Another type is the cross fox, which has reddish yellow background fur with a dark brown cross extending from the nape of the neck to the tail. This form occurs occasionally in Ciscaucasia and Transcaucasia. Peculiar silver foxes with chocolate-purple fur are occasionally found in Dagestan. Silver foxes rarely occur in the Zakataly and Nukha regions in Transcaucasia, only 1–2 specimens being found in 20,000 animals.

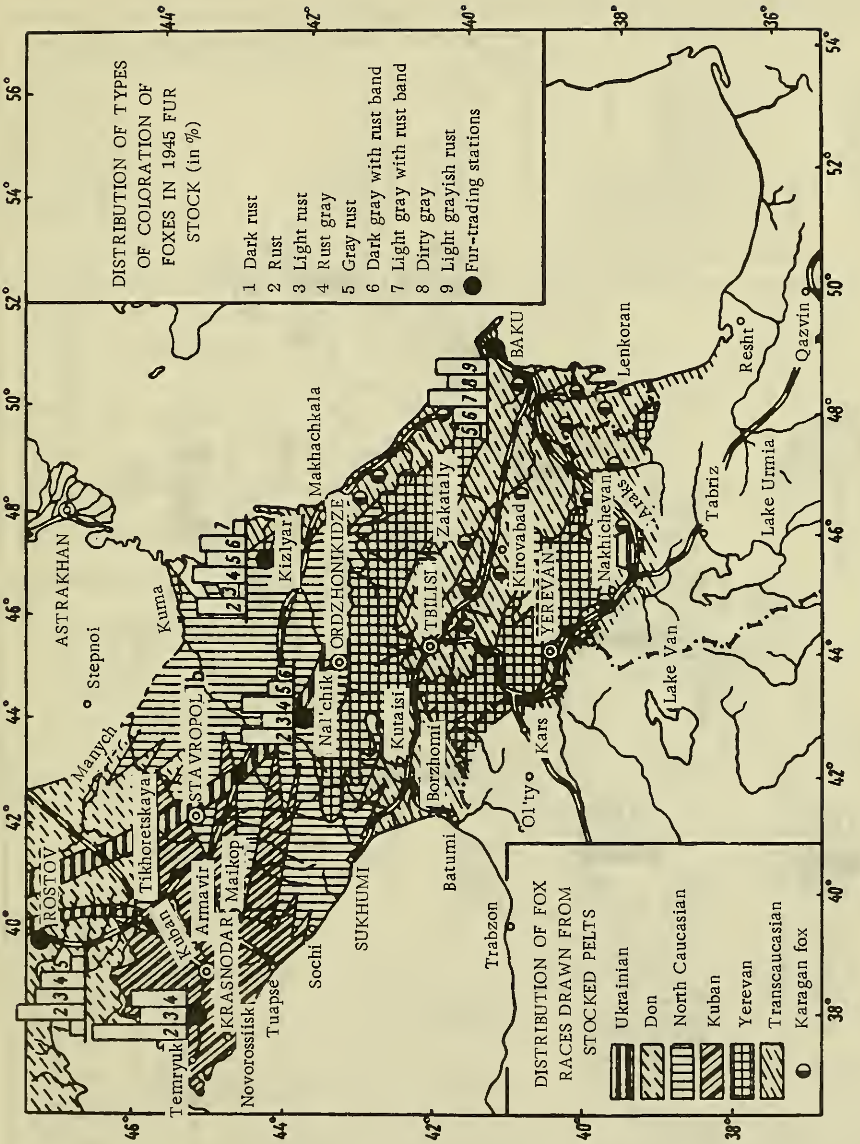
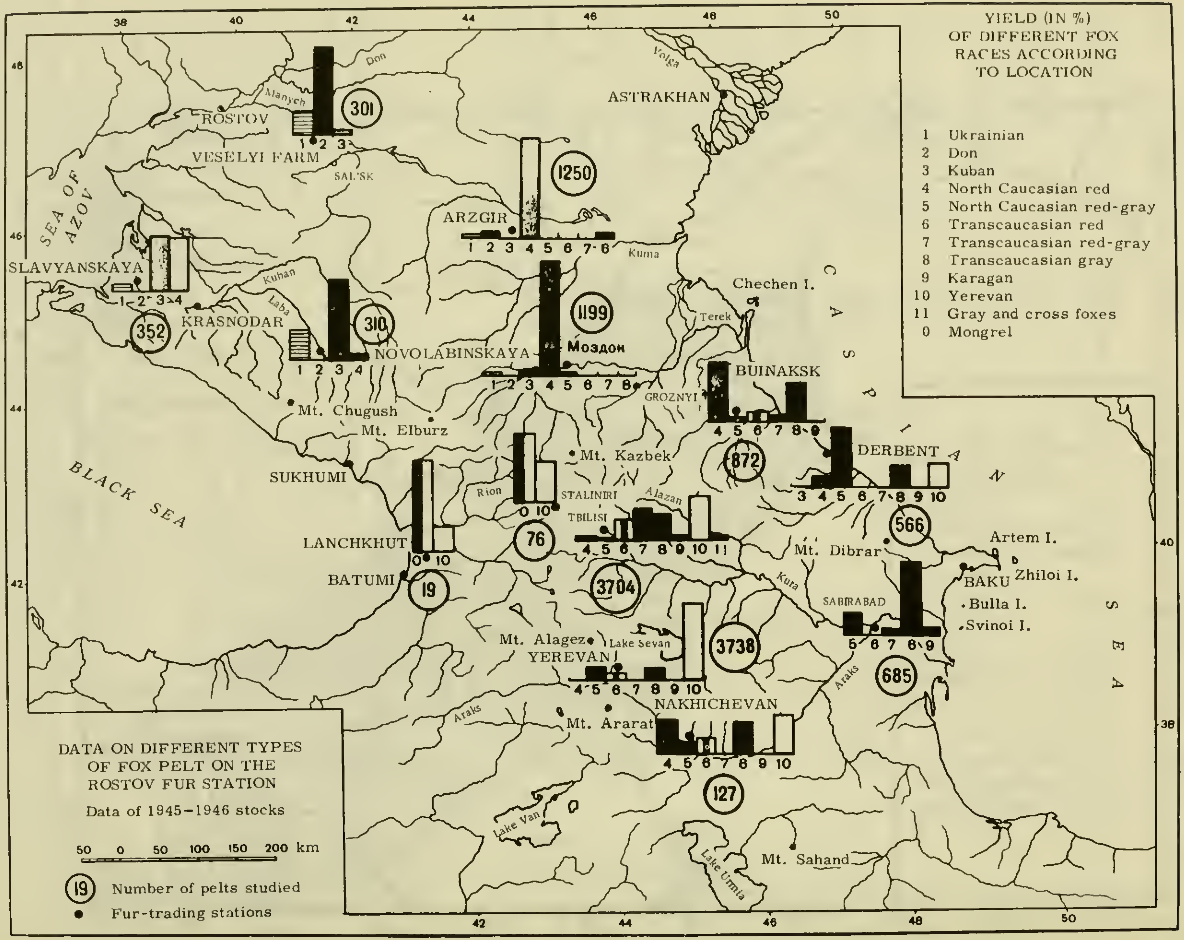

DISTRIBUTION OF TYPES OF COLORATION OF FOXES IN 1945 FUR STOCK (in %)
1 Dark rust
2 Rust
3 Light rust
4 Rust gray
5 Gray rust
6 Dark gray with rust band
7 Light gray with rust band
8 Dirty gray
9 Light grayish rust
● Fur-trading stations
DISTRIBUTION OF FOX RACES DRAWN FROM STOCKED PELTS
Ukrainian
Don
North Caucasian
Kuban
Yerevan
Transcaucasian
Karagan fox
ASTRAKHAN
Stepnoi
Kuma
Manych
ROSTOV
Tikhoretskaya
STAVROPOL
Kuban
Armavir
KRASNODAR
Maikop
Temryuk
Novorossiisk
Tuapse
Sochi
SUKHUMI
Nal'chik
ORDZHONIKIDZE
Kizlyar
Makhachkala
Kutaisi
TBILISI
Zakataly
Borzhomi
Batumi
Trabzon
Ol'ty
Kars
Kirovabad
YEREVAN
Nakhichevan
Araks
BAKU
Lenkoran
Lake Van
Tabriz
Lake Urmia
Resht
Qazvin
36°
38°
40°
42°
44°
46°
48°
50°
52°
54°
56°

FIGURE 162



DATA ON DIFFERENT TYPES OF FOX PELT ON THE ROSTOV FUR STATION

Data of 1945–1946 stocks

TABLE 79. Geographic variation of skull dimensions (in mm) of foxes from the Caucasian Isthmus*

(396)

Regions and collection sites	Basic length of skull	Width between ends of auditory canals	Number of skulls studied
Western Ciscaucasia and Don area			
Tarasovka area	131.5 125-138	47.0 46-49	5
Azov area	128.0 125-137	46.8 46-48	5
(397) Sal'sk area	129.0 123-138	47.0 45-49	5
Trans-Kuban Plain, Maikop	133.5 128-142	47.5 46-51	10
Central Ciscaucasia			
Kursavka area	133.0 124-141	47.5 46-50	37
Eastern Ciscaucasia			
Ipatovo, Beshpagir	134.5 123-150	47.0 46-49	7
Ordzhonikidze	132.0 123-141	48.5 46-51	48
Kizlyar, Makhachkala	129.0 120-143	46.9 46-49	11
Greater Caucasus			
Gvilety	133.0 122-138	47.7 46-50	4
Black Sea coast			
Tuapse-Gagry	128.0 126-135	45.8 43-48	6
Eastern Transcaucasia			
Kirovabad	121.5 115-129	44.4 43-46	14
Lesser Caucasus			
Borzhomi	125.0 118-133	45.0 44-46	3
Yelenovka	128.0 119-138	47.2 44-50	7

Note. Mean values in the numerator, observed ranges in the denominator.

* Material used is in the ZIN and Moscow University collections. Skulls used for measurements were those of mature males and females, with replaced teeth or teeth in early stages of wearing.

Fur traders do not subdivide the fox skins from the western plains of Transcaucasia into races. These foxes are small and their fur is the
398 usual type of rust in color. As far as the pelts at the Batumi station show, rust gray foxes predominate in Adzharia; they amount to 71% of all the foxes. Foxes similar in color and size to the Transcaucasian race number 16%. Foxes of the type transitional from the Yerevan to Transcaucasian occur on the margins of the Dzhavakhetia Highland (Bogdanovka, Tsalka).

Dimensions of skins and skulls of foxes of some of the races mentioned are given in Table 78 and 79.

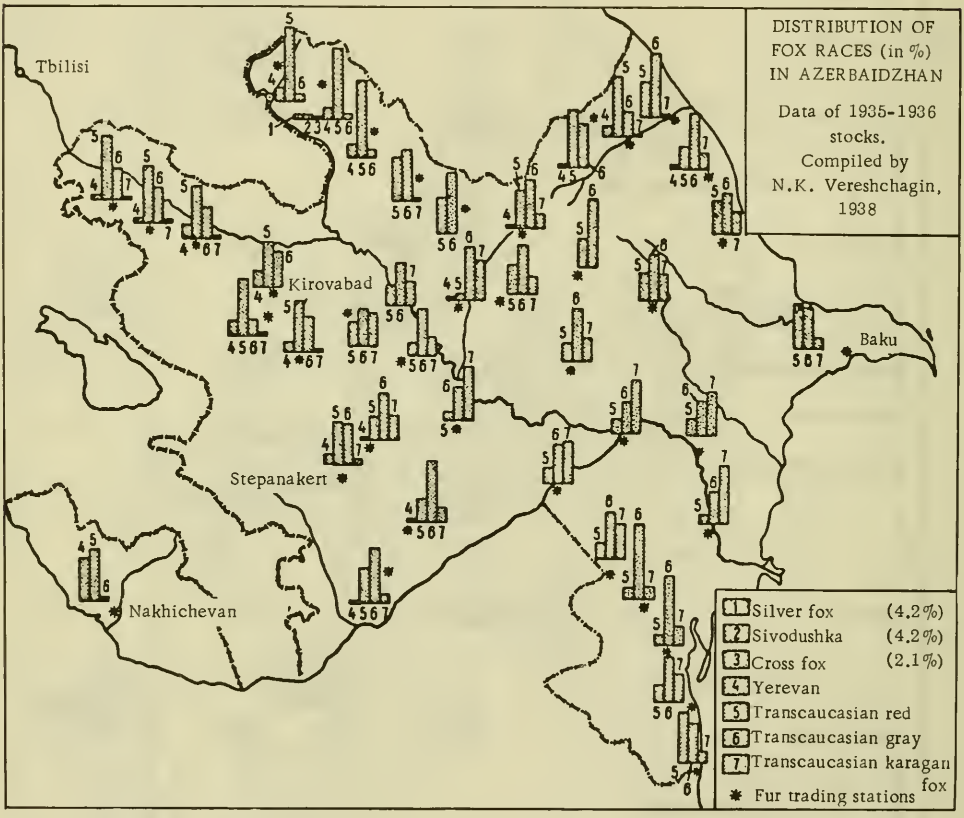


FIGURE 164

Analyses of all the data on the distribution of the coloration types and dimensions of skins and skulls produce a very complex picture of the geographic variation of foxes on the Caucasian Isthmus. It is clear that on the Ciscaucasian plains the foxes become consistently smaller and paler in color from west to east. In Transcaucasia the altitude factor is superimposed on this regularity. Nevertheless, the smallest and least brightly-colored foxes are characteristic of the easternmost populations inhabiting the hot Kura-Araks Lowland. Another example of the connection between fur color and landscape are the foxes in eastern Transcaucasia.

Data on their distribution were obtained from 41 fur stations for the 1935/36 season. The total number of pelts used in the construction of the diagram (Figure 164) was 28,250.*

399 From the review of the diagram it is possible to conclude that the palest-colored foxes occur in the zone of semideserts. Westward, towards the foothills and mountains, the abundance of bright-colored specimens increases.

In the Zakataly forest-mountainous region, 4.2% of the furs are silver foxes, 4.2% sivodushka, and 2.1% cross foxes.

It may be mentioned that to the south and southeast of the Caucasus are located the areas of distribution of the small races of the same polytypic group of the Palearctic black-eared foxes: V. vulpes flavescens Gray, V. vulpes persicus Blanf., V. vulpes leucopus Blyth.

Taking into account such taxonomic variability of the Caucasian foxes and following the generally accepted criteria for establishing the area of origin of the species, the subprovince of the east Mediterranean and southwest Asia is the area from which the Holarctic fox most probably originated.

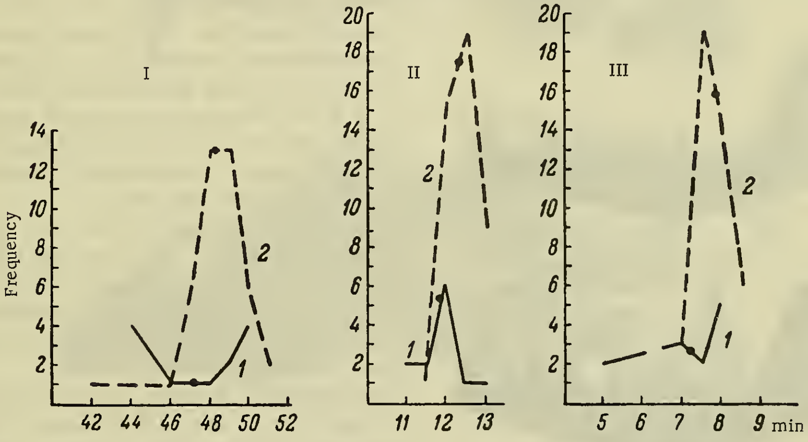


FIGURE 165. Variation in size of teeth of corsac fox in the Middle Pleistocene

I — length of lower molar row; II — length of M_1 crown; III — length of M_2+M_3. 1 — Recent Vulpes corsac, Central Asia; 2 — fossil V. aff. corsac, eastern Transcaucasia, Binagady. Dots indicate the mean values

The evolution of the skull of the corsac fox was much more pronounced than in the common fox. The remains from the Binagady asphalt indicate that the Middle Pleistocene east Caucasian corsac fox was somewhat smaller than the Recent Ciscaucacian and central Asian varieties (Vereshchagin, 1951b). In addition, the size of M_2 and M_3 has considerably decreased, and M_3 has even completely disappeared since the Middle Pleistocene (Figures 165, 166). The normal sized M_3 was present in the Binagady

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* For the sake of brevity the numbers were not tabulated.

corsac fox (43 cases), whereas in the Recent species this tooth is present in 66% (8 out of 12 cases). The Recent corsac foxes increase in size to the east, in their presumed country of origin, i.e., the steppes of the Baikal region and Transbaikalia, where they attain their maximum size.

Brown bears in the Caucasus have noticeably decreased in size since the Middle Pleistocene. The Binagady bear from the Middle Pleistocene beds of the Apsheron Peninsula is closely related to the Recent large Caucasian bear, Ursus arctos caucasicus, but the Binagady species, which is probably ancestral to the Caucasian bear, is characterized by
400 bigger molars of a more carnivorous type. This is particularly noticeable in the shape of the sharp pointed heel of M_2^2. The decrease in the size of the animals and their teeth towards the Holocene was accompanied by the flattening of the grinding surface of the teeth with the development of herbivorous habits. The Binagady Pleistocene bear may actually be identified as a distinct species (Vereshchagin, 1951c).

The biggest was the Middle Pleistocene bear of the Russian Plain, known from the Lower Kama (Mysy). This bear, a contemporary of the Binagady bear, has been identified by us as U. kamiensis N. Ver. sp. nov. The skull is elongate with a low forehead (Figure 167). In size (basic skull length 381, 386 mm) it was no smaller than the cave bears of the Pleistocene. In the Upper Pleistocene the bears of the Kama area (Tatar A.S.S.R.) began to decrease in size and to develop a convex forehead. The latter feature is particularly noticeable in the skulls of the bear U. karmalkiensis N. Ver. sp. nov. (Figure 167, 2) from the asphalt near the village of Nizhnie Kalamalki on the Shemsha rivulet. In postglacial time the bears of the Russian Plain and the Caucasus decreased considerably in size, as confirmed by the size of the last molars. Our diagram (Figure 168), which combines the elements of the stratigraphic, geographic and individual variability in the size of M^2 of bears, illustrates these facts.

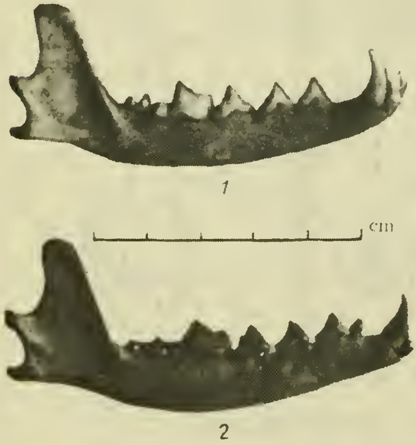

FIGURE 166. Lower jaws of corsac foxes

1 – Recent, Central Asia, No.9470, ZIN;
2 – fossil, eastern Transcaucaasia, Binagady, No.23674, ZIN

The Recent populations of bears of the Caucasus are genetically highly heterogeneous. In the present case it is probably impossible to speak of the regularities in the geographic distribution of one monotypic species since, according to Smirnov's (1916a) studies, the region is inhabited by the big Caucasian subspecies and two small races — the northern and the southern, or Mediterranean. The interbreeding of these three forms (the northern race has probably migrated to the region relatively recently) makes the studies of the geographic variation of the species very difficult.

There is a high degree of variability in skulls of badgers from the Middle Pleistocene of Binagady. Skulls with features of both the sand badger (Meles meles leptorhinus) and the common badger occur at the same locality. Most of the badgers, however, were closest to the Recent badger of eastern Transcaucasia and northern Iran — M. meles minor and M. meles canescens Blanf. It is interesting that the brain of the Recent badgers has become smaller, which attests to a decrease in metabolic rate (Figure 169). The first upper molar of the badgers from eastern Transcaucasia has decreased 8% in width, relative to length, since the Middle Pleistocene. However, badgers from the Bronze Age of the Armenian Highland had a wider M^1 than the early Apsheron forms (Vereshchagin, 1951b).

401

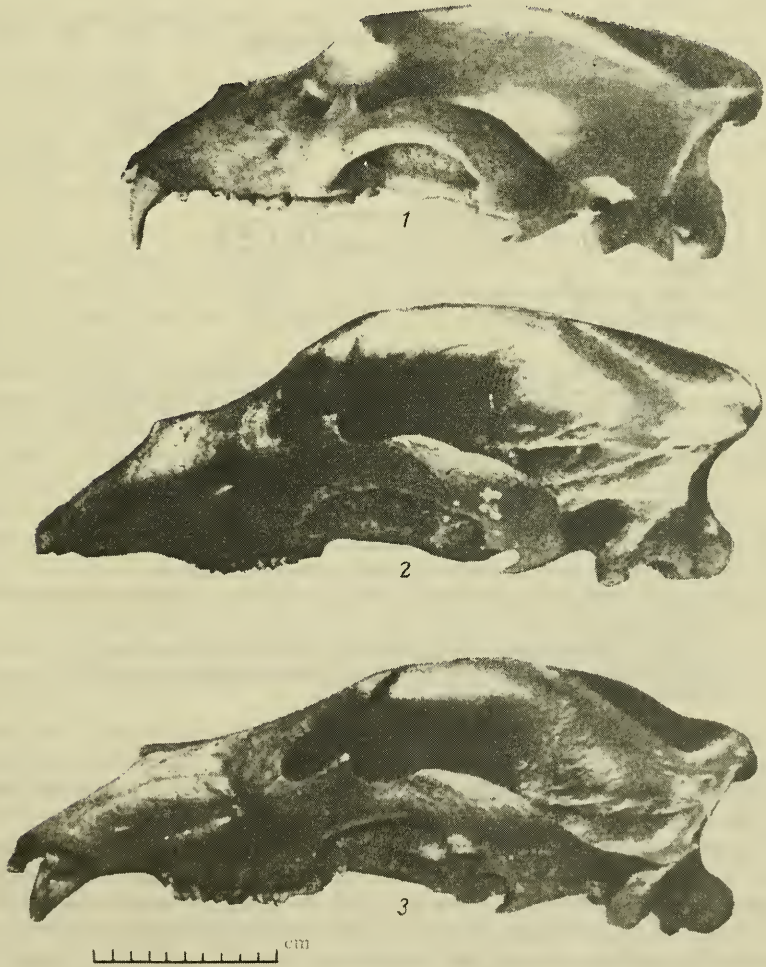

FIGURE 167. Skulls of bears

1 — Recent Ursus arctos caucasicus, Greater Caucasus, No. 6169, ZIN; 2 — U. karmalkiensis N. Ver. sp. nov, Tatar A.S.S.R., Nizhnie Karamalki, Upper Pleistocene, No. 3, Kazan University; 3 — U. kamiensis N. Ver. sp. nov., Tatar A.S.S.R., Mysy, Middle Pleistocene, No. 1, Kazan University

The Recent badgers of Ciscaucasia are larger in size, while those from Transcaucasia are the smallest.

Skulls of Vormela peregusna of eastern Transcaucasia have not altered appreciably since the Middle Pleistocene. The Recent tiger polecat decreases somewhat in size from the west to east in the steppe and desert zones of the U.S.S.R.

The Upper Paleolithic gluttons from western Transcaucasia (Figure 57, 2) differ from the Recent tundra-taiga species in the deeper mandibles and larger molars, in this respect exceeding even the older, Middle Pleistocene forms from the Russian Plain and the Urals (Table 80). This is at variance with Bergmann's rule, but the phenomenon may be satisfactorily explained
402 by the large size of the local prey: Caucasian ungulates.

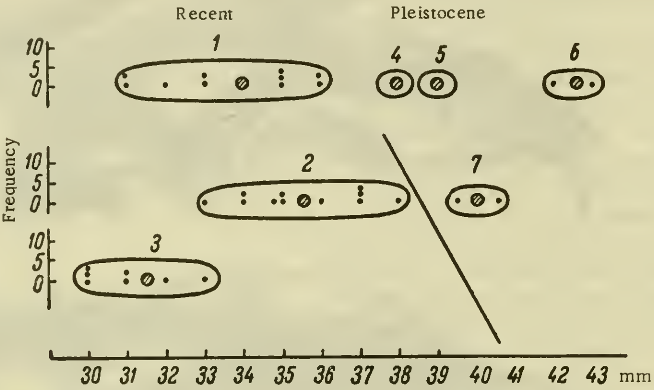

FIGURE 168. Stratigraphic and geographic variation in length of M^2 of Pleistocene and Recent bears

1 — Ursus arctos arctos, Karelia; 2 — U. arctos caucasicus, Greater Caucasus; 3 — U. arctos meridionalis, Lesser Caucasus, Talysh; 4 — U. arctos arctos (subfoss.), Voronezh, Holocene; 5 — U. karmalkiensis N. Ver. sp. nov., Tatar A. S. S. R., Nizhnie Karmalki, Upper Pleistocene; 6 — U. kamiensis N. Ver. sp. nov., Tatar A.S.S.R., Mysy, Middle Pleistocene; 7 — U. arctos binagadensis, eastern Transcaucasia, Binagady. Dots indicate individual measurements; hatched circles, mean values

The smallest glutton was collected in the Middle Pleistocene of the middle Urals.

There are no data on the evolution of the Caucasian martens of genus Martes in the Quaternary. However, the Recent martens are represented in the area by distinct forms. The skull of the Caucasian pine marten (M. martes lorenzi) is on an average 2.0-2.5 mm longer than the skull of the central Russian marten (M. martes ruthena Ogn.); jugal width is greater in M. martes lorenzi. The Caucasian species is distinguishable from the Swedish marten (Martes martes martes L.) by a more highly-developed facial region, a relatively small brain case, and a narrower postorbital bridge (Kuznetsov, 1941). The coloration of the fur has more pronounced differences.

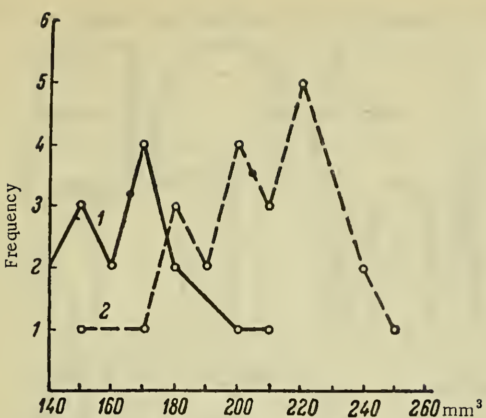

FIGURE 169. Variation in brain volume of badgers from eastern Transcaucasia in the Middle Pleistocene

1 — Recent Meles meles minor; 2 — fossil M. meles aff. minor, eastern Transcaucasia, Binagady. Dots indicate the mean values

These differences should not be considered significant, even if it is taken into account that the species migrated to the Caucasus relatively recently, as the differences may be due to specific features of the Caucasian habitats. The Recent pine marten varies little in size and color within its distribution area in the Caucasus.

403 Individual and age variability are much more pronounced, as expressed, for example, in the shape and color of the neck spot.

This variability, based on the material of the Rostov fur station, is shown in Figure 170.

The biometric differences between the Caucasian populations of the older stone marten (M. foina nehringi) and the West European M. foina foina Erxl. are, as expected, insignificant. Nevertheless, the skulls of these Caucasian martens are 2-2.5 mm larger than those of the Swiss martens, and 5-6 mm larger than the skulls of the Crimean martens (M. martes rosanovi Martino).

The skull of the Caucasian mink (Lutreola lutreola turovi) is also considerably larger than the skull of the central Russian species (Bobrinskii, Kuznetsov and Kuzyakin, 1944). It is known that the increase in size is fairly characteristic of populations in newly established marginal sections of an area of distribution.

Detailed morphological and ecological studies are needed for the clarification of the genetic affinities between the small and big Caucasian weasels: Mustela nivalis caucasica and M. nivalis dinniki.
404 These often occur side by side and may therefore be regarded as separate species.

Cats such as the panther, cheetah, European wildcat and lynx are of interest from the point of view of their origins and speciation in the Caucasus.

The size and proportions of the teeth and skeletal elements of leopards have remained practically the same since the Middle Pleistocene (Table 81; Figures 61, 6; 85, 1), as have the teeth of cheetahs (Vereshchagin, 1951b).

The Recent Caucasian panthers are smaller, with thinner fur and brighter coloration in Transcaucasia than in Ciscaucasia (Dinnik, 1914a; Satunin, 1915a). They are larger than the south Asian and African varieties.

The Recent European wildcat of the Caucasus (Felis silvestris caucasicus) is generally larger than the European variety (F. s. silvestris): the condylobasal skull length of an adult male of the former is 99.1 (89.8-102) mm, and of the latter 86-96 mm. The lengths of the upper tooth row are 33.1 (30-34.7) and 28-32 mm respectively.

(403) TABLE 80. Stratigraphic and geographic variation in dimensions (in mm) of teeth and lower jaws of gluttons of the Caucasus and Eastern Europe *

Measurements	Upper Pleistocene	Middle Pleistocene			Recent
	Caucasus, Gvardzhilas cave, Museum of Georgia	Ukraine, Gontsy, Zoological Institute of the U. S. S. R. Acad. of Sc.	Tatar A.S.S.R., Mysy on Kama, Kazan University	Northern part of the central Urals, Kizel cave, ZIN, 3 specimens	Norway, Anadyr, ZIN, 5 specimens
Height of jaw behind M_1	30.3	22.0	28.0	$\frac{20.5}{19.5-21.0}$	$\frac{24.0}{21.0-26.0}$
Height of jaw near Pm_3	23.3	21.5	–	$\frac{17.8}{17.5-18.0}$	$\frac{19.3}{18.0-21.0}$
Length Pm_2	7.1	9.0	9.0	$\frac{7.5}{7.3-7.6}$	$\frac{7.0}{6.0-8.0}$
Width Pm_2	5.0	–	–	$\frac{4.8}{4.5-5.1}$	$\frac{5.3}{4.5-6.0}$
Length Pm_3	13.2	12.7	13.5	$\frac{10.5}{10.0-11.0}$	$\frac{11.0}{11.0-11.1}$
Width Pm_3	9.0	–	–	$\frac{6.5}{6.0-7.0}$	$\frac{7.4}{7.0-8.0}$
Length M_1	24.0	22.0	24.0	$\frac{19.5}{19.0-20.0}$	$\frac{22.1}{21.0-23.2}$
Width M_1	10.8	–	–	$\frac{9.0}{8.0-9.5}$	$\frac{9.8}{9.0-10.2}$

Note. Mean values in the numerator, observed ranges in the denominator.

* Author's unpublished material.

As a rule, cats inhabiting the reed thickets of the Lower Kuban are more uniformly colored than those which live in beech forests. Melanic individuals occur infrequently in the big beech forests near Nukha, Zakataly and Madagiz (Lesser Caucasus). In order to make sound conclusions on the scale of isolation of the Caucasian populations, pelts and skulls from the north of Asia Minor, the Balkans and the Carpathians must be studied.

The Recent Caucasian lynx (Felis lynx orientalis) is usually regarded as a subspecies of the European lynx. Its body and skull size
405 sometimes exceed those of the European form, and its coloration is brighter than that of the northern form. Morphological changes of the Caucasian lynx include decrease in size and simplification of the form of the internal nares in the populations of the Lesser Caucasus.

(404)

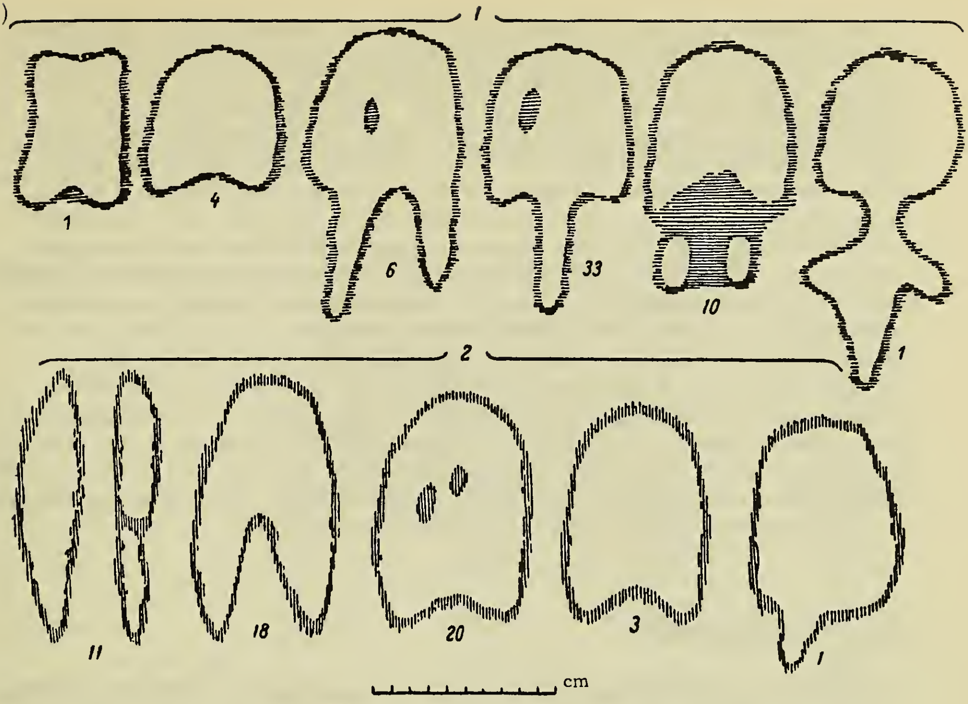

FIGURE 170. Variation in the size and shape of the throat spot of Caucasian pine martens (1) and stone martens (2). Numbers indicate frequency

TABLE 81. Dimensions of teeth (in mm) of Recent and fossil leopards in the Caucasus

Locality and age	Species	Crown length Pm^4	Crown length M_1
Western Caucasus, Recent	Panthera pardus	$\frac{25.0}{24.5-26.2}$	$\frac{18.1}{17.8-19.3}$
Baksan gorge, Sosruko grotto, Early Holocene (Mesolithic)	P. aff. pardus . . .	–	18.8
Upper Rion, Kudaro cave, Middle Pleistocene (Lower Paleolithic)	P. cf. pardus . . .	26.0	–

Note. Means in the numerator, observed ranges in the denominator.

Order LAGOMORPHA

According to I. Gromov's measurements (1952), the following morphological changes have occurred in the European hare of Transcaucasia since the time of deposition of the Binagady bitumens: narrowing of the facial region of the skull, development of more angular orbits, decrease in the volume of auditory bullae, and narrowing of the ilium. The Recent European hares of the Caucasus well illustrate Bergmann's rule in that they increase in size from south to north. The European hares of Transcaucasia (Lepus europaeus cyrensis) have the following characteristics: skull length 93-97 mm, liveweight up to 3.5 kg, pale yellowish brown in color. The skull length of the Ciscaucasian Lepus europaeus caucasicus varies from 95 to 105 mm, the liveweight reaches 4.5 kg, and the color is predominantly brownish-yellowish gray (Bobrinskii, Kuznetsov, Kuzyakin, 1944). According to our measurements, the condylobasal length of the skull of mature hares (females and males) from the Kura Lowland in eastern Transcaucasia is 85.3 (79-94) mm (32 specimens), whereas in western Ciscaucasia it is 88.4 (83-96) mm (25 specimens). The liveweight of mature east Transcaucasian hares (females and males) is 3.78 kg (14 specimens), whereas the weight of the Ciscaucasian hares is 4.76 kg (9 specimens). The increase in the size of the hares is most noticeable in the region of the Khachmas Lowland, on the Kusary Plain and in the forests of the Lower Samur. This longitudinal type of variation confirms the southern origin of the species.

Order RODENTIA

Only few species of post-Pliocene Caucasian rodents are known, so that the phylogenetic lineages of most of them are too short to study their stratigraphic variation. However, the wide distribution and numerical abundance of many of the species permits easy tracing of their geographic variability.

The geographic (latitudinal) variation of morphological and physiological features of the little suslik is reflected in the increase in size and in the
406 darkening of color, as well as in the shortening of the period of estivation from semidesert to steppe habitats.

According to Ognev's measurements (1947), the skulls of the subspecies Citellus pygmaeus kalabuchovi from the Sal'sk steppes are on average almost 2 mm larger than the skulls of C. pygmaeus pallidus from the Kuma region semidesert. The variation with altitude is even more pronounced: the isolated populations of susliks of Ciscaucasia regularly increase in size and darken in color with height (Table 82).

From the semideserts on the Lower Terek to the Upper Baksan the length of the body of the susliks increases on an average by 14 mm, tail length by 12 mm, foot length by 5 mm, and condylobasal skull length by 3 mm (Figure 171).

However, the mountain populations of susliks also show considerable variation in adaptation to hot and dry glacial valleys (altitude 900-1200 m) and mountain slopes and subalpine meadows (altitude 2500-2800 m). As a rule, populations inhabiting the bottoms of the gorges are similar to the plain dwellers, particularly in color.

The European suslik (Citellus citellus), according to Vinogradov and Gromov (1952), increases in size and in the relative length of its tail when the populations are traced from east to west (from the Ukraine to the Balkans). The Asia Minor subspecies, however, shows pronounced morphologic and physiologic variation according to altitude: the body increases in size and weight, the tail becomes shorter, and the fur color darker (Table 83). According to Avetisyan (1950), the hibernation of the suslik in the Alagez area ends by the middle of March, while estivation begins in the second half of July. In the upland steppes, hibernation ends only in early April.

TABLE 82. Geographic variation in size (in mm) of little suslik on the Caucasian Isthmus

Dimensions	Lower Terek Citellus pygmaeus planicola 25 specimens	Dagestan foothills Citellus pygmaeus satunini 40 specimens	Terek-Sunzha Plateau Citellus pygmaeus boehmii 7 specimens	El'brus slopes Citellus pygmaeus musicus 48 specimens
Body length	$\frac{206.7}{182\text{-}230}$	$\frac{208.5}{182\text{-}230}$	$\frac{207.5}{193\text{-}215}$	$\frac{220.0}{205\text{-}240}$
Tail length	$\frac{35.6}{30\text{-}40}$	$\frac{36.3}{32\text{-}43}$	$\frac{37.8}{28\text{-}40}$	$\frac{47.4}{45\text{-}50}$
Foot length	$\frac{32.1}{27\text{-}35}$	$\frac{32.1}{30\text{-}36}$	$\frac{33.2}{28\text{-}34}$	$\frac{37.4}{36\text{-}38}$
Condylobasal skull length	$\frac{40.7}{39.5\text{-}42.0}$	$\frac{40.0}{37.9\text{-}42.6}$	$\frac{41.0}{37.8\text{-}41.9}$	$\frac{43.5}{42.5\text{-}45.2}$

Note. Means in numerator, observed ranges in denominator.

Some general evolutionary trends and specialization rates can be studied in the jerboas (genus Allactaga).

407

TABLE 83. Changes in size (mm) and weight (g) of Asia Minor suslik (males and females) at different altitudes

Dimension	Zone 1255-1550 m above sea level	Zone 1550-2190 m above sea level
Body length	$\frac{203}{175\text{-}230}$	$\frac{215}{180\text{-}390}$
Tail length	$\frac{45}{33\text{-}37}$	$\frac{43}{21\text{-}59}$
Weight	$\frac{239}{188\text{-}372}$	$\frac{278}{184\text{-}430}$

Note. Means in the numerator, observed ranges in the denominator.

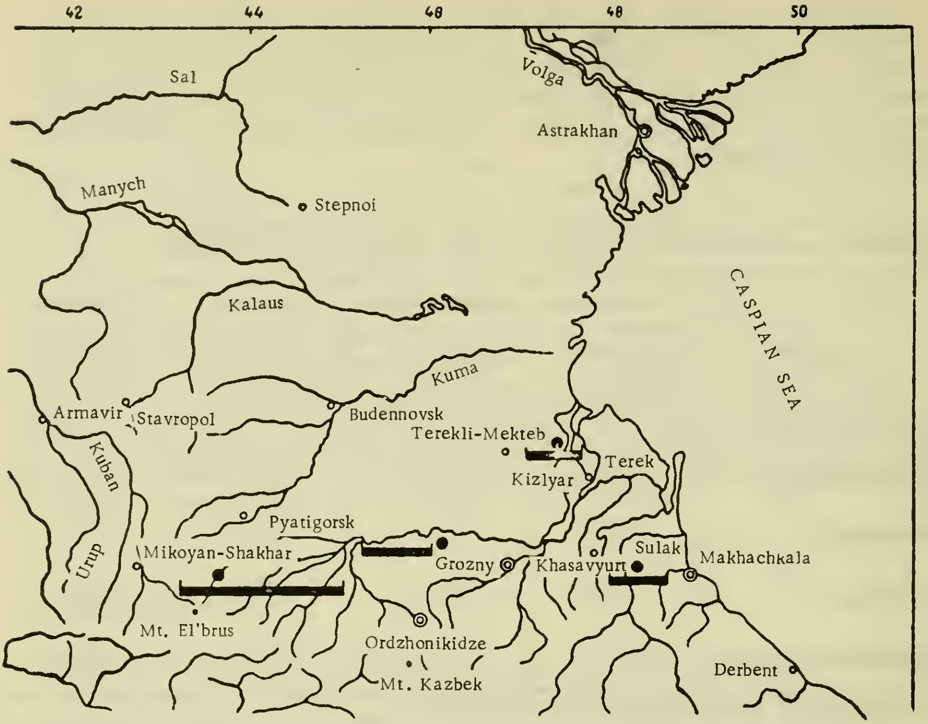

FIGURE 171. Variation in size of little suslik in Ciscaucasia. Rectangles indicate the length of a foot squared. Populations from the Lower Terek taken as an entity. Black dots — points of trapping

The jumping ability of Recent jerboas of Ciscaucasia and the Apsheron Peninsula has improved since the Middle Pleistocene (Binagady) due to the increased length of the tibia relative to the femur, as shown in the increase
408 in the jumping index (length of tibia/length of femur × 100) of the small and Asia Minor jerboas (Table 84).

I. Gromov (1952) has pointed out that the structure of the metapodia in the great jerboa from the Binagady asphalt (Allactaga jaculus bogatschevi) is more primitive than in the Recent form in the wider spacing of the distal part of the foot and in the longer free end of the second metatarsal (mtt_2).

Hamsters (Cricetinae) have occurred in the Caucasus since the Middle Miocene. It is difficult, however, to establish the affinity of the Miocene (Palaeocricetus, Belomechetka) and Pliocene (Stavropol) hamsters with the Quaternary genera Cricetus and Mesocricetus. Hamsters from the Lower Pliocene alluvium of Stavropol (Kosyakin quarry) are characterized by large molars. The hamster from the Binagady asphalt (Mesocricetus auratus planicola) is intermediate in size between M. auratus raddei and M. auratus nigriculus. The Binagady species differs from the forms of Mesocricetus known in the U.S.S.R. in its hard palate and short incisor foramina. The structure of the postcranial skeleton of the Upper Pleistocene hamsters from the Chiaturi manganese region indicates that the population was no less specialized than the Binagady population.

TABLE 84. Changes in jumping index of Middle Pleistocene jerboas*

Species	Jumping index	
	Binagady	Recent
Allactaga jaculus	125.0	127.0
A. williamsi	126.1	129.5
A. elater	129.5	136.8

* We calculated the indexes from the mean values given by I. Gromov (1952); he tried to reconstruct the ancient landscapes of the Apsheron on the basis of certain morphological features of the Binagady jerboas. His assumptions, however, on the existence of either soft ground, mosaic landscapes or diversified relief at Binagady are poorly founded.

The geographic variation in the Recent populations of hamsters in Asia Minor is mainly reflected in changes in the depth and brightness of the rusty color of the back and sides, and the black color on the abdomen (Argiropulo, 1937). Also the mountain populations are, as a rule, larger than those of the Ciscaucasian foothills, though the ecological variability of the species is great. On the high Armenian plateaus, hamsters begin to hibernate at the end of October or early November, whereas on the lower Kakhetian plateau they begin only in early December.

The Recent gray hamsters of the Apsheron Peninsula have developed a narrower anterior palatal region, larger molars, a more protruding coronoid process, and a slightly recurved lower incisor and M_3 with shortened heel. These changes have occurred since the Middle Pleistocene. The functional significance of these minor changes and the evolutionary trends of the species are difficult to explain. It is simpler to record the facts, as has been done by I. Gromov (1952).

The process of morphological and ecological evolution of the species as polymorphic as the house mouse (Mus musculus) in the Caucasus is
409 very complex. This species was widely distributed in the Middle Pleistocene of eastern Transcaucasia (Binagady), and also occurs in this region today. The morphological and ecological differentiation of the species has led to evolution of the following subspecies: white abdomen and short-tailed (steppe and semidesert forms), M. musculus hortulanus, M. musculus tataricus; gray abdomen and long-tailed (mountain-forest forms), M. musculus abbotti, M. musculus formosovi; and introduced domestic forms, M. musculus musculus. This variability is as developed as the variability of the common field mice of the Caucasus (discussed below); however, it cannot yet be studied using the modern methods of morphological investigation (see Geptner, 1930; Gulii, 1930; Sviridenko, 1935a).

The systematics of the common field mice of the Caucasus (genus Apodemus) has not been extensively studied, but on the basis of the studies of Argiropulo (1940a, 1946), Sviridenko (1936), Kuznetsov (Bobrinskii, Kuznetsov and Kuzyakin, 1944), Shidlovskii (1953a) and our observations, the genus may be considered as being subdivided into four species: A. mystacinus, A. flavicollis, A. fulvipectus and A. sylvaticus (see also Chapter V). This classification is tentative and subject to future experimental ecologic studies.

The Asia Minor mouse (A. mystanicus), distributed in the Balkans, Asia Minor and western Transcaucasia, is considerably smaller in size in the Caucasus than in the Balkans. According to Shidlovskii's measurements (1953a), the condylobasal length of the skull of the Balkan specimens is 28.4 mm (34 specimens), and of the Transcaucasian specimens 26.5 mm (200 specimens). The length of the upper molar row is 4.9 and 4.5 mm respectively. The Balkan populations are lighter in color than those in Asia Minor and Transcaucasia. According to Shidlovskii (1953a), this animal migrated to the southern slopes of the Greater Caucasus (Map 55) recently, during the last few decades. In the present case, the body size of the animal, which migrated into a new mesophytic environment, has decreased considerably. Paleontological studies of the Imeretian caves will clarify whether this is a primary or a secondary immigration and will consequently shed light on the degree of morphological divergence of this east Mediterranean species.

The picture of the geographic variation of the other three species on the Caucasus Isthmus is much more complex. The yellow-necked mouse of the European type, with feet 24-25 mm long (close to A. flavicollis samariensis) occurs only in the river valley forests on the Lower Sulak in eastern Ciscaucasia.* In the far southwest the southern boundary of the distribution of this species reaches the Lower Don (Map 55).

The relatively small A. fulvipectus**, with a foot 22-23 mm long, occurs in the deciduous forests of the lower mountain belt in the Krasnodar area, in Abkhazia, Adzharia and northwestern Azerbaidzhan, and in some places in northern Armenia (Map 56). This species is easily distinguishable from the common field mouse, even in juvenile states, by its larger dimensions, greater length (relatively shortened) of the foot and the presence of an oval yellow spot on the breast. The species comes out into the sun to feed only rarely. It is a good climber and often lives in hollows in trees. It also differs from the common field mouse in its weaker response to light.
410 It seems likely that the relatively short foot and tibia, the longer tail of the yellow-spotted mouse and its relatively narrow internal nares (Argiropulo, 1946), as compared with these features of the common field mouse, are adaptations to slower movement and better climbing.

The populations of this species vary even within their area of distribution. As a rule, the southern forms are somewhat smaller, while to the east their size increases. Morgilevskaya (1954) has published data on five mixed populations of the yellow-spotted and common field mice. According to her data, the condylobasal length of the skull is (accordingly to locality): Sukhumi — 23.8, Gagry — 22.3, Batumi — 23.1, Akhalkalaki — 22.7, Lagodekhi — 23.7 mm; length of hind foot: Sukhumi — 22.6; Gagry — 21.3, Batumi — 21.4, Lagodekhi — 22.7 mm.

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* This is true only if the labels on the material in the Moscow Zoological Museum have not been mixed. Geptner and Formosov (1941) have identified 5 specimens from this region and I studied one specimen, but the origin of this species is not yet clear to me.

** We have assigned to this species the Caucasian subspecies A. flavicollis ponticus, A. flavicollis parvus and A. sylvaticus fulvipectus of earlier authors.

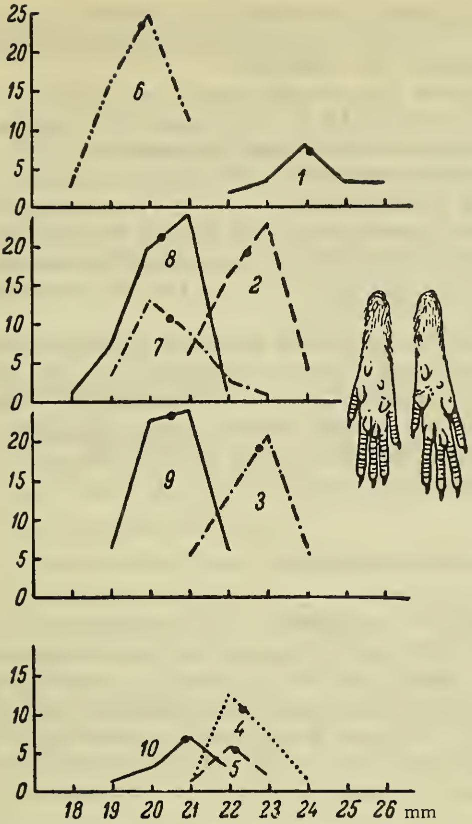

FIGURE 172. Variation in foot length of common field mice on the Caucasian Isthmus

Apodemus flavicollis: 1 — Rostov region. A. fulvipectus: 2 — Caucasian Reservation; 3 — Alazan-Agrichai valley (Transcaucasia); 4 — Lesser Caucasus (Delizhan); 5 — Talysh. A. sylvaticus: 6 — Rostov region; 7 — Caucasian Reservation; 8 — North Ossetia (Lars, Zamarag); 9 — Alazan-Agrichai valley (Zakataly); 10 — middle Araks valley. On the left — foot of A. sylvaticus; on the right — A. fulvipectus. Ordinate — number of specimens

Populations of yellow-spotted mice are common in a number of valleys in Central Ciscaucasia (Urukh, Ardon, Terek) and on the piedmont plains of eastern Ciscaucasia. In this region the animals vary considerably in size from one valley to another, which is due to both genetic isolation and differences in habitats. The higher degree of ionization of the air in the area of tectonic fracture has been suggested as the reason for the larger size of the mice in the Armkha ravine (tributary of the Terek) (Ushatinskaya-Dekalenko, 1933). If this is true, then the size of mice in the mountain populations may be an indicator in surveys of radio-isotopes.

In eastern Transcaucasia this species primarily occurs in the piedmont lowlands. Careful measurements in a series of preserved specimens of A. fulvipectus and common field mice of the same age group gave the data on the geographic variation in foot length, as shown in Figure 172.

Isolated bones of the common field mouse (A. sylvaticus subsp.) occur in the Middle Pleistocene asphalts of the Apsheron Peninsula. No morphological differences between these and the Recent forms have been recorded in this material. In Ciscaucasia, this species is widely distributed on the plains, in the foothills and in the mountains, particularly in areas of sparse vegetation (Map 57). The mountain populations of this species are characterized by higher counts
411 of erythrocytes in their blood (Kalabukhov, 1940). In Transcaucasia the common field mouse is somewhat larger, which sometimes makes it difficult to distinguish from A. fulvipectus. A yellow spot is almost always present on the breast of mature specimens.

The Caucasus is thus an ancient and self-contained center of speciation of domestic and field mice; this confirms their Pliocene origin in this country.

The red-tailed gerbil from the Binagady bitumens (Meriones erythrourus intermedius) is a form intermediate between the Recent gerbils occurring to the west and east of the Caspian.

The primitive features of the Middle Pleistocene gerbil are reflected in the shortness of the tibia, which is only 113.8% the length of the femur, as compared with 125.9% in the Recent gerbils of the Apsheron.*

Insofar as the lengthening of the tibia relative to the femur indicates an adaptation for jumping (jerboas), it can be stated that the Recent gerbils became "jerboaized" (N. A. Smirnov's term) since the Middle Pleistocene.**

Evolution in space and time can be studied in the case of the Caucasian voles (genera Prometheomys, Arvicola, Microtus) as rewardingly as in mice.

The teeth and lower jaws of Prometheomys from the Acheulean beds of Kudaro I and the Upper Paleolithic beds of the Gvardzhilas cave are not noticeably different from the Recent forms. This is understandable, since the morphological features of burrowing rodents reflect conservativeness in habit. The data on the geographic variation in the color of Recent populations are summarized in Table 85.

TABLE 85. Variation in abundance of melanic varieties in the distribution area of Prometheomys *

Color	Upper Laba and Belaya		Upper Bzyb		Upper Terek	
	no.	%	no.	%	no.	%
Grayish brown	13	52	16	100	15	100
Black	12	48	–	–	–	–

* Collections of ZIN AN SSSR.

The increased proportion of the melanic varieties is probably restricted to the western part of the distribution range.

The Recent populations of water vole (Arvicola terrestris) vary noticeably within the Caucasian and adjacent regions. At least 9 varieties have been described in the Caucasus, and not less than 6 varieties from neighboring areas in Iran, Turkey and the Russian Plain. It is difficult, however, to trace the geographic variation in the morphological characters of the species.

412 As a rule the northern marshland forms from the Lower Don, Kuban and Volga are somewhat larger than the mountain and south Caucasian forms (Table 86).

Populations of this species from some sections of the distribution range are characterized by minor morphological adaptive features. The upper incisors of the mountain "burrowing" populations of Balkaria, Ossetia, and Dagestan resemble those of mole voles. The curvature of the incisors is greater than in the marshland forms, and the degree of differentiation

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* Indices of the mean values were computed by us from the measurements given by I. Gromov (1952).

** I. Gromov has also indicated that the Binagady gerbil was of a "more running" type (i.e., less of a jumping type) than the Recent species.

of the fur is less marked. The change in shape of the incisors is due to their adaptation for digging.

TABLE 86. Variation in skull size of the water vole in the Caucasian Isthmus*

Dimensions	Lower Don Arvicola terrestris tanaiticus 10 specimens	Lower Kuban Arvicola terrestris cubanensis 11 specimens	Eastern Dagestan Arvicola terrestris kuruschi 32 specimens	Transcaucasia Arvicola terrestris persicus 32 specimens
Condylobasal length of skull . . .	$\frac{41.2}{41.0-41.5}$	$\frac{41.0}{39.5-42.6}$	$\frac{38.5}{38.2-38.3}$	$\frac{39.6}{37.3-41.9}$
Length of upper molar row . . .	$\frac{10.2}{10-10.4}$	$\frac{9.9}{9.2-10.5}$	9.4	$\frac{10.1}{9.6-10.8}$

Note. Means in the numerator, observed ranges in the denominator.

* Measurements by Ognev (1933).

Up to 8 subspecies of the snow vole known from Palestine to Kopet-Dagh are also found in southwest Asia, the Caucasus and Central Asia, The geographic variation of the Asia Minor snow vole occurring between the Lesser Caucasus and Kopet-Dagh is expressed in lighter coloration correlated with increasing draught and isolation, in the shortening of M^3 along the west—east gradient, and in a general decrease in size (Table 87).

(413)

TABLE 87. Geographic variation in size (in mm) of Asia Minor snow vole*

Dimensions	Northwestern Caucasus, Mt. Pambak Microtus nivalis loginovi 7 specimens	Lesser Caucasus, Lake Sevan shores Microtus nivalis satunini 8 specimens	Talysh, Mt. Kelakhan Microtus nivalis subsp. 1 specimen	Kopet-Dagh, Mt. Shakh-Shakh Microtus nivalis dementievi 3 specimens
Body length	$\frac{109.4}{99-121}$	$\frac{121.9}{109-142}$	115.0	$\frac{103.2}{97-120}$
Tail length	$\frac{58.1}{52-68}$	$\frac{54.0}{32-90}$	52.0	$\frac{55.3}{51-60}$
Foot length	$\frac{18.8}{12.2-20.0}$	$\frac{17.9}{13-20}$	18.5	$\frac{18.5}{17-20}$
Total skull length	$\frac{26.4}{25.0-27.8}$	$\frac{27.8}{26.3-29.6}$	27.3	$\frac{27.2}{25.8-28.5}$
Length of upper molar row	$\frac{5.9}{5.5-6.2}$	$\frac{6.3}{6.1-6.7}$	6.3	$\frac{6.1}{5.5-6.5}$

Note. Means in the numerator, observed ranges in the denominator.

* Author's measurements on the ZIN material.

The snow vole from the Greater Caucasus is the smallest variety, indicating that humid mesophytic regions are not suitable for this animal. The decrease in size of this species towards the southeast, and its disappearance from the intermediate heights of the southern slopes of the Armenian uplands, indicate that the southeastern sections of the present distribution area are in a state of decline. This also indicates that in the past a more humid phase existed, during which the distribution area of the species extended further to the east.

The geographic variation in the Caucasian snow vole on the Greater Caucasus is reflected in the decrease in size and lighter coloration from west to east. The change in color is probably due to the fur becoming bleached in sunny woodless Dagestan. The inversion of the zones in the central part of the Greater Caucasus is somewhat superimposed on the trend of brightening of the color.

The decrease in size from west to east is shown by the measurements given in Table 88.

413 It should, however, be mentioned that size variation of this species of vole has not yet been traced through the altitudinal and landscape zones.

TABLE 88. Geographic variation in size (in mm) of Caucasian snow vole*

Dimensions	Western Caucasus Microtus gud nenjukovi 128 specimens	Central Caucasus Microtus gud gud 116 specimens	Eastern Caucasus, Dagestan, Microtus gud lghesicus 8 specimens
Body length	120-152	102-149	100-121
Tail length	68-106	61.0-85.0	58-78
Foot length	19.0-26.9	18.0-23.0	18.5-21.2
Condylobasal length of skull	26.4-28.6	25.0-29.2	26.4-27.2
Length of upper molar row	6.7-7.8	6.0-7.0	6.0-6.6

* Measurements of Ognev (1950) and author's (for Dagestan).

The Middle Pleistocene Apsheron vole (Microtus (Pitymys) apscheronicus) differs from the Recent pine vole of the Caucasus in its larger size, its longer tooth row (6.3 mm as compared with 5.7 mm of the Recent species) and in details of the shape of the lower jaw. It is also possible that the extinct species was of a less mesophilous character than the Recent form.

Geographic variation of the Recent pine vole is poorly developed. The subspecies described for the Caucasus reflect the subjective approaches
414 of investigators or the ecological variants (and age groups) arising due to variation in living conditions from year to year. The subspecies described are: M. majori majori from northeast Asia Minor, the Kars Highland, Dzhavakhetia, Mingrelia, and the central and western parts of the Greater Caucasus; M. majori ciscaucasicus from the northern slope of the

Bol'shoi Range, in its western and central parts; M. majori suramensis from the central sections of both slopes of the Bol'shoi Range, Surami and the Lesser Caucasus; M. majori dagestanicus from inner Dagestan, Tushetia, northwestern Azerbaidzhan, the northeastern slopes of the Lesser Caucasus and Dhavakhetia; M. majori schelkovnikovi from the forests of Talysh.

TABLE 89. Geographic variation in size (in mm) of common vole in the Caucasus*

Dimensions	Foothills of northern Caucasus Microtus arvalis macrocraninus 162 specimens	Inner valleys of central Caucasus Microtus arvalis gudauricus 52 specimens	Armenian Highland Microtus arvalis transcaucasicus 133 specimens	Talysh Highland Microtus arvalis mystacinus 4 specimens
Condylobasal length of skull	$\frac{26.3}{25.8-27.3}$	23.8-27.3	$\frac{25.3}{24.0-26.9}$	$\frac{25.2}{24.0-26.0}$
Length of upper molar row	$\frac{6.0}{5.8-6.5}$	$\frac{5.7}{5.3-6.2}$	$\frac{5.9}{5.2-6.0}$	$\frac{5.5}{5.2-5.7}$
Foot length	17-18.2	15.5-19.6	14.1-18.0	$\frac{16.2}{15.0-17.0}$

Note. Means shown in the numerator, observed ranges in the denominator.

* Measurements of Krasovskii (1930), Ognev (1950) and author's (for Talysh).

The Talysh specimens are distinguishable by their intense rusty color on the sides and their small size. M. majori dorothea Ellerm. from the Elburz Range is probably synonymous with the latter subspecies. The pronounced differences between the M. schelkovnikovi subspecies and the pine voles of the Lesser and Greater Caucasus attest to the long period of isolation of this animal in the southeastern section of its distribution range. The overlap of the distribution ranges of the former four subspecies is self-explanatory. The rather vague systematic diagnosis of the forms described indicates that in order to understand their geographic variation special ecologic and morphologic studies must be made.

It is known that the common vole (Microtus arvalis) decreases in size from north to south on the Russian Plain. On the Caucasian Isthmus, with its diversified relief and inversion of the zones, Bergmann's rule does not strictly apply to the distribution of the species. Studies of the geographic variation of this species must be done systematically across the altitudinal and landscape zones, taking into account seasonal and annual variation.

Some numerical results of the studies of the Caucasian subspecies are given in Table 89.

415 Animals inhabiting the dry longitudinal valleys east of the El'brus and inner Dagestan are characterized by a lighter color than those inhabiting the humid foothills.

The type of geographic variation described and the characteristic features of the area of distribution attest to the ancient origin of the species on the mesophytic uplands of the Mediterranean.

The Middle Pleistocene steppe vole, Microtus socialis, from the Binagady asphalt is almost identical in skull structure to the Recent species (Gromov, 1952).

According to Ognev (1950, p. 400) these subspecies increase in size from north to south; their auditory bullae also increase in size and the structure of M^1 and M^3 becomes more complex. However, these facts need further study, particularly in relation to the specific ecologic features and to height above sea level. Considering the great size of the total area of distribution, the variation mentioned is not particularly significant.

All this indicates that the relationships between the steppe vole and the xerophytic landscapes of the Mediterranean have remained stable; they date at least from the Lower Pleistocene.

Order PROBOSCIDEA

In the south of the Russian Plain, in the Caucasus and in southwest Asia (as in the Mediterranean in general), the first known true elephants are represented by highly specialized forms: Elephas (Archidiskodon) planifrons, E. (Hesperoloxodon) antiquus, E. (Archidiskodon) meridionalis from the Middle Pliocene (Trouessart, 1898-1899c; Pavlova, 1910a; Bogachev, 1923-1924; Osborn, 1942; Simpson, 1945). The small elephant (Phanagoroloxodon mammontoides), as described by Garutt (1957a) from some Upper Tertiary beds of western Ciscaucasia*, is probably of the same age. The affinities of this species to those mentioned above are not clear. However, the species is considered to be close to E. (Hesperoloxodon) antiquus or E. (Parelephas) trogontherii, so that Garutt's identification of this form as Early Pleistocene is undoubtedly false. The absence of direct ancestors of the species listed in the Oligocene, Miocene and Lower Pliocene beds is probably not due simply to change. It is worth noting that the remains of elephants definitely do not occur in the immediately post-Pontian beds in Ciscaucasia and in the northern Black Sea area as they do, in the alluvium of the Kosyakin quarry near Stavropol and in the clay fissure-fillings in the Pontian limestone, exposed in the Odessa catacombs. In spite of the "taphonomic universality" of both burials, the proboscideans are represented only by mastodons (and Dinotherium at the Kosyakin quarry).

Evolution of the elephants in the region must be studied mainly from tooth material, on which the poorly-developed hypothesis of the evolutionary lineage E. planifrons-E. meridionalis-E. trogontherii-
416 mammoth has been based. The systematic position of the so-called ancient

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* The Phanagorian elephant has been described from a permineralized skull (with broken teeth) of unknown locality in the Krasnodar museum. Garutt's (1957a) photographs show teeth of elephants collected from the conglomerates near Sennaya and Akhtanizovskaya on the Taman Peninsula, but his identification of the material as belonging to the Phanagorian elephant is not certain; these teeth seem rather to belong to the southern and ancient elephants (Vereshchagin, 1957a). There is unfortunately no space for discussion of the opinions of Sherstyukov (1954), which are lacking in clarity.

elephant [E. antiquus] is not sufficiently clear. Russian paleontologists have either identified this form with the Loxodonta group or have related it to E. planifrons and E. meridionalis. It has been identified as Palaeoloxodon by Dubrovo (1957). Because of the scarcity of remains of the ancient elephant, it is only possible to construct a distribution map (Map 76). Over 400 casts and descriptions of various teeth of Upper Pliocene and Quaternary elephants, collected from the Russian Plain and the Caucasus, have been studied by us in the Russian museums and collections. In addition to distribution maps showing occurrence of teeth (Maps 74-76), we can give a general description of the teeth of various phylogenetic grades and a summary in table form of the main morphological features. Most teeth and bones of Pliocene and Quaternary elephants in the Caucasus occur in redeposited sediments. All the material has been washed out of the primary bone-bearing lenses by streams and redistributed in conglomerates, gravels and sands. The localities with E. planifrons and E. meridionalis in Ciscaucasia are situated in delta zones of ancient streams and mudflows, which once flowed from the Greater Caucasus to the Akchagyl and Apsheron seacoasts. The bones often occur in ferruginous gravels and sands of the high (third or fourth) river terraces on the inclined piedmont plains. According to Bogachev (1923-1924), most of the bones of southern elephants on the coast of the Sea of Azov (Lower Don) have been washed out of the Middle Pliocene beds and redeposited in Late Pliocene gravels.

In eastern Transcaucasia the bones occur mostly in loesses, loams and gravels, around the ancient coasts of the Kura bay of the Akchagyl and Apsheron seas. On the Lesser Caucasus uplands, bones of Upper Pliocene and Lower Quaternary elephants occur in river and lake-river sediments, like those near Leninakan and Erzurum. Elephant bones occur at Tsalka in conglomerates between doleritic lava flows, dated as Günz and Günz-Mindel (see also Burchak-Abramovich, 1951a).

Teeth of Elephas planifrons* and E. meridionalis are relatively small, with short and weak roots. Their enamel pockets are coarse-ribbed, comb-like plates, formed of enamel cylinders intergrown longitudinally. With a covering of dentine and cement, these widely-spaced pockets form enamel bellows; upon wearing, the pockets became transversally flattened, forming enamel loops with thick walls protruding 5-6 mm above the surface in mature individuals (Figure 173). The working surface of the tooth was used for grinding large pieces of plant material. The bases of the enamel pockets, near the pulp cavity, form a uniform roller with poorly-developed papilla. The cement of the teeth of these early elephants has been altered and weakened to such an extent that the roots, as a rule, have been destroyed and the pulp cavity is full of earth.** On the Russian Plain remains of Upper Pliocene elephants occur mostly in the south, none having been recorded north of the latitude of Moscow and Kazan.

417 As far as diet is concerned, E. planifrons and E. meridionalis were probably still fairly close to the mastodon. Striations and scratches in the enamel of the teeth of these elephants strongly resemble those on mastodon teeth, though in mastodons the grooves are usually transverse

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* Garutt (1957b) has expressed an opinion, not yet well founded, that the so-called E. planifrons known from the U.S.S.R. is merely an early form of E. meridionalis.

** The cement and dentine of these teeth usually resemble alabaster and marl.

to the jaw, while in elephants they are longitudinal. This is probably due to differences in the mode of grazing. The grooves were undoubtedly formed by sand grains and small stones taken up together with roots and grasses.

The seasonal feeding of elephants in the thickets and swamps and along the shores of lakes and in river valleys undoubtedly explains their relatively frequent burials in water-laid sediments.

Tooth replacement in Upper Pleistocene elephants has not yet been studied thoroughly, but it is generally assumed that in each jaw 5 molars were worn off and replaced by the appearance of new molars from behind and above in each jaw, in a manner similar to the replacement of the molars of the Recent Indian and African elephants. The last, 6th tooth, the biggest, with thickest enamel, was characterized by the absence of a posterior crushing surface; it functioned only in the last stages of the animal's life. This type of molar replacement, which was probably also characteristic of mammoths, is taken into account in the discussion which follows.[*]

Towards the Lower Anthropogene, the number and size of enamel pockets and consequently the height of the teeth have considerably increased; the enamel wall has become thinner and less folded. The teeth, particularly the lower teeth, have become relatively narrower and longer, and their volume and weight have increased both absolutely and relatively. This stage in the morphogenesis of elephants is represented by a series of burials on the lower (second and third) river terraces of Elephas (Parelephas) wüsti and E. (Parelephas) trogontherii.[**] The occurrences of bones of E. trogontherii are best known in the gravels of the third 418 terrace on the left bank of the Dniester, near Tiraspol, and in the Araks valley, near Yerevan and Leninakan (Map 75).

FIGURE 173. Section through M^5 of the southern elephant from the northern coast of the Sea of Azov

Section shows enamel pockets and specific features of loop formation (a — loop; b — pocket)

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[*] Fragment of the skull of a southern elephant from Khapry (collections of Institute of Geological Sciences AN SSSR) shows that the replacement of the second upper tooth by the third took place directly from above, similarly to the mode of replacement in mastodons, rather from than above and behind as in mammoths and Recent elephants.

[**] The latter name poorly reflects the actual situation, since the increase in abundance and area of distribution of the "trogontherial" beaver occurred probably as early as the Upper Pliocene.

The Middle Pleistocene sees the beginning of the final stage in the evolution of elephants. It coincided with the rapid development and proliferation of Middle Paleolithic man, who rapidly perfected the art of hunting, including the elephant hunt. By that time E. trogontherii had decreased in size and evolved into the mammoth, E. (Mammonteus) primigenius, and had completely changed in appearance, having developed a woolly coat*, longer and more sharply curved tusks, and stouter metacarpals and metatarsals. The evolutionary trends in the teeth included closer spacing of the enamel loops and increase in their number per unit length, thinning of the enamel, and smoothing of the enamel surface (Figure 174). Sharp edges developed on the bottom of the enamel pockets; pointed papillae situated along the sharp rim protruded into the pulp cavity. The teeth roots developed into long, curved or straight hollow tubes and the closely spaced enamel lamellae make a finer, and possibly more durable, grinder. Traces of vegetable matter are found only rarely on the truncated surfaces of the thin enamel of the teeth of mammoths and E. trogontherii. While feeding on twigs and tree branches undoubtedly continued, grass as a diet began to gain in importance, as has been definitely established by the contents of the stomachs of the frozen mammoths in Siberia.

Remains of true mammoths in the Caucasian Isthmus are more common in Ciscaucasia than in Transcaucasia. As as rule, they occur in the young (first and second) river terraces. The state of preservation of the enamel, dentine and cement of the mammoth teeth is always strikingly different from the preservation of these components in the teeth of earlier elephants, as roots and the pulp cavities of mammoth teeth are often preserved in their entirety.

The earliest remains of mammoth-type elephants from the Caucasus were found in the Girei quarry on the second terrace of the Kuban. Only the materials from the Il'skaya site in the Trans-Kuban region have been dated. Four fragments of molars, many pieces of tusk, and up to 40 assorted incomplete skeletal elements including tarsals and carpals have been collected from this site.

The last occurrence, stratigraphically speaking, is part of a left upper jaw with a very worn 6th tooth from the travertines of the northern slope of Mt. Mashuk. The whitish enamel, the light cement—light brown color of the bone in fresh fracture, and the characteristic smell of raw bones upon scratching — all these features are highly unusual for a burial so far south. The small size of the tooth, the thin enamel (1.0-1.2 mm), and the small diameter of the tusk indicate that the fragment belongs to a stunted, very late variety of mammoth of Late Paleolithic and even Neolithic age.

In Transcaucasia, mammoth teeth have so far been found only in the Gori depression (Burchak-Abramovich, 1946; Gabuniya, 1952a). The tooth described by Gabuniya (1952a), an unworn M^4, was collected on the first terrace of the Kura River in the town of Gori. On the basis of the small size of the tooth with 12 lamellae over 10 cm and enamel thickness of 1.5 mm Gabuniya has related the tooth to the "stunted" mammoths of the west
419 Mediterranean. On the basis of the mode of its occurrence the specimen
has been dated as early post-Würm, i.e., Lower Mesolithic to Neolithic.

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* So far there is no information on the woolly coat of E. trogontherii.

Gromova (1948) has assumed, without any evidence, that "some mammoths lived in the Caucasus in pre-Riss time." Burchak-Abramovich (1946) considered (incorrectly) that the Transcaucasian mammoth is a representative of the northern tundra. At variance with these investigators, Gabuniya has correctly emphasized the probability of evolution of small local forms of mammoth in the south of eastern Europe and in Transcaucasia.

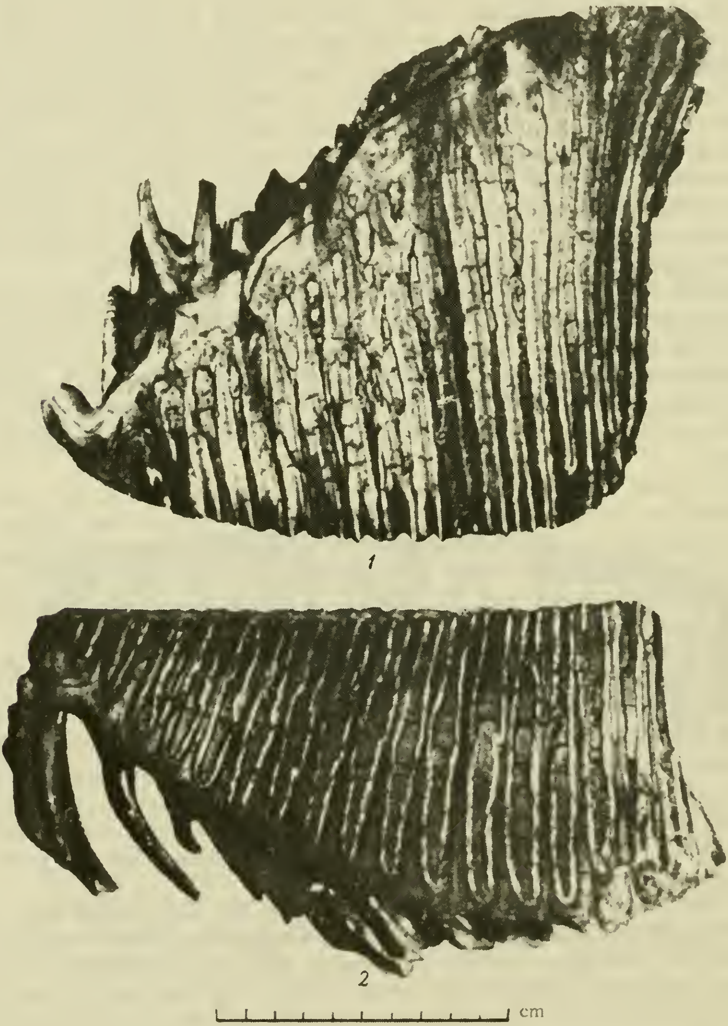

FIGURE 174. Longitudinal sections

1 — M^6; 2 — M$_6$ of mammoths from the Russian Plain

Even if the northern mammoths migrated to the Caucasus during the maximum height of the cold periods, it is doubtful that they could migrate farther south than Ciscaucasia. In the Upper Pleistocene the western migratory route of the northern mammoths through forests and steep rocks was difficult, and the eastern route passed through a country too dry and hot for mammoths.

420 Thus Transcaucasia was probably the southern boundary of the distribution of the mammoths, and this is confirmed by the absence of reliably identified remains of mammoths from the Armenian Highlands, Iran and Southwest Asia in general. The xeromorphic environment with poorly-developed wood vegetation, which evolved (at least in the low valleys of these regions) towards Middle Pleistocene time, was not suitable for the elephants of late and northern types.

North of the Ciscaucasian plain, mammoth remains are the most common paleontological finds in the valleys of the Don, the Volga and the Ural, and farther north the proportion of mammoth bones also steadily increases by comparison with the bones of earlier elephants. The results of our counts, done in 1950-1955, are given in Table 90.

TABLE 90. Number of teeth of fossil elephants in regional museums

Museums	Mammoths		Elephas trogontherii		Elephas meridionalis	
	no.	%	no.	%	no.	%
Arkhangel'sk	12*	100.0	–	–	–	–
Veliki Ustyug	33*	100.0	–	–	–	–
Vologda	23*	100.0	–	–	–	–
Kazan University	59	98.4	1	1.6	–	–
Ural'sk	10	83.3	2	16.7	–	–
Kuibyshev	10	77.0	3	23.0	–	–
Saratov	21	81.0	5	19.0	–	–
Astrakhan	51*	43.5	71*	56.5	–	–
Novocherkassk	3	18.7	4	25.0	9	56.3
Temryuk and collections from Taman and at the Paleontological Institute	3	7.3	8	19.5	30	73.2
Krasnodar	7	33.3	11	52.4	3	14.3
Stravropol	3	25.0	2	16.7	7	58.3
Pyatigorsk	4	44.5	2	22.2	3	33.3
Makhachkala	1	33.3	–	–	2	66.7

Note. Asterisk indicates cases when bones other than teeth were counted.

The distribution of the species, as given in Table 90, indicates more than the apparent decrease in the frequency of burial of mammoths in the south and the increase in erosion and exposure of older beds containing remains of southern elephants. Recorded distribution of the proportions of the species is due to the fact that the mammoths were very abundant in the north, the main area of their distribution, whereas the distribution areas of E. trogontherii and E. meridionalis were further south.

FIGURE 175. Print of worn surface (enamel loops) and outlines of teeth M^6_6 of fossil elephants of the Russian Plain and the Caucasus (M^6 – a; M_6 – b)

Elephas (Mammonteus) primigenius: 1a, 1b – Sukhona valley, No.10401, 10870, Tot'ma Museum; 2a – peat in Don valley, un-numbered, Voronezh Museum; 3a – Kirillovskaya Upper Paleolithic site near Kiev, No.302, Institute of Zoology of the Academy of Sciences of the Ukr. S. S. R.

FIGURE 175 (continued)

4b — Middle Paleolithic site, Chokurcha, in the Crimea, un-numbered, Simferopol Museum; 5a — second terrace of Kuban, Girei quarry, near Kavkazskaya, un-numbered, Armavir Museum; 6a — Terek valley near Naurskaya, un-numbered, Georgian Museum; 7a, 7b — Khazar age of Volga valley, Chernye Yar, un-numbered, PIN [Paleontological Museum] ("Late" Elephas trogontherii and "Early" mammoth);

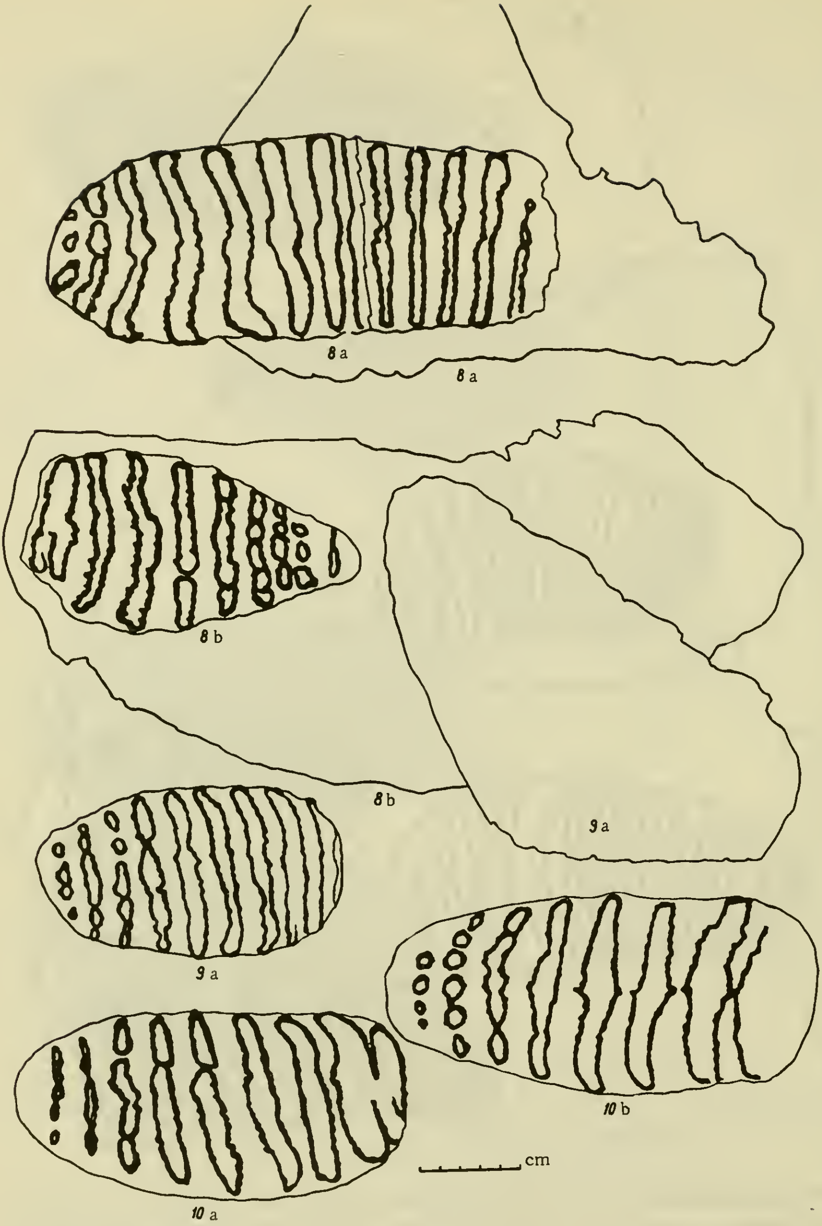

FIGURE 175 (continued)

Elephas (Parelephas) trogontherii: 8a, 8b – third terrace of Dniester at Tiraspol, un-numbered, Moscow Geological Prospecting Institute. Elephas (Archidiskodon) meridionalis: 9a – Araks valley, Leninakan, Kazachii Post, un-numbered, Geological Institute AN Arm. S. S. R.; 10a, 10b – conglomerates of Taman Peninsula, No. 1249/222, No. 1249/42, PIN (Phanagorian (?) elephant);

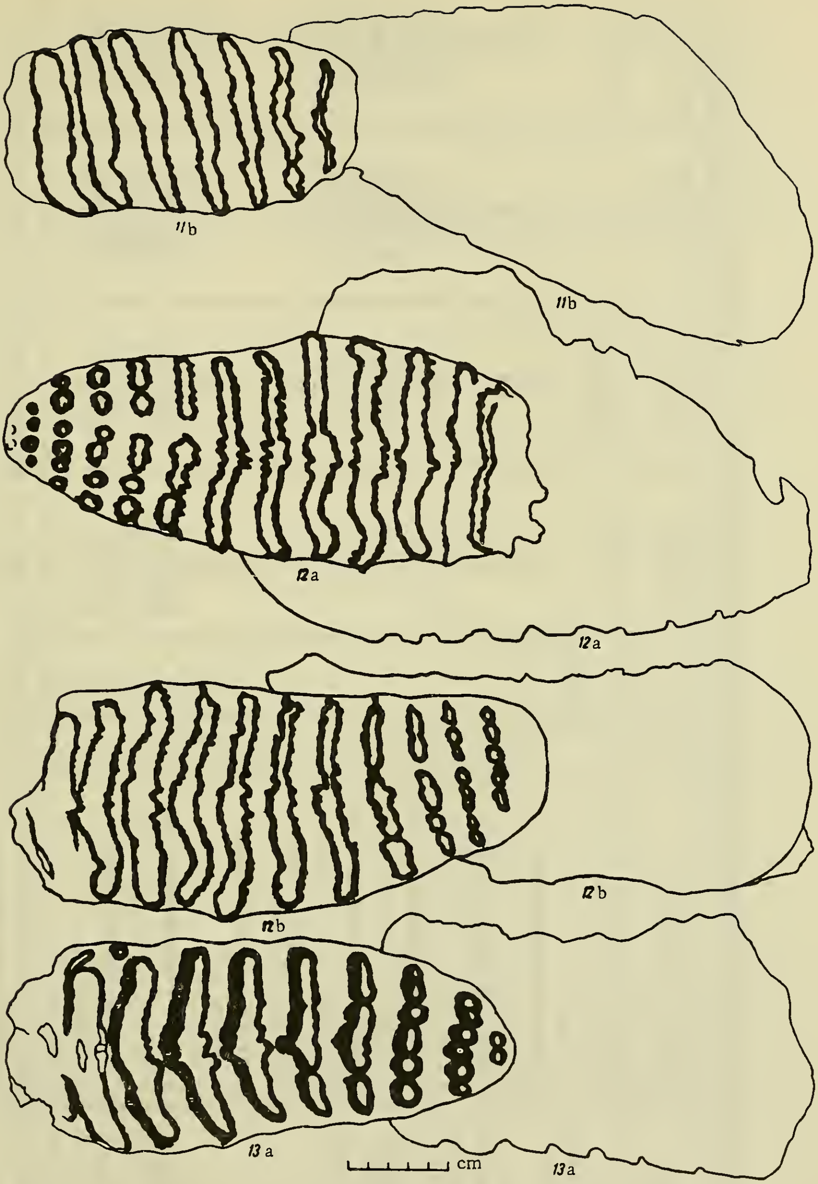

FIGURE 175 (continued)

11b — conglomerates of Taman Peninsula, No. 1249/232, PIN (Phanagorian (!?) elephant); 12a, 12b — Obitochnoe, Ukraine, No. 24239, ZIN; 13a — Stavropol, No. 25284, ZIN

TABLE 91. Changes in basic morphometric indices of teeth (M_1^1-M_6^6) of elephants from the Anthropogene and Pliocene beds in the Caucasus and the Russian Plain*

Epoch and stages	Localities	Indices	M_1^1	M_2^2	M_3^3	M_4^4	M_5^5	M_6^6
			Mammoths					
Pleistocene Upper Khvalynsk age	Low terraces of Northern Dvina and Sukhona; museums: Volgoda, Totma, Velikii Ustyug, Sol'vychegodsk, Arkhangel'sk	Number of teeth studied	—	—	$\frac{2}{1}$	$\frac{1}{3}$	$\frac{2}{8}$	$\frac{18}{22}$
		Maximum number of enamel pockets ....,.........	—	—	$\frac{12}{12}$	$\frac{—}{18}$	$\frac{17}{20}$	$\frac{25}{29}$
		Number of enamel pockets over 10 cm	—	—	$\frac{12}{12}$	$\frac{9}{8.7(8-10)}$	$\frac{9.3(8.5-10)}{8.9(7.5-10)}$	$\frac{8.8(7-12)}{8.7(6.2-12)}$
		Thickness of enamel wall (in mm)	—	—	$\frac{1.0}{1.0}$	$\frac{1.0}{1.0-1.2}$	$\frac{1.4(1.1-1.6)}{1.6(1.0-2.0)}$	$\frac{1.4(1.0-1.8)}{1.5(1.0-2.5)}$
	Upper Desna, Eliseevichi site (Upper Paleolithic)	Number of teeth studied	—	$\frac{—}{1}$	$\frac{2}{3}$	$\frac{3}{1}$	$\frac{4}{2}$	$\frac{5}{—}$
		Maximum number of enamel pockets	—	$\frac{—}{10}$	$\frac{12}{14}$	$\frac{15}{17}$	$\frac{—}{17}$	$\frac{23}{—}$
		Number of enamel pockets over 10 cm	—	$\frac{—}{14}$	$\frac{11.5(11-12)}{11.3(10-12)}$	$\frac{9.3(8-11)}{9.5}$	$\frac{8.1(7-10)}{8.8(8-9.5)}$	$\frac{8.2(7-9)}{—}$
		Thickness of enamel wall (in mm)	—	$\frac{—}{0.9}$	$\frac{1-1.1}{1.3(1.1-1.5)}$	$\frac{1.5(1.0-1.9)}{1.8}$	$\frac{1.9(1.6-2.2)}{2.1(1.9-2.2)}$	$\frac{1.7(1.2-2.0)}{—}$

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* Unpublished author's material. Measurements and casting of teeth done at excavation sites (Mezin) and in museums of the R. S. F. S. R., Belorussia, the Ukraine, the Crimea and the Caucasus. Sex variation has not been studied.

Pleistocene	Upper Khvalynsk age	Middle Desna*, Mezin site (Upper Paleolithic)	Number of teeth studied	—/1	—/1	3/1	2/2	4/6	1/3
			Maximum number of enamel pockets	—/0	—/15	—/16	—	—	—
			Number of enamel pockets over 10 cm	—/13	—/12	11(10-12)/10	9(8-10)/10.5(9-12)	9.5(9-10)/9.3(8.5-10)	8.5/8.3 (8-8.5)
			Thickness of enamel wall (in mm)	—/0.8	—/0.9	1.2(1.0-1.4)/1.1	1.5-1.7/1.4-1.4	1.6(1.5-1.7)/1.6(1.4-1.8)	1.6/1.9(1.8-2.0)
		Middle Dniester, [former] Kirilovskaya site at Kiev (Upper Paleolithic)	Number of teeth studied	—	—	—/3	—/11	—/2	3/4
			Maximum number of enamel pockets	—	—	—/13	—/17	0/0	22/22
			Number of enamel pockets over 10 cm	—	—	—/11(10-12)	—/8.9(7-12)	—/8.5(8-9)	8.9(8-10)/8.5(8-9)
			Thickness of enamel wall (in mm)	—	—	—/1.2(1.0-1.4)	—/1.7(1.2-2.0)	—/1.9-2.0	1.9(1.8-1.9)/2.0(1.8-2.3)
	Khazar age	Northern foothills in Crimea, Chokurcha cave (Middle Paleolithic-Mousterian	Number of teeth studied	—	—	—/2	4/1	1/2	—/3
			Maximum number of enamel pockets	—	—	—/14	18/18	20/20	—/25
			Number of enamel pockets over 10 cm	—	—	—/10-11	9.8(8.5-11)/10	11.5/7-8	—/8.0(7-9.5)
			Thickness of enamal wall (in mm)	—	—	—/1.2(0.8-1.5)	1.5(1.3-1.9)/1.4	1.6/2.1(1.9-2.2)	—/2.0(1.8-2.1)

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* Thickness of enamel measured on prints. Counting the number of enamel pockets (loops) at Mezin was difficult since teeth were preserved in situ in the jaw.

TABLE 91 (continued)

Epoch and stages	Localities	Indices	M^1_1	M^2_2	M^3_3	M^4_4	M^5_5	M^6_6
		Mammoths						
Pleistocene Middle Khazar age	Gravels and loams of low terraces of rivers of Ciscaucasia and Transcaucasia: Il'skaya Girei, Labinskaya, Dusheti and others	Number of teeth studied	–	–	$\frac{2}{-}$	$\frac{1}{2}$	$\frac{5}{3}$	$\frac{7}{5}$
		Maximum number of enamel pockets	–	–	$\frac{13}{-}$	–	$\frac{-}{21}$	$\frac{24}{-}$
		Number of enamel pockets over 10 cm	–	–	$\frac{10\text{-}10}{-}$	$\frac{9}{8\text{-}10}$	$\frac{8.4(7\text{-}10)}{7.2(6.5\text{-}8)}$	$\frac{7.7(6\text{-}9.5)}{7.5(7.0\text{-}8.0)}$
		Thickness of enamel wall (in mm)	–	–	$\frac{1.3(1.1\text{-}1.5)}{-}$	$\frac{1.4}{2.0\text{-}2.1}$	$\frac{1.6(1.5\text{-}1.7)}{1.6(1.4\text{-}1.9)}$	$\frac{1.9(1.2\text{-}2.2)}{1.8(1.5\text{-}2.2)}$
		Elephas trogontherii						
Lower Baku age	Gravels at the base of high terraces of Dniester, Don, Tiraspol, Rostov (fossil valleys of proto-rivers)	Number of teeth studied	–	–	–	–	$\frac{3}{4}$	$\frac{2}{8}$
		Maximum number of enamel pockets	–	–	–	–	$\frac{-}{17}$	$\frac{18}{23}$
		Number of enamel pockets over 10 cm	–	–	–	–	$\frac{6.5(6\text{-}7)}{6.7(6\text{-}8)}$	$\frac{5\text{-}6.5}{6.8(5.5\text{-}8)}$
		Thickness of enamel wall (in mm)	–	–	–	–	$\frac{2.4(1.8\text{-}3.3)}{1.9(1.8\text{-}2.3)}$	$\frac{2.9(2.3\text{-}3.4)}{2.4(1.9\text{-}3.3)}$

Pleistocene	Lower Baku age	Gravels at the base of high terraces of rivers of Ciscaucasia: Girei, Labinskaya, Pregradnaya, Pyatigorsk, Stavropol (fossil valleys of proto-rivers)	Number of teeth studied	—	—	—	$\frac{-}{1}$	$\frac{4}{2}$	$\frac{4}{5}$
			Maximum number of enamel pockets	—	—	—	—	—	$\frac{26}{-}$
			Number of enamel pockets over 10 cm	—	—	—	$\frac{-}{5.5}$	$\frac{6.1(5-8)}{6.4(6.2-6.5)}$	$\frac{7.0(6-8)}{7.0(5.5-8)}$
			Thickness of enamel wall (in mm)	—	—	—	$\frac{-}{1.9}$	$\frac{2.3(1.7-3.2)}{2.4(2.2-2.5)}$	$\frac{2.8(2.5-3.0)}{2.2(1.4-2.8)}$
			Elephas meridionalis						
Pliocene	Upper Apsheron age	Sands and gravels of middle Araks valley. Leninakan (Kazachii Post)	Number of teeth studied	—	—	—	—	$\frac{1}{1}$	$\frac{1}{7}$
			Maximum number of enamel pockets	—	—	—	—	—	$\frac{-}{25}$
			Number of enamel pockets over 10 cm	—	—	—	—	$\frac{6.5}{7}$	$\frac{6.2}{6.4(5.3-8)}$
			Thickness of enamel wall (in mm)	—	—	—	—	$\frac{2.8}{2.1}$	$\frac{2.3}{3.0(2.7-3.6)}$
		Conglomerates of Taman Peninsula: Sennaya, Tsimbal	Number of teeth studied	—	—	$\frac{-}{2}$	$\frac{1}{2}$	$\frac{4}{5}$	$\frac{2}{3}$
			Maximum number of enamel pockets	—	—	$\frac{-}{9}$	$\frac{-}{9}$	$\frac{10}{-}$	$\frac{12}{11}$
			Number of enamel pockets over 10 cm	—	—	$\frac{-}{8-9}$	$\frac{7}{8-8}$	$\frac{5.4(5-5.5)}{5.7(5-6.3)}$	$\frac{5.7(4.8-6.5)}{4.7(4.5-5.0)}$
			Thickness of enamel wall (in mm)	—	—	$\frac{-}{1.4(1.0-1.8)}$	$\frac{1.8}{1.6(1.1-2.0)}$	$\frac{2.8(2.1-3.8)}{2.9(2.8-3.5)}$	$\frac{2.7-2.9}{3.5(2.9-4.0)}$

TABLE 91 (continued)

Epoch and stages	Localities	Indices	M^1_1	M^2_2	M^3_3	M^4_4	M^5_5	M^6_6
Pliocene Upper Akchagyl age	Sands and gravels of proto-rivers of Ciscaucasia: Psekups, Girei, Voskresenskaya, Georgievsk, Malgobek, Groznyi and others	Number of teeth studied	–	–	–	$\frac{-}{4}$	$\frac{2}{8}$	$\frac{3}{4}$
		Maximum number of enamel pockets	–	–	–	$\frac{-}{8}$	$\frac{-}{11}$	$\frac{12}{13}$
		Number of enamel pockets over 10 cm	–	–	–	$\frac{-}{5.5(5\text{-}6)}$	$\frac{5\text{-}6}{5.3(5\text{-}6)}$	$\frac{4.8(4.5\text{-}5)}{5.0(4.5\text{-}5.5)}$
		Thickness of enamel wall (in mm)	–	–	–	$\frac{-}{2.9(2.4\text{-}3.3)}$	$\frac{3.5(2.8\text{-}4.1)}{3.2(2.7\text{-}3.9)}$	$\frac{3.1(2.3\text{-}3.5)}{3.7(3.0\text{-}4.5)}$
	Sands and gravels of proto-rivers of northern Azov coast: Leventsovka, Aksai, Khapry, Morskaya, Taganrog, Mariupol and others	Number of teeth studied	–	–	$\frac{-}{1}$	$\frac{-}{1}$	$\frac{-}{3}$	$\frac{2}{4}$
		Maximum number of enamel pockets	–	–	$\frac{-}{9}$	$\frac{-}{8}$	$\frac{-}{11}$	$\frac{16}{15}$
		Number of enamel pockets over 10 cm	–	–	$\frac{-}{7}$	$\frac{-}{5}$	$\frac{-}{4.4(4.2\text{-}4.5)}$	$\frac{4.8(4.5\text{-}5)}{4.6(4.0\text{-}5.0)}$
		Thickness of enamel wall (in mm)	–	–	$\frac{-}{2.0}$	$\frac{-}{3.5}$	$\frac{-}{3.0(2.8\text{-}3.3)}$	$\frac{3.5(3\text{-}3.9)}{3.8(3.5\text{-}4.1)}$

The above-mentioned morphological changes in the teeth of the supposed evolutionary sequence can be traced on the photographs of their longitudinal sections (Figures 173, 174) and by casts and diagrams (Figure 175). Table 91, which gives the morphometric indices of the teeth from some "key" burials in the Caucasus and the Russian Plain, is of practical significance in stratigraphic correlations.*

430 The changes in tooth structure may be summarized as follows. From the time elephants appeared in the region of the Black and Caspian seas to the time of their extinction in the Lower Holocene, the maximum number of enamel loops of M_6^6 increased from 16/15 to 25/19; the number of loops over 10 cm of the worn or lateral surface increased by 4.1/4.2. Thickness of the enamel wall decreased by 2.05/2.30 mm.

The apparently saltatory changes in the tooth structure of Quaternary elephants, described so briefly in the preceding section, may be better explained from the geological (taphonomic) rather than the biological standpoint. The apparently isolated stages of morphogenesis of elephants (and other animals) may correspond to the changes in the structure of river networks and distribution, and in cycles of sedimentation which produced the conditions necessary for the burial of bones. Evolutionary inertia, which almost always operates in the evolutionary process, results in the lag of adaptive changes behind rapidly changing environmental factors. The accumulation of sediments depends, of course, on environmental factors; however, we tend to regard the evolutionary changes described as a continuous (not necessarily saltatory) accumulation of minor features, terminated by evolutionary extinction.

Unfortunately, there are no data so far which would indicate that the development of mammoth features in the elephant stock occurred in the Caucasus at the same time as on the Russian Plain. Future comparisons of the results of geological and paleontological studies will undoubtedly reveal the truth.

Order PERISSODACTYLA

Very little work has been done on the phylogeny of perissodactyls, and as yet there is no agreement among paleontologists about whether the rhinoceroses of the Upper Pliocene and Anthropogene (Rhinoceros etruscus, R. mercki, R. tichorhinus) represent a single phylogenetic series. The pronounced morphological differences between these stratigraphically separated species are less sharp in the transitional stratigraphic stages. The skulls of the still poorly known R. binagadensis from the Middle Pleistocene of the Apsheron Peninsula (Binagady) differs from the Upper Pleistocene woolly rhinoceros in its deeply concave intertemporal region, the smaller second horn and greater inflation and callosity of the base of the first horn, the shorter postorbital part of the skull, thin mastoid processes and small (spherical) occipital condyles. The teeth of this species were considerably bigger (broader and longer) than those of the woolly rhinoceros, and the aboral edge of the last

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* In the construction of the table it was taken into account that the direct affinity of the Upper Pliocene forms to the Quaternary forms has not been proved in all cases.

molar protruded far beyond the anterior edge of the orbit (Figure 176, 2). The preorbital foramina are very small. The relatively narrow occipital region of the skull of the Binagady species indicates that its head was held in a more horizontal position than that of the woolly species. The Binagady rhinoceros probably thrived more on tree branches than on grasses, as did the woolly rhinoceros. The more slender metapodials, forearm bones and tibia of the Binagady rhinoceros indicate that it was more lightly built and was more active than the woolly rhinoceros. The abundance of this species in the clearly xerophytic landscape of the Apsheron, very different from the habitats of the woolly rhinoceros, attests to the distinct specific and even generic identity of the Binagady form (see Dzhafarov, 1955). All the data
431 presented above do not preclude the possibility that the woolly rhinoceros migrated from the north to eastern Transcaucasia and farther south into southwest Asia in Upper Pleistocene times. This seems very likely, as it is known that other large mammals like the primitive bull migrated in the Upper Pleistocene from the north to the Apsheron Peninsula. Since the remains of the woolly and early rhinoceroses in the Caucasus are represented by fragmentary material, at present we can only give a map of their occurrence (see Map 77), without going into a detailed analysis of their origin and stratigraphic variation of morphological and phylogenetic features.

FIGURE 176. Rhinoceros skulls: 1 — Rhinoceros tichorhinus, Upper Pleistocene, Russian Plain, Vladimir, No. 10699, ZIN; 2 — Rh. binagadensis, Middle Pleistocene, eastern Transcaucasia, Binagady, No. 24402, ZIN

The evolutionary trends of Elasmotherium (E. caucasicum — E. fischeri), known only from its Upper Pliocene to Middle Pleistocene representatives, included a considerable decrease in the size of teeth and development of plicated enamel plates (Borisyak, 1914).

The problem of the direct and indirect continuity of evolution of morphological characters in horses from the Anthropogene of the Caucasus and Russian Plain is as difficult as the problem of the evolution of rhinoceroses. The great ability to migrate and the almost universal adaptability to various types of habitat make it very difficult to solve the
432 problem of the origin of the east European and Caucasian horses in the Quaternary satisfactorily. For example, it is still not clear whether Przewalski's horse is an evolutionary successor of the local Upper Pleistocene horse (broad-footed horse from the Upper Paleolithic of the Don area), or whether it migrated from the south in relatively recent times (i.e., Holocene). However, it is clear that local races of horses evolved in the Caucasian Isthmus and the Russian Plain, replacing one another at different geological periods. The general trend in horse evolution was reflected in the development of hypsodonty and monodactylism, but the details of the process varied from region to region.

Considering the data presented above, it is only possible at this stage to speak of general stratigraphic and geographic changes in the post-Tertiary horses of Russia, without relation to the evolution of any particular species. As far as the Caucasian and east European material shows, the evolution of horses proceeded as follows. The Upper Pliocene horses of the Equus stenonis type from the Azov area were large, relatively heavy, with large teeth, characterized by a relatively thin and much folded enamel plate. The metapodia were neither highly specialized for fast running in semideserts and steppes nor broad-footed and thus adapted to the meadows and peat bogs of the taiga and tundra.

The horses of the Upper Pliocene-Lower Pleistocene of the E. süssenbornensis type (from the conglomerates of the Taman Peninsula) had completely equuid teeth; their metapodia were lightly built, indicating that this form was adapted for fast running on savannah and steppes, which were regularly burnt during the summer. These horses were bigger than the Quaternary horses (Vereshchagin, 1957a), but a smaller horse occurred in the Middle Pleistocene of eastern Transcaucasia, characterized by more antero-posteriorly flattened metapodial diaphyses. Protuberances of the lower epiphysis ridge of the canon bone and metacarpus are indexes that the osteochondrous type of pastern fixation is somewhat less marked in the Binagady horse than in the Upper Pliocene forms. The laterial ligaments, however, are stronger. The hoof phalanges of this horse are relatively small, with a steeply rising angle anterior to the wall, an adaptation to the xerophytic habitats and the rough ground of this region. The fossil representatives of Upper Pleistocene and Holocene horses of the Caucasus are still poorly known; however, horses of the southern type, of "dry" contsitution (see Chapter III), undoubtedly inhabited Transcaucasia. The Upper Pleistocene horse of the Russian Plain was characterized by very massive legs and a brood foot, which can be seen particularly well in the representatives from the Upper Paleolithic beds at Kostenki on the Don (Figure 177).

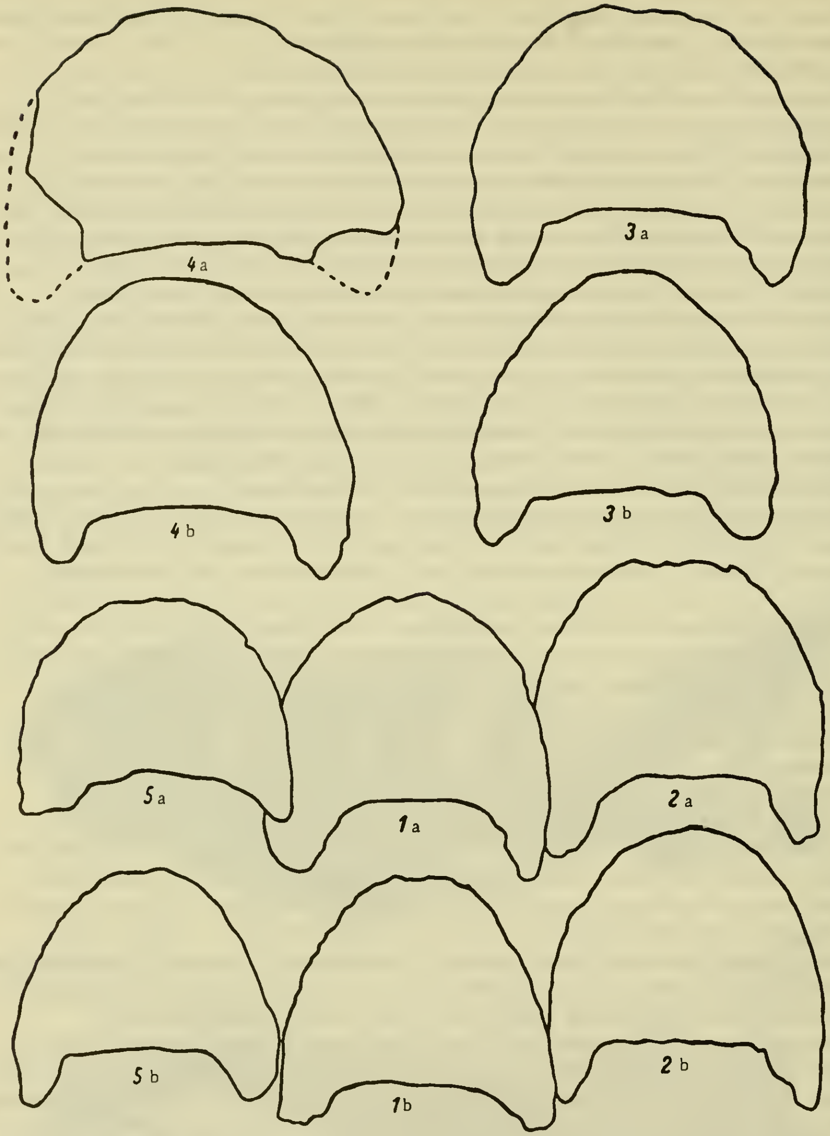

FIGURE 177. Stratigraphic and geographic variation in the shape and supporting surface area of the hoof phalanx of Eurasian horses. a — fore legs; b — hind legs. ½ natural size

1a, 1b — Equus caballus gmelini, Recent "tarpan", Russian Plain, No.521, ZIN; 2a, 2b — E. przewalskii, Recent Przewalski's horse, Dzungaria, No.17591, ZIN; 3a, 3b — E. caballus subsp. (foss.), Lower Holocene, Novosibirskie Islands, No.4419, ZIN; 4a, 4b — E. caballus latipes, Upper Pleistocene (Upper Paleolithic) Voronezh, Kostenki XV, No.25183, ZIN; 5a, 5b — E. caballus subsp., Middle Pleistocene, eastern Transcaucasia, Binagady

These horses probably grazed on soft meadows, tundra and taiga swamps on the floodplains of rivers. A similar structure of the hoof phalanx, though not as wide, is characteristic of the horses of the extreme northeast of Siberia, which probably lived on somewhat harder terrain under conditions of thinner snow cover.*

434 TABLE 92. Stratigraphic and geographic variation of the supporting surface (mm^2) of hoof phalanges of horses from the Anthropogene of Asia

Dimensions	Middle Pleistocene, eastern Transcaucasia, Binagady Equus caballus 4 specimens	Upper Pleistocene, upper Don, Kostenki Equus caballus latipes 4 specimens	Upper Pleistocene, Novosibirskie Islands Equus caballus subsp. 8 specimens	Ukraine Equus caballus gmelini Ant. No.521, ZIN	Dzungaria Equus przewalskii Pol. No.17591. ZIN
Fore leg.	$\frac{28.8}{27-32}$	$\frac{43}{39-50}$	$\frac{40}{27-48}$	34	37.5
Hind leg	25.5	$\frac{40.9}{37-46}$	$\frac{37}{33.5-40.5}$	31.5	33.5
Index of difference (2:1 x 100)	88.5	95.0	92.5	92.6	89.3

Note. Means in the numerator, observed ranges in the denominator.

The size of the area of the fore and hind leg hoof phalanges of different horses and their interrelationships are given in Table 92. The data in Table 92 show that in the southern and steppe varieties of horses the anterior hoofs were relatively larger.

During the period of maximum cooling and development of mesophytic landscapes, the broad-footed horse migrated far southward, probably to the foothills of the Caucasus. There are reasons to believe that the xerothermal stage and the extensive development of steppes on the Russian Plain resulted in further divergence of these Upper Pleistocene horses in the development of morphological characters related to forest and steppe tarpans; confirmation is difficult, however, due to the absence of good skeletal material of these so recently extinct forms (see Gromova, 1949; Geptner, 1955).

Order ARTIODACTYLA

The large amount of work done on this order allows easy tracing of the main evolutionary trends of some of the Caucasian forms.

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* A.A. Sludskii (pers. comm.) related the occurrence of wide hoofs on the fore legs of the northern and Upper Pleistocene hoofed mammals to the need to dig through the snow in search of food.

Pigs of the group Sus scrofa — S. vittatus appear in Eastern Europe and the Caucasus for the first time in the Upper Pliocene, and their main morphological features by then have already been eatablished.

Amon (1938) noted the extreme variation in skull morphology of the Pliocene-Pleistocene pigs, which already inhabited vast areas of Eurasia by the Lower Pleistocene. Therefore there are reasons for believing that any stratigraphically younger pigs found in Russia are members of a continuous evolutionary lineage.

The Taman boar (S. tamanensis) from the Upper Pliocene beds of the Taman Peninsula differs from the younger Caucasian boars in its
435 larger size and, in mature males, a much wider lower jaw in the region of the diastema (Vereshchagin, 1957a). The boar from the Middle Pleistocene beds of the Apsheron Peninsula (S. apscheronicus) does not differ in size from the Recent species, but the Apsheron species is characterized by auditory bullae elongated downward and by the lachrymal bones of the type intermediate between S. scrofa and S. vittatus (Burchak-Abramovich and Dzhafarov, 1948). Widths of the lower jaw of Quaternary boars measured behind the tusks are given in Table 93.

TABLE 93. Changes in size of boars by the dimensions of the lower jaw (in mm)

Locality and geologic age	Species	Width of lower jaw behind tusks	Number of specimens studied
Caucasus, Recent	Sus scrofa attila ...	$\frac{46.0}{45-55}$	5
Middle Don, 10-13th centuries A. D.	S. scrofa attila	$\frac{59.0}{55-64}$	3
Volga area, Tunguz Peninsula, Middle Pleistocene	S. cf. scrofa	65.0	1
Transcaucasia, Apsheron Peninsula, Middle Pleistocene	S. apscheronicus	$\frac{52.0}{50-54}$	2
Ciscaucasia, Taman Peninsula, Upper Pliocene	S. tamanensis	73.0	1

Note. Means in the numerator, observed ranges in the denominator.

A number of lower jaws and skulls of boars of the Anthropogene are shown in Figure 178. The relative size of the bones of the axial and visceral cranium has changed considerably since the Middle Pleistocene; however, there have only been minor changes in tooth size since that time. The sizes of M_3^3 are identical in the Binagady and Recent Caucasian boar. However, the heel portion of the tooth of the Recent species has become more complex due to development of 1-2 columnar papillae on the heel (see Figure 178, 1, 4).

The abrupt saltatory decrease in the size of teeth, particularly noticeable in M_3^3, occurred only in the Neolithic in domesticated populations.

The remains which have been reliably identified as the red deer group (Cervus elaphus s. lato) occur in the U.S.S.R. for the first time in the beds of the Lowermost Anthropogene.* These deer evidently evolved from some Pliocene Mediterranean forms. Pavlova (1926) has described a skull and very simple unbranched antlers of a deer (Cervus tschelekensis) from the Akchagyl (Upper Pliocene) beds of the Transcaspian region. Isolated fragments of antlers (with the first outgrowth somewhat above the crown) of a small variety of Pliocene deer occur in 436 the Lower Pleistocene conglomerates of the Taman Peninsula. Their identification with the red deer group is not certain (Vereshchagin, 1957a), though it seems possible that they are ancestral forms. The Lower Anthropogene deer, known from the Tiraspol gravels (on the Dniester), are characterized by antlers with two closely spaced low supraorbital outgrowths and by the primitive, crownless type of the terminal branching.

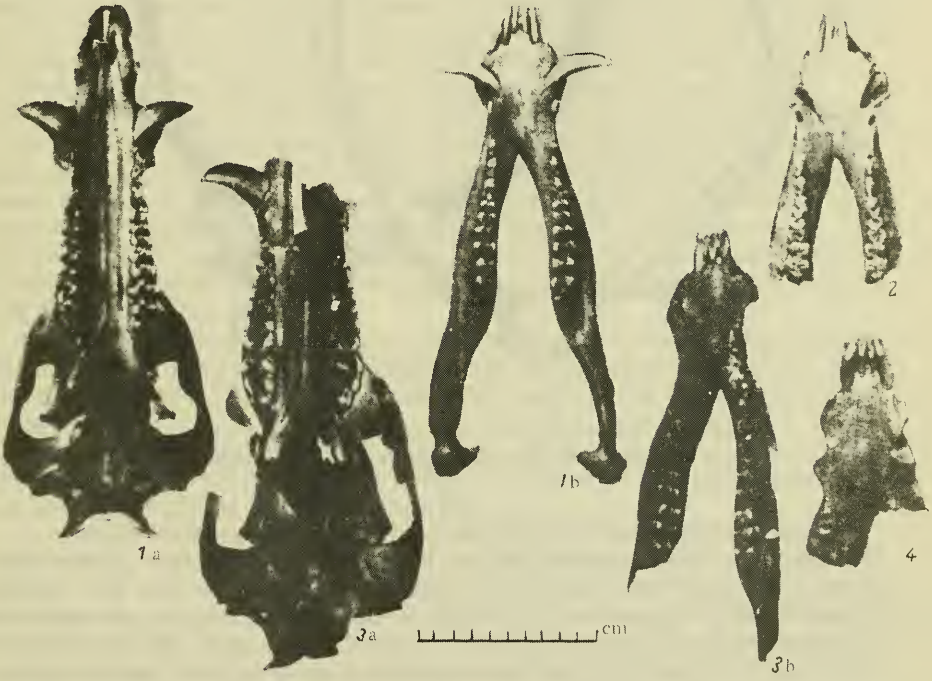

FIGURE 178. Skulls and lower jaws of boars

1a, 1b — Sus scrofa attila, Recent, Greater Caucasus, No. 10485, ZIN; 2 — S. scrofa attila, 10-13th centuries A.D., Lower Don, Sarkel; 3a, 3b — S. apscheronicus, Middle Pleistocene, eastern Transcaucasia, No. 26031, ZIN; 4 — S. tamanensis, Upper Pliocene, Caucasus, Taman Peninsula, No. 26000, ZIN

This type of "tightly" branching antler was remarkably stable, persisting through the Anthropogene in Eastern Europe and the Caucasus. However, the Middle and Upper Pleistocene deer of the Volga valley and areas farther east are characterized by a "looser" position of the first outgrowths on the

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* Indications of earlier occurrences, as for example, in the Middle Pliocene of Transcaucasia (Bogachev, 1938c), are not certain. They probably refer to the deer of the genus Eucladocerus.

antler stem similar to that of the Recent Siberian and American wapiti. Development of the fairly large antlers in the European noble deer began probably in the Middle Pleistocene. A weakly-developed type of vestigial crown is noted in some antlers washed out of the Khazar alluvium of the Volga (Figure 179) and Don valleys, and the crown is well developed in some antlers from the bitumens of the Apsheron Peninsula.

(437)

FIGURE 179. Antlers of red deer (*Cervus elaphus* subsp.) from the Middle Pleistocene alluvium of the proto-Volga valley. Kuibyshev museum

The extensive descriptions of deer from the Binagady materials (Alekperova, 1952) indicate that the Middle Pleistocene deer of eastern Transcaucasia are not appreciably different in size from the Recent deer
437 of the Greater Caucasus. The Middle Pleistocene species is characterized by lighter antlers. According to Akeperova's drawings, antlers with poorly-developed and widely-spaced supraorbital outgrowths also occur in the bitumen. This material is not sufficient for the study of the role of the migrations and local speciation of the noble deer of Eastern Europe and the Caucasus in the Anthropogene under the conditions of changing landscape and ecology. Nevertheless it is clear that during the Quaternary in Eastern Europe and the Caucasus there was a "struggle" between the *elaphus*-type (*Cervus elaphus* — with developed crown) and the wapiti-type (*C. canadensis* — without crown and with widely-spaced first outgrowths). For the Caucasian population the development of this process can be traced by using Dinnik's (1914a) descriptions and very complete collections as those of the Digorized cave in North Ossetia and the museum of the Borzhomi nature reserve. The *elaphus*-type of antler is usually suppressed in the Recent Caucasian deer, but in the Digorized collection, which in 1948 consisted of 62 pairs and 121 single horns, 27% were

elaphus-type antlers (Figure 134) and 73% wapiti-type.* The reliability of these estimates is somewhat questionable due to the fact that many antlers in this collection have an intermediate type of terminal branching, i.e., vestiges of a small crown.

Smirnov (1923-1924) pointed out that the Caucasian deer has decreased in size since the Upper Paleolithic, his conclusions being based on the occurrence of teeth in the Gvardzhilas cave. Indeed the teeth found there by us and D.M. Tushabramishvili are of striking size, almost like those of elks.

438 Since the collections contain mostly Quaternary deer material, it is only possible to speak in greater detail of stratigraphic variation in antler size. The antlers, and probably the animals themselves, gradually increased in size from the Lower to the Upper Pleistocene, the largest example occurring in the Upper Paleolithic of the Russian Plain (Kostenki, near Voronezh). Later, in the Holocene, they somewhat decreased in size again, though not as sharply as bison, for example; in the Middle Ages the deer of the middle Don valley (Fortress Sarkel, near Tsimlyanskaya) were still very large (Figure 180, 181). It is of interest that size change in deer somewhat lags behind such changes in bison (see below).

The stock of particularly large individuals which colonized the Russian Plain at the end of the Upper Pleistocene was probably derived from the Caucasian population of deer which survived the Quaternary cool phases under most favorable conditions. The migration of the Caucasian deer to the north probably followed the Don and Volga valleys. In any event, Flerov's (1952) statement that they attained their maximum size in the Middle Pleistocene (Mindel-Riss) and then gradually began to decrease in size is undoubtedly wrong.

The Recent Caucasian deer are characterized by body dimensions and size of antlers intermediate between the West European and Asian-American forms. This has been correctly noted in the first description by Ogilby.

Geographic variation of the Recent deer C. elaphus maral in the Caucasus has not been studied in detail; variation is to a large extent masked by individual and age variability.

440 According to Dinnik (1914a), the deer of the northwestern Caucasus (Kuban area) are the largest, their size approaching that of Manchurian wapiti. The size of the Caucasian deer decreases to the east and south, and those inhabiting the foothills of Dagestan and the tugaic lower reaches of the Terek and Sulak are particularly small. Both the fossil material and the Recent populations are characterized by light horns, with only a few (5-6) outgrowths, and almost always devoid of crown. The deer which inhabited the Armenian Highlands and Talysh were also of relatively small size. All this is accounted for by the optimum conditions of the northwest — abundance of food, vast areas of forests and mountains, etc. — as compared with the hot and dry east and south with their ancient civilizations.

Thus it can be seen that the picture of the development of the morphological type and range of distribution of the red deer in Eastern Europe and the Caucasus in the Cenozoic is extremely complex. This also shows that some of the excellent paleozoogeographic analyses of Geptner and Tsalkin (1947) can be confirmed or disproved only by means of additional collecting and detailed study of paleontological materials.

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* Dinnik's statement on the 500 pairs of horns at Digorized is somewhat exaggerated.

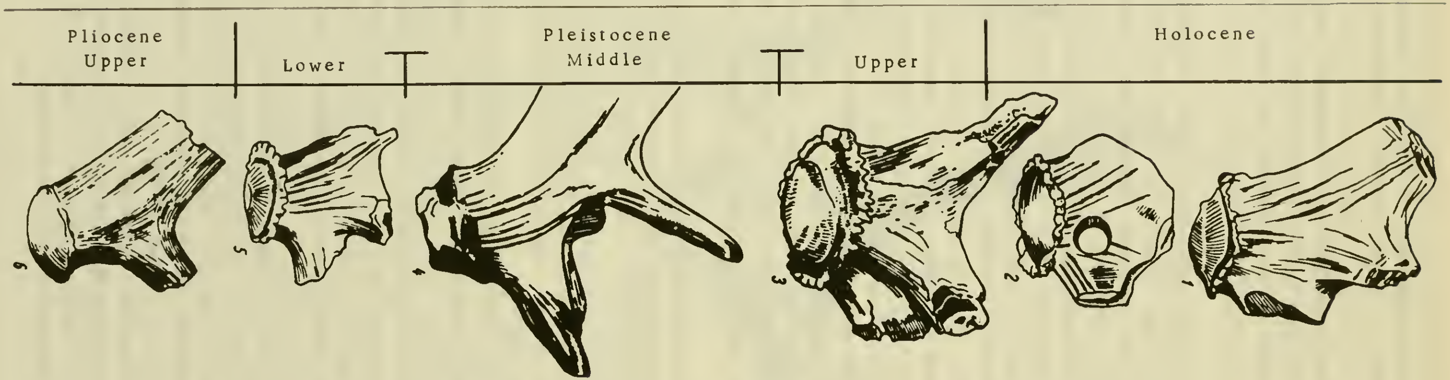

FIGURE 180. Fragments of antler bases of the noble deer (Cervus elaphus group)

1 — 10-13th centuries A.D., Don valley, Sarkel; 2 — 10-13th centuries A.D., Kura valley, Samtavro; 3 — Upper Pleistocene (Upper Paleolithic), Don valley, Kostenki XIV; 4 — Middle Pleistocene, alluvium of proto-Volga, un-numbered, Saratov Museum; 5 — Lower Pleistocene, alluvium of proto-Dniester; Tiraspol, un-numbered, Moscow Geological Survey Institute; 6 — Upper Pliocene, Caucasus, Taman Peninsula, No. 26005, ZIN

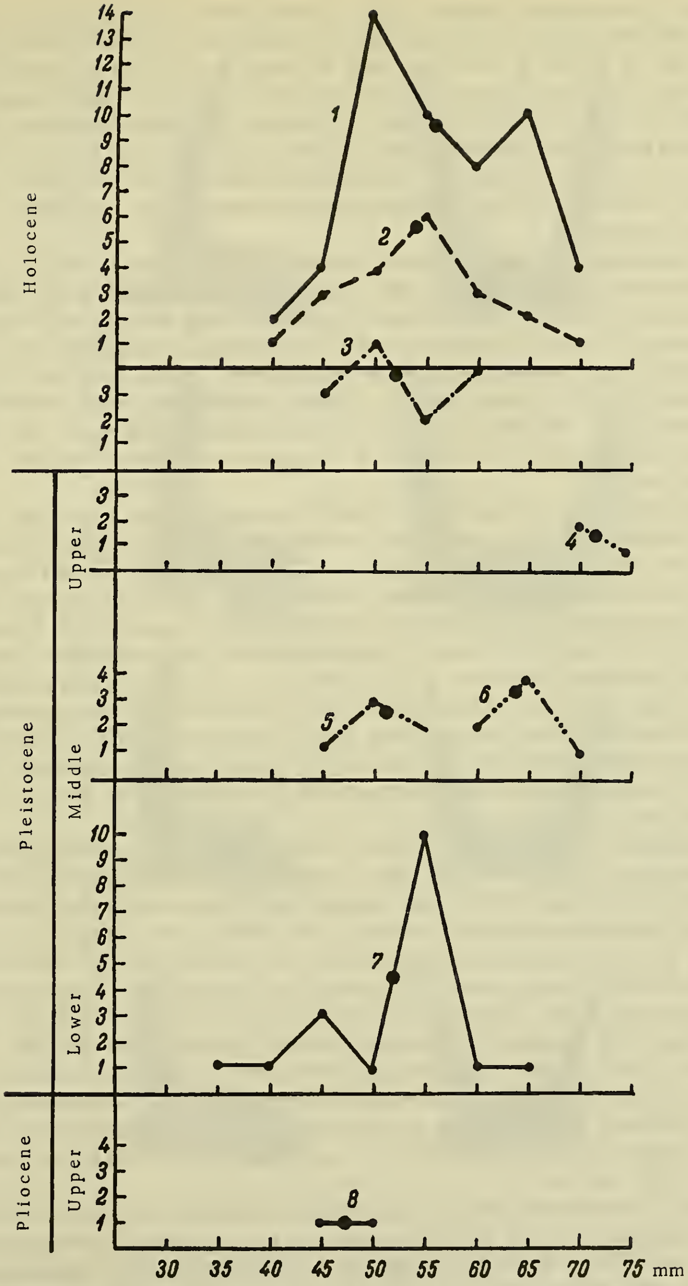

FIGURE 181. Change in antler size in red deer of the Cervus elaphus group. One-half of the sum of the diameters of the antler bases under crown. Black dots indicate means. Ordinate — frequency

1 — 15-19th centuries A.D., North Ossetia, Digorized cave; 2 — 10-13th centuries A.D., Don valley, Sarkel; 3 — 1st millennium B.C., Caucasus, burial, Makhachkala, Samtavro and Lake Sevan shores; 4 — Upper Pleistocene (Upper Paleolithic), Don valley, Kostenki XIV; 5 — Middle Pleistocene, bitumens of Apsheron Peninsula, Binagady; 6 — Middle Pleistocene, alluvium of proto-Volga; 7 — Lower Pleistocene, alluvium of proto-Dniester, Tiraspol; 8 — Upper Pliocene, Caucasus, Taman Peninsula

The phylogenetic lineage of the Recent elks of the genus Alces is so far known only from the Middle Pleistocene. Nevertheless, there is no doubt that Alces alces evolved at least in the Upper Pliocene, since by the Middle Pleistocene the animals were already indistinguishable from the Recent forms. The elk-like cervids of the side lineages which became extinct in the Lower Pleistocene, Tamanalces and Alces latifrons, had, by the Upper Pliocene, developed some features of skull and antlers similar to those of elks. These features developed, evidently, long before the Anthropogene.

The adaptations of the Recent northern elk to life in the taiga swamps and deep snow (long legs, large supporting surface of hoofs, brachydonty and feeding on twigs) could have originated long before the elks invaded the taiga and moss swamps.* Until recently, elks inhabited (in 1951) the floodplain marshes of the middle Volga area. Thus, Flerov's (1950, 1952) statements on the recent origin of these adaptations and on the feeding of elks mainly on leaves and bark do not correspond with the facts. It is known that for 7-8 months of the year elks feed mainly on hard (frozen) twigs.

The skulls and antlers of Middle Pleistocene elks from the Khazar beds of the Middle Volga region were already practically indistinguishable from the Recent forms. The Caucasian elk, A. alces caucasicus, known in the Caucasus since the Upper Pleistocene, was a relatively small animal in the 18th century with clearly pronounced features of the European form. The skull is relatively broad, particularly in the preorbital and frontal regions; the nasal section is narrower than in the northern elks. The molars differ in their branchydonty with complicated wedge-shaped folds on the labial surfaces of Pm^3 and Pm^4. In general, the morphological features of the Caucasian elk are sufficiently well pronounced, which enables one to date its appearance and beginning of isolation in the Caucasus as at least the Middle Pleistocene.

The saiga (Saiga tatarica) is an example of considerable morphological stability since the Middle Pleistocene. However, the Russian and West European collections consist mostly of teeth and frontal-
442 occipital fragments with horn cores. The oldest and probably most primitive type of the frontal-horn fragment was collected in the Khazar beds of the central Volga area. The skull of the Middle Pleistocene East European saiga is relatively small, with absolutely straight, fairly short and only slightly diverging horns (Figure 182, 4a, 4b), quite similar to the skull of the saiga from the Binagady asphalt in eastern Transcaucasia. While no different from the Khazar skull type in the divergence of the horns, the horn stems of the Binagady skulls are longer, with a noticeable posterior curvature in the sagittal plane (Figure 182, 3a, 3b).**

Upper Pleistocene skulls from the Khvalynsk beds of the Ural valley (our collections, 1950) are characterized by greater divergence of the horns, curvature of the horn stems in the frontal plane, massive structure in some specimens and even greater length in other specimens (Figure 182, 2a, 2b).

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* It should be mentioned that all these features developed also in the absence of snow in Tertiary giraffes and in some antelopes of the Mediterranean and Africa.

** Unfortunately, Alekperova's (1955) detailed description of the Binagady saiga does not help in drawing conclusions.

(441)

FIGURE 182. Stratigraphic and geographic variation in structure of horn cores and frontal-occipital fragments of saiga skulls. 1/5 natural size

Frontal and side view: 1a, 1b — Saiga borealis Tscher., Lower Holocene, Yakutia, Vilyui valley, No.13636, ZIN; 2a, 2b — S. tatarica, Upper Pleistocene (Khvalynsk age), alluvium of proto-Ural, No.24201 (10), ZIN; 3a, 3b — S. tatarica binagadensis, Middle Pleistocene, bitumens of the Apsheron Peninsula, Binagady, No.22385, ZIN; 4a, 4b — Saiga sp., Middle Pleistocene (khazar age), alluvium of proto-Volga, No.1084, ZIN

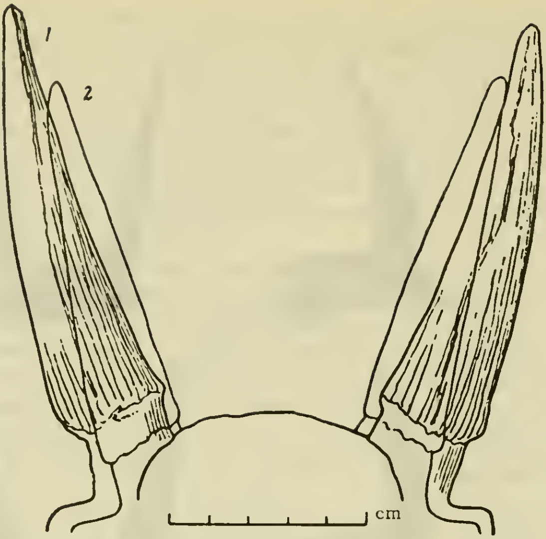

FIGURE 183. Outline of horn stems and frontal-occipital section of skull of the Recent saiga

1 — Saiga tatarica, Volga-Ural steppes, No. 7064, ZIN;
2 — S. tatarica mongolica, northwestern Mongolia, No. 8465, ZIN

This type of frontal-occipital has persisted from the Upper Pleistocene to Recent times in vast areas of Eastern Europe, central Asia and west Siberia. In Yakutia, however, on the Vilyui and Lena rivers, morphologically distinct populations of the northern saiga (S. borealis Tscher.) are known from the Upper Pleistocene and Lower Holocene, characterized by the elongation of the region posterior to the horns, and straight and long laterally compressed horns with weak divergence (Figure 182, 1a, 1b).

The frontal-occipital region of the skulls in Recent saigas shows wide variability; however, their skulls are practically indistinguishable from the fragments of skulls from the central Urals (Figure 183, 1).

The geographic variation in Recent populations is probably related to their occurrence on different types of pastures. In the upland semidesert of Inner Mongolia, for example, an undernourished population has developed, the subspecies S. tatarica mongolica Bann. (Figure 183, 2).

The sizes and frontal-occipital indexes of saigas are given in Table 94. 443 Generally speaking, horn stems increased in length from the Middle Pleistocene to the Holocene; the skull became wider between the orbits and the region posterior to the horns shorter. At a later stage the horn stems became shorter.

The size and proportions of the limb bones, the length of the tooth row and the tooth structure of the Pleistocene saigas do not differ essentially from the Recent forms. For example, the index of lateral compression of the metapodial diaphyses, i.e., the ratio of anteroposterior diameter of the diaphyses of metacarpus and metatarsus to the transversal diameter (in the middle of the bone), varies in the Binagady saiga within the following limits: metacarpus, 90-105% (5 specimens), metatarsus, 128-140% (3 specimens); whereas the indexes of the Recent Volga-Ural saiga are 90-102 and 114-146% respectively (5 specimens). The jumping index, i.e., the length ratio of tibia to femur, is 114.9% (3 specimens) in the Binagady saiga, and 114.2% (5 specimens) in the Recent species.

TABLE 94. Stratigraphic and geographic variation in size (in mm) and proportion (in %) of frontal-occipital fragments of saigas*

Species, localities, geologic age	Horn stem length measured along chord	Size index (circumference at stem base as % of its length)	Maximum orbital skull width	Length index (length of skull section behind horns as % of its orbital width)
Northwestern Mongolia, Recent Saiga tatarica mongolica, 1 specimen	99	62.7	106	62.0
Dzungaria, Recent Saiga tatarica, 2 specimens	127 124-130	76.7 76.7-76.9	125 125-125	47.5 46.5-49.5
Central Don, 10-13th centuries A.D. Saiga tatarica, 100 specimens . . .	139 110-165	78.5 71-91	62** 130-144	45 44.2-47.0
Yakutia, Olenek, Lena Delta, Upper Pleistocene, Saiga borealis, 2 specimens	146 139-153	70 66.7-73.4	122.0 117-127	56.1 55.0-57.2
Ural valley, Upper Pleistocene, Saiga tatarica, 10 specimens	156.1 141-179	77 65.9-87.1	134.5 129-142	51.8 49.2-55.6
Apsheron Peninsula, Middle Pleistocene, Saiga tatarica binagadensis, 2 specimens	135.5 135-136	75 74.3-76.0	130	52.2
Volga valley, Middle Pleistocene, Saiga sp., 1 specimen	115	82.6	127	57.5

Note. Means in the numerator, observed ranges in the denominator.

* Unpublished author's data, from ZIN collections. Selected measurements giving significant differences.

** Based on 4 specimens.

In other words, the Binagady saigas were able to move as fast as the Recent saigas; this feature also confirms to some extent the long-standing stability of the morphological structure of this animal as mentioned above.

The stratigraphic variation of the Caucasian goats (Capra caucasica, C. cylindricornis) is of particular interest in the study
444 of the origin and rates of evolution of the mountain mammals. However, it is unfortunate that the bones found so far are mostly Upper Pleistocene and Holocene.

The Upper Pleistocene (Upper Paleolithic) goats of the western Caucasus differ from the Recent species in their larger size, which is shown by measurements of the teeth and metapodia (Table 95). (The metapodia of goats from the Gvardzhilas cave (Figure 184) are of remarkable size.)

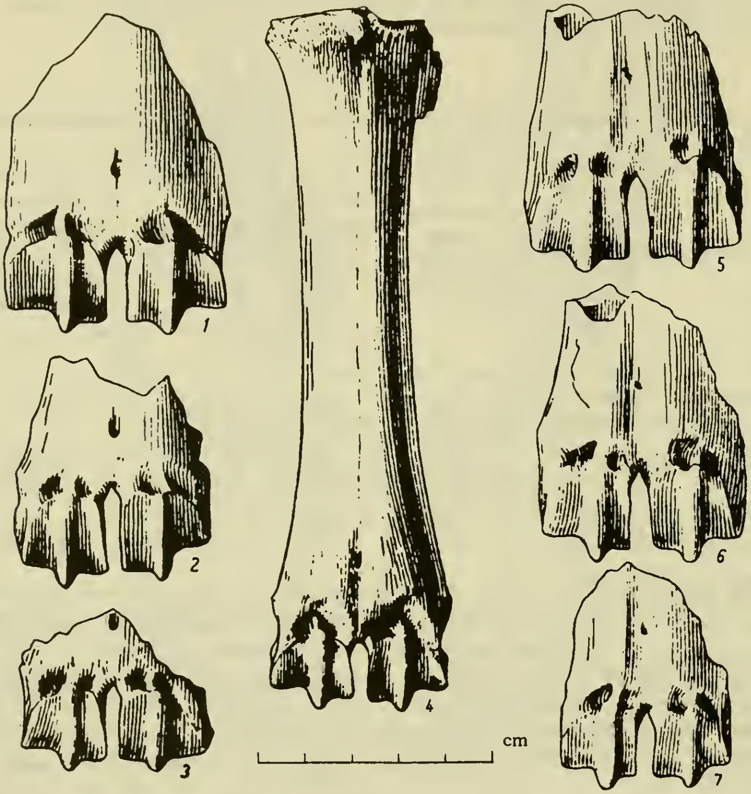

FIGURE 184. Lower epiphyses of metacarpus (1-3) and metatarsus (5-7) of Caucasian goats, Capra caucasica (foss.), from the Gvardzhilas cave, Upper Paleolithic; metacarpal bone (4) of Recent 5-year-old C. caucasica

As far as the structure of the teeth and metapodia is concerned, no reliable distinctive features are apparent in the Upper Pleistocene and Lower Holocene goats (Figure 97); the only exception is the somewhat greater eurosomality (wide bones). In general, the main morphological and physiological characters of the Caucasian goats — species adapted to mountainous terrain — may be said to have developed by the Lower Anthropogene.

The geographic variation with longitude of the Recent Caucasian goats is more clearly observable on the degree of specialization of the horns of males, the structure of the horns becoming more complex from west to east.

Four species of goats were identified in the Caucasus by the structure of the horns, or, more correctly, horn sheaths: (from west to east)

C. dinniki, C. severtzovi, C. caucasica and C. cylindricornis
445 (see Dinnik, 1914a). Actually there are only two main forms: west and east Caucasian.

TABLE 95. Stratigraphic variation in size of teeth and metapodia (in mm) of goats*

Dimensions of teeth and metapodia	Upper Pleistocene, Sakazhia and Gvardzhilas caves			Recent, west Caucasus		
	mean	range	number of specimens	mean	range	number of specimens
Anteroposterior diameter M^3	24.8	24-25	3	23.8	22-26.5	10
Anteroposterior diameter M_3	31.6	25-36	16	26.8	26-29	6
Transverse diameter of lower epiphysis of metacarpus	45.6	42-48	5	38	35-42	3
Transverse diameter of lower epiphysis of metatarsus	41.7	36-45	3	32	30-36	3

* Measurements based on the largest individuals (8-12 years old for teeth and 5-7 years old for metapodia) available in the ZIN collections.

The west Caucasian goat is more variable than the east Caucasian form. The former is transitional from the central Caucasian C. caucasica caucasica to the west Caucasian C. caucasica severtzovi and C. caucasica dinniki. However, transitional forms, probably hybrids of the east Caucasian and Caucasian goats, occur in Svanetia, on the Upper Ingur (Radde, 1899; Vereshchagin, 1938a).

The westernmost goats are characterized by massive and short horns, sabre-like in profile, with slight divergence and ends slightly bent forward and outward. In some specimens the horn sheaths display slight positive coiling, "homonimity" of Nasonov (1923). The adjacent western goats (C. caucasica severtzovi) are characterized by horns of predominatly neutral "ibex" type with marked protuberances on the outer curved surface. The ends of the horn sheaths diverge sharply; homonimity is slightly developed, i.e., the right sheath coils to the right, and the left one to the left. The central Caucasian goats (Güldenstaedt's turs) are characterized by strong divergence of their horns, with ends slightly curved inward and slight "heteronimity" of the sheaths, i.e., the right horn coils to the left and the left one to the right. The east Caucasian forms (Pallas or Dagestan tur) have widely divergent horns; in old individuals the sheaths are bent backwards and inwards, forming a low spiral. Slight heteronimity is also observable. These forms of the geographic variation are illustrated in Figure 185. In addition, the frontoparietal suture in west Caucasian goats is straight, while its shape becomes more like an obtuse angle in the skull of the east Caucasian populations.

If the original primitive form of the goat horns is the sabre-shaped profile (ibex and wild goat), then it can be assumed that the horns of the east Caucasian goat are phylogenetically the "youngest."

446 In view of the observed horizontal migrations and hybridization, the origin of the "latitudinal" variation and morphological differentiation of both forms of goat in the Caucasus can be accounted for by very high rates of evolution of certain morphological characters. Taking into account the Recent ecology of both species (Chapter III), there is no evidence which would indicate that their isolation is the result of the glaciation of the region. It is of interest to note that the genus Ovis, distributed over the vast areas of Eurasia, represents another example of progressive development of more complex horns in its range of distribution from west to east.

FIGURE 185. Skulls and horns of goats of the Caucasus

1 – *Capra caucasica severtzovi*, western Caucasus, No.12325, ZIN; 2 – *C. caucasica caucasica*, central Caucasus, No.697, ZIN; 3 – *C. cylindricornis*, eastern Caucasus, No.6964, ZIN

The origin of the Caucasian goats and their closest generic affinities are not quite clear. The ecology and morphology of the skull and horns of Recent forms is similar to those of other goats of the ibex type inhabiting Eurasia, being closest to the Alpine ibex (Capra ibex L.), yet it differs
448 strongly from the geographically closest Sinai ibex (C. sinaitica Ehrenb.) and Siberian ibex (C. sibirica Meyer). Even greater are the morphologic differences in the structure of the skull and horns between the Caucasian and the Spanish ibex (C. pyrenaica Schinz.).

The two Caucasian forms — western and eastern — have, of course, many more morphological and ecological features in common with each other than with any other named species of goat. For example, the lachrymal bones and the portion of the skull posterior to the horns are identical in the east and west Caucasian goats. Therefore the identification of C. ibex severtzovi Menz., C. ibex nubiana F. Cuvier and C. ibex sibirica Pall. as one species — C. ibex L., as was done recently by Ellermann and Morrison-Scott (1951), may be regarded as an unfounded extrapolation.* In spite of the fact that the Sinai and the Siberian ibex resemble one another in the shape of the horns, the structure of the lachrymal bone and the region of the skull posterior to the horns, it would be erroneous to identify these species with the Alpine and west Caucasian ibex. Moreover, for some reason C. caucasica is designated as a species, whereas C. cylindricornis is designated as one of its subspecies.

The morphologic distinction of the Caucasian goats from other Eurasian forms attests to the isolation of their ancestors in the Caucasus in the Middle Quaternary.

Among other cavicornia, the best-developed continuous series of morphologic changes traceable since the Upper Pliocene is that of bison (genus Bison).

The evolution of bison, like the evolution of elephants of the mammoth lineage, took place in the vast areas of the Holarctic region as in Asia and North America. However, the outcome and the features leading to extinction of the Holocene populations of bisons on these continents were entirely different (Vereshchagin, 1956).

Some American investigators, for example Skinner and Kaisen (1947), regard the geologically distinct stages of the morphogenesis of bison on the level of genus, which is probably incorrect.

In the Caucasus and the Russian Plain the phylogeny of bisons is known from several geologic phases of accumulation of freshwater sediments during the entire Quaternary era to the Recent: 1 — flat-horned small Bison sp. (tamanensis N. Ver.) in the Apsheron age of western Ciscaucasia (Taman Peninsula) and eastern Transcaucasia (Kabristan); 2 — considerably larger B. schoetensacki from the third terrace of the Dniester (near Tiraspol); 3 — huge long-horned B. longicornis** from the alluvium of the high terraces in Ciscaucasia and the Khazar alluvium of the Volga and Ural river valleys; 4 — B. priscus, a smaller form from the drift and alluvial loams and gravels of the first and second terraces in Ciscaucasia (post-Mousterian site, Il'skaya) and caves in western Transcaucasia (Aurignacian site, Sakazhia, etc.), and also from the Khvalynsk age and its equivalents on the Russian Plain (asphalt-impregnated loams at Nizhnie Karamalki in Tataria and other localities); 5 — the sharply decreased size of the postglacial B. bonasus of the historical epoch with two subspecies surviving to Recent times: the Lithuanian B. bonasus bonasus and the Caucasian B. bonasus caucasicus (see Figures 186, 187).

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* Tsalkin (1955) has recently arrived at a similar conclusion.

** For the sake of nomenclatural consistency, the long-horned bison from the Khazar alluvium, which is older than B. priscus Boj., must be regarded not as a subspecies of the latter but assigned the rank of species.

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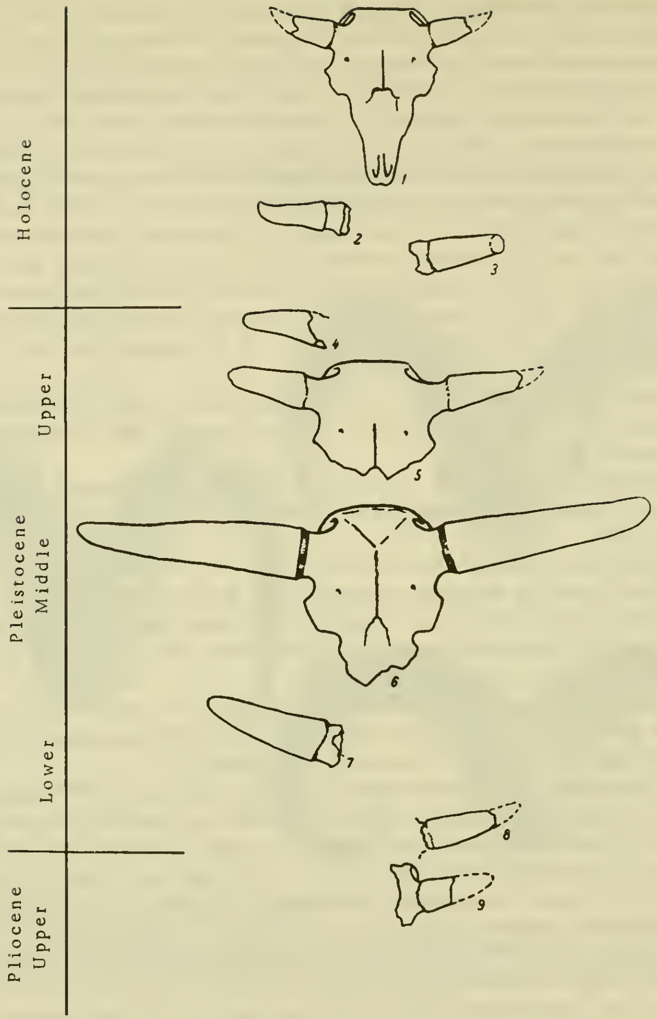

FIGURE 186. Stratigraphic and geographic variation in skulls and horn stems of bison of the Russian Plain and the Caucasus. Contours of frontal surface of skulls and stems. 1/15 natural size

1 — Bison bonasus caucasicus, 15-18th centuries A.D., North Ossetia, Digorized cave; 2 — B. bonasus bonasus L., 10-13th centuries A.D., Don valley, Sarkel; 3 — B. bonasus bonasus L., 12th century A.D., Belorussia, Grodno; 4 — B. priscus (aff. deminutus), Upper Pleistocene (Upper Paleolithic), Transcaucasia, Sakazhia cave, un-numbered, Odessa University; 5 — B. priscus deminutus, Upper Pleistocene, Tatar A.S.S.R., Nizhnie Karamalki, No.1, Kazan University; 6 — B. longicornis, Middle Pleistocene (Khazar age), alluvium of proto-Volga, Stalingrad Hydroelectric Station, No.26134 (1), ZIN; 7 — B. schoetensacki, Lower Pleistocene, alluvium of proto-Dniester, Tiraspol, Moscow Geological Survey Institute; 8 — B. cf. schoetensacki, Lower Pleistocene Caucasus, Taman Peninsula, No.26009, ZIN; 9 — B. sp. (tamanensis N. Ver.), Upper Pliocene, Caucasus, Taman Peninsula, No.26010, ZIN

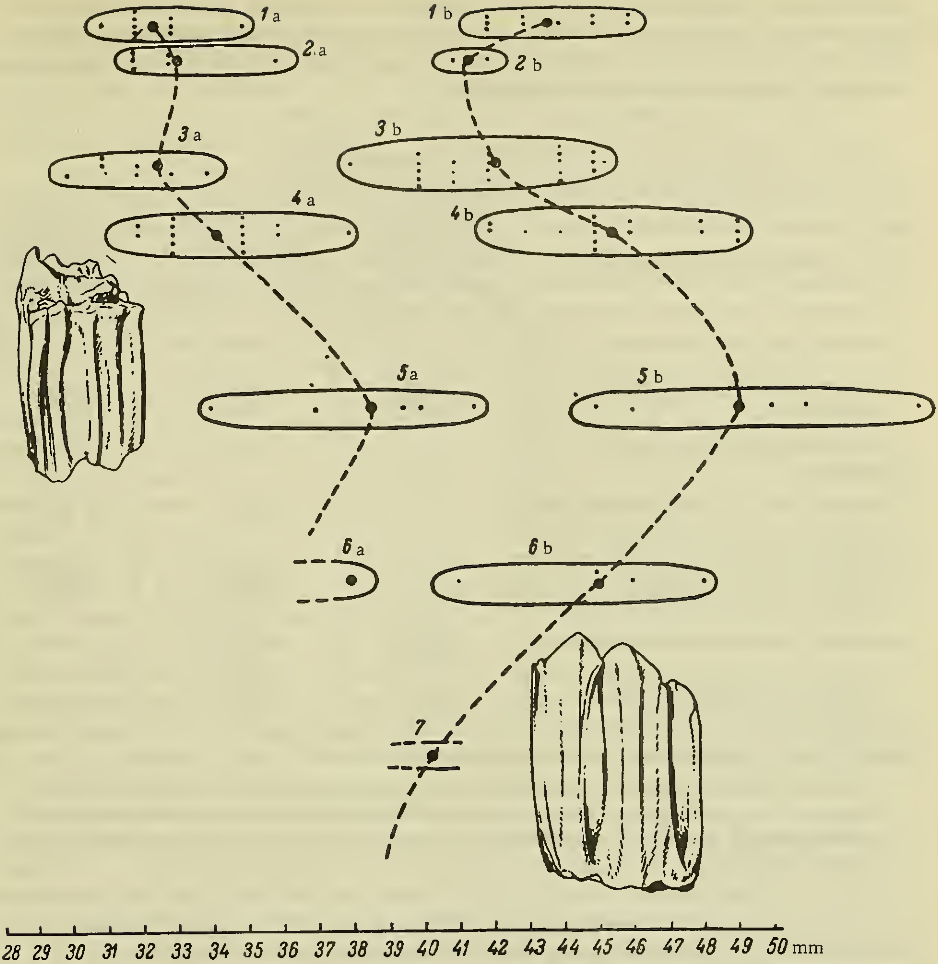

FIGURE 187. Stratigraphic and geographic variation in tooth size of bisons from the Russian Plain and the Caucasus. Anteroposterior diameter M^3_3 on the level of alveola (M^3 – a; M_3 – b)

1a, 1b – Bison bonasus bonasus L., Belorussia, Belovezh, Recent; 2a, 2b – B. bonasus caucasicus, Caucasus, Recent; 3a, 3b – B. priscus, Upper Pleistocene, western Transcaucasia, Gvardzhilas and Sakazhia caves; 4a, 4b – B. priscus, Upper Pleistocene, Trans-Kuban Plain, Il'skaya site; 5a, 5b – B. longicornis, Middle Pleistocene (Khazar age), alluvium of proto-Volga, Stalingrad Hydroelectric Station; 6a, 6b – B. cf. schoetensacki, Lower Pliocene, alluvium of proto-Dniester, Tiraspol; 7 – B. sp. (tamanensis N. Ver.), Upper Pliocene, Caucasus, Taman Peninsula

Even the Upper Pliocene fragments of skulls and long bones give an idea of the stabilized morphological features of the genus which evolved in the Pleistocene. The rest of the lineage, as far as the available material shows, was characterized by evolution of quantitative (size, length, volume) rather than qualitative characters. The isolated teeth and long bones of the long-horned bison from the Khazar alluvium of the Volga are essentially

only larger "copies" of the Lower Pleistocene bisons from the Tiraspol
450 gravels and the Upper Pliocene bisons from the Taman conglomerates.
Nevertheless even minor changes in the skeleton often attest to pronounced changes in the external environment.

TABLE 96. Dimensions (in mm) of skull fragments of Pleistocene bison*

Locality and geologic stage	Length of horn stem proper along the chord (number of specimens in parentheses)	Anteroposterior diameter of base of horn stem proper (number of specimens in parentheses)	Postorbital forehead width (number of specimens in parentheses)
Caucasus, Digorized cave, 16-18th centuries A.D.	128(18) 95-185	60.1 (63) 44-90	223 (27) 186-263
Caucasus, Sakazhia cave, Upper Paleolithic	210	85	–
Tatar A.S.S.R., Nizhnie Karamalki, Upper Pleistocene	270	87	291
Volga area, Stalingrad Hydroelectric Station localities, Middle Pleistocene	350 (7) 371-560	120 (8) 105-140	328 (7) 301-352
Moldavia, Tiraspol, Lower Pleistocene: . .	308(8) 290-340	106 (8) 85-120	–
Caucasus, Taman Peninsula, Upper Pliocene	210-260 (5)	80-90 (2)	140

Note. Means in the numerator, observed ranges in the denominator.

* The table is based on unpublished work of the author: measurements of male and female skulls in Digorized cave, and of mature Pleistocene males in the collections of the Kazan Geological Museum, Moscow Geologic Survey and a number of muzeums in cities on the Volga, the Odessa Paleontological Museum, and ZIN.

For stratigraphic purposes, the dimensions of the skull fragments (Table 96), in addition to Figures 186 and 187, are of importance, particularly in the study of sexual dimorphism, age and individual variability.

Studies of the morphogenesis of bisons in the Caucasus and adjacent areas suggest that these hollow-horned forms evolved here during the Anthropogene, and relict populations have survived in the mountain forests of the regions into Recent times.

The history of the primitive bull (genus Bos) developed along different lines, as in the Pleistocene the Caucasus was inhabited by forms of diverse origins (Burchak-Abramovich, 1957).

In a discussion of the morphological evolution of Caucasian and east European mammals in both time and space, it becomes clear that the Quaternary index forms (carnivores, proboscideans and ungulates) evolved

in the Caucasian Isthmus in a manner analogous to the vast areas of northern
451 Eurasia. Some features of their evolution are identical with those described by Hooijer (1949) for the southeast Asian mammals. As a rule, most of the animal species increased in size during the Pleistocene, followed by strong decrease in size at the end of the Pleistocene as if Bergmann's rule applied to distribution in time.

From study of the morphological changes in mammals during the Anthropogene one concludes that most of the evolution of the Quaternary forms took place some time before the Quaternary. Lower Pleistocene and even Upper Pleistocene mammals (carnivores, rodents, proboscideans and ungulates) show the characteristic features of Upper Pleistocene and Holocene forms at the rank of genus, and even subgenus and species; thus we recognize the fox from the group of the red fox, hamsters of subgenera Cricetus and Mesocricetus, deer of the group Cervus elaphus, etc.

Since the onset of the Anthropogene, successive stages of related mammals (in most cases) differ mostly in questions of proportion and in relatively minor adaptations (Severtsov, 1939). For example the red deer of the Upper Paleolithic and the historical epoch of the Don area is an enlarged copy of the Lower Pleistocene deer of the Tiraspol gravel. There is an apparent absence of qualitative saltatory changes in the Quaternary history of mammals. This probably requires a revision of the criteria for the identification of species. It is due to these facts that some Russian paleontologists, among them Flerov (1952) and Gromov (1948), are mistaken in their interpretations about the geologically young age of certain mammals (reindeer, elk) and their morphologic-physiologic adaptations to the conditions of taiga and tundra. Their assumptions only indicate lack of understanding of the genesis and evolution of the landscape of the northern part of the Holarctic region.* To us it is beyond doubt that the Anthropogene was the period of development of distribution areas and ecological assemblages of species which have reached the final stages of their evolution.

The Anthropogene mammals mostly exploited ecological (physiological) plasticity, developed since the Pliocene in response to changes in the landscape behind which the morphological evolution often lagged. In other cases animals became extinct or migrated into other areas.

The activity of man may possibly be partly responsible for the striking interruption of the evolution of many Quaternary species and their sudden extinction.

452 Among other general phenomena is the variability in the rates of speciation and the heterogeneity of characters in different phylogenetic lineages, sometimes even in taxonomically closely-related forms. We may also point out the conservative nature of the skull characters of foxes, as compared with the characters of the corsac fox, the slower rates of increase and decrease in size of deer and elks as compared with bisons, etc.

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* Most recent geological and paleontological studies in northern Siberia, particularly in Yakutia, have shown that during the Cenozoic this country underwent considerable climatic changes together with changes in landscape structure and fauna. The changes were similar to those which occurred in the Mediterranean. Consequently, occurrences of Lower Quaternary reindeer, elks and saigas may be anticipated.

In a number of cases it is not clear whether we are concerned with minor adaptations to environment and initial stages of divergence, as has been demonstrated by Vinogradov (1946) for the rodents, or whether we are dealing with continuously developing characters within the framework of a general evolutionary trend. For example, it is difficult to decide without additional studies whether the increase in the length of the tibia and increased mobility of the Recent jerboas and gerbils of the Apsheron Peninsula, as compared with the Pleistocene forms, is the result of development of xerophytic (desert) landscapes, or whether it is the product of evolution of the organisms in a certain direction. The latter explanation is presumably favored by examples of specialization in the teeth of wolves, corsac foxes and elephants.

The main forces behind changes in morphology during the Anthropogene were, of course, marked environmental and climatic changes.

Minor responses to ecologic variation include the independent development of relict forest-mountain forms, which led to far-reaching divergence and conservatism (Caucasian voles, goats), and also the rapidly-developing initial stages of speciation which led to the establishment of local ecological varieties (moles, foxes, common field mice, water voles, etc.).

The Caucasian populations of Eurasian species formed, as a rule, local subspecies from which not only their origin and the antiquity of their areas of distribution can be determined, but also the rates of morphological divergence.

The geographic changes in Recent mammals of the Caucasian Isthmus are mainly expressed in decrease in size and brightening of the coloration towards the southeast (foxes, snow voles), increase in body size with altitude (susliks), and more complex structure of the horns of cavicorn species towards the east of their area of distribution (Caucasian goats). These examples are often only small-scale reflections of similar phenomena observable over the vast expanses of Eurasia, and contribute to the understanding of the origin and history of colonization of the ecological niches in this area. It becomes increasingly clear that in the process of development of this Anthropogene mammal fauna the main role was played by the immigrations and the fluctuations in abundance and extinctions of organisms, whereas the divergence and morphogenesis in general were of secondary significance.

453 *Part Three*

GEOGRAPHIC ZONATION AND LATEST EVOLUTIONARY TRENDS OF MAMMALIAN FAUNA OF THE CAUCASIAN ISTHMUS

455 *Chapter V*

ANALYSIS OF HOLOCENE MAMMALIAN FAUNA AND SCHEME OF ZONATION

Through our studies of the origin and ecology of a number of Caucasian mammals (Chapter III) it is possible to identify the principal ecological and geographic groupings of those species whose ranges lie in more or less clearly defined regions of diverse origins and ages. A study of the distribution of the other Holocene animal species and an evaluation of their origins and histories in the Caucasus would be a considerable contribution to the zoogeography of this region. The zonation of the area into mammalian geographic districts is necessary in order to understand the regularities in faunal evolution as they relate to changing landforms and to gain some perspectives for the planned restoration of the fauna.

However, since the ranges of individual species and the composition of ecological assemblages and faunal complexes are not constant, these zoogeographic boundaries cannot be regarded as permanent. The more the landscapes and the boundaries between landscape zones change, the greater is the rate of evolution; and the less adaptable the animals are to these changing environmental conditions, the greater is the rate of change within the ecological and faunal complexes. Therefore, a zonation, particularly on the scale of subregions or provinces, can be established only for relatively short periods of geologic time. This fact is not always recognized by zoogeographers. The concept of geographic boundaries of a range of a "faunal type," a "faunal complex," etc. is only a convention. Such a boundary only holds for an individual species on a specific date. At any given moment in geologic time, it can only establish an approximate coincidence of a number of species which are similar in their ecological characteristics.

The schemes of zoogeographic zonation and zoogeographic categories based upon characteristics of the species complexes presented by contemporary zoogeographers are usually based on relict species, which have survived during the historical epoch under various anthropogenic influences. Only tentative, inadequate attempts have been made to employ historical data on the occurrence of some extinct forms in the near past and to infer from this history the dynamics of the ranges of individual species.

The error in this approach lies in the exclusion of those species which have recently become extinct, particularly those exterminated through
456 human activity. This omission rules out any possibility of gaining perspective on the restoration of the fauna, which is the practical goal of zoogeographic studies.

From the second half of the 19th century, almost every investigator who, in one way or another, was concerned with the zoogeographic division of Eurasia turned his attention to the origin of the fauna of the Caucasian Isthmus and its zoogeographic zonation. Wallace (1876) divided the Isthmus longitudinally along the Bolshoi Range, including Ciscaucasia in the European region, and Transcaucasia in the Mediterranean region.

Severtsov's scheme (1877) was exceedingly simple and very nearly correct. He assigned the northern Caucasus, western Transcaucasia and the Caucasian Range to the Mediterranean region, the rest of Transcaucasia to the western Asian region, and northeastern Ciscaucasia to the central Asian region. This zonation reflected the heterogeneous origin of the fauna of the Isthmus.

W. and Ph. Sclater (1899) combined the Caucasian Isthmus with Asia Minor, assigning both areas to the Europaeo-Asian region.

It was Satunin who most clearly recognized the heterogeneous origin of the Recent fauna of the Caucasian Isthmus in his papers of 1901d, 1903b, 1904-1906, 1909-1910, 1912b, and 1913.

His main hypotheses were the monophyletic origin of species and their unvarying migrational tendency.[*] He evidently assumed that the focus of speciation lay somewhere to the south of Transcaucasia and from there, as from a cornucopia, the species spilled forth in northward migrations via the Balkans and the Caucasus — the highly mobile species and those less mobile. Satunin was the first Russian zoologist to attempt to synthesize the history of faunal development on the Caucasus with the geological data available in his time on the Tertiary and post-Tertiary seas, straits and glaciations. He reasoned his migrational hypothesis from his belief that evolution proceeds very slowly in mammals, and that the Caucasian Isthmus is geologically much younger than the adjacent areas of southwest Asia and southern Russia. Consequently, he concluded that no independent speciation could take place on the Caucasus. According to Satunin, the Manych strait and the Aral-Caspian basin in the northeast constituted barriers to mammal migrations from the north to the Caucasus.

Satunin made an interesting attempt in 1901 to establish the geologic age of mammals which migrated to the Caucasus. He considered that Microtus arvalis and Arvicola amphibius already lived in the Caucasus in glacial time. After the disappearance of the Manych strait "only Putorius foetidus, Vulpes corsac, Cricetus vulgaris, Sminthus subtilis, Castor fiber, Allactaga saliens, Lepus europaeus and Saiga tatarica migrated to the Caucasus from the north.

"In addition to Cricetus vulgaris, mentioned above, Mus agrarius and M. minutus should be included among the most recent immigrants from the north."

Later (1900-1910) Satunin examined the origin of the fauna of the entire
457 Caucasian area and divided it into the northern Caucasus, the Range and
Transcaucasia. He defined nine subdistricts in these three major districts.
His work gave particular emphasis to the great antiquity and independent

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[*] We are in agreement with Pidoplichko (1953) that local development of a number of mammalian species, assemblages and complexes was a significant factor in the evolution of the Palaearctic, particularly the eastern Mediterranean fauna. His point, however, by no means excludes the possibility suggested by paleontological data of a dispersion of species and faunas during the Cenozoic, particularly in the Quaternary.

origin of the alpine fauna and to the occurrence of immigrants in the forest zone and on mountain slopes. He further hypothesized that the ancestors of the mountain fauna of the Caucasus migrated from the mountains of southwest and central Asia. He pointed out that the absence of ptarmigan and blue hare in the highlands indicated that the arctic fauna never reached the Caucasus, that the mountain fauna of southwest Asia is autochthonous in nature, that there were no African elements in the Transcaucasian fauna, and that the fauna remained purely Asian in character.

He accounted for the emergence of "Aral-Caspian" fauna in the Caucasus by the glacial advance and the flooding of the Caspian steppes, and for the isolation of the Aralik section in the Araks valley by vulcanism in the area of the southeastern spurs of the Zangezur Range. He regarded the fauna of the wooded parts of Talysh as the northwesternmost sector of the Indian fauna.

Satunin briefly summarizes the general characteristics of the fauna of the Isthmus in this way: "In this region the following occurrences can be observed — an ancient autochthonous fauna of the Greater Caucasus, a relict Mediterranean fauna in western Transcaucasia, the original, endemic fauna of the uplands of eastern Asia Minor, the northwesternmost advance of the Indian fauna and, finally, the faunas which migrated from the steppes of southern Russia and the deserts of central Asia."

Satunin's zoogeographical studies culminated in his work "On Zoogeographical Districts of the Caucasian Territory" (1912b). He subdivided the territory into five subregions and eleven districts. His zoogeographic scheme of the Caucasus has been well accepted.

He saw his main achievement in the fact that his zonation almost completely coincided with the phytogeographic divisions of the Caucasus. The coincidence is not fortuitous — Satunin travelled widely over the territory and placed great importance upon direct observation. He held that the fauna does not merely depend upon a specific landscape, but forms an integral part of it.

Satunin's compilations of mammals for various districts of the Caucasus are extremely accurate and comprehensive. The interpretation of the data, however, was hindered by prevailing notitions and by too little knowledge of the ranges and faunas of adjacent territories.

Some of Satunin's errors were repeated in the last work cited: the zoogeographic scheme remained "geomorphological" in nature, based on the features of the "phytolandscapes" rather than on the actual distribution areas of species and complexes. The boundaries either followed the mountain divides or were drawn along the foothills, and in the south of the country they were drawn from inference. The migration route of the Aral-Caspian fauna was still considered to be through eastern Transcaucasia along the ravine and valley of the Araks to the foothills of the Ararat and Alagaz, although the Lesnoi district of eastern Transcaucasia was mapped as a remarkable wedge-like extension, reaching to Artvin in the west and including, on the northeast, half of the woodless interior of Dagestan.

Dinnik (1911), among other Caucasian faunologists, recognized the predominantly southern aspects of the mammalian fauna of the Caucasus. He pointed out the occurrences of three species of European, five species of Eastern European and thirteen species of Asian mammals in the steppes of the northern Caucasus. According to Dinnik, the mountain species migrated to the Caucasus from the south, mainly from Asia Minor.

458 In a criticism of Satunin's work published 27 years later, Lyaister (1931) made the point that 85% of the mammals in the Aralik section of the Araks valley, which Satunin included in the steppe district of eastern Transcaucasia, are shared with adjacent Iran, and that only 41% are also common to the Transcaspian region.

Actually only two species of the Aral-Caspian fauna are found in the middle Araks valley: small five-toed jerboa and manul, and the ancient links of these species with the Transcaspian region were through northern Iran, rather than through eastern Transcaucasia and Ciscaucasia.

Lyaister, like Satunin, in holding to the theory that most of the animals characteristic of the Armenian Highlands migrated from Iran, was only paying lip service to the unfounded hypothesis of "migrationism." The existence of dry land in this area since the Oligocene means that the Recent Lesser Caucasus uplands can be regarded as a marginal part of the ancient focus of speciation in southwest Asia.

Menzbir (1934), who was also well acquainted with paleontological material, included all the plains of western Ciscaucasia in the Pontian-Barabanian subprovince of the European-Siberian subregion, eastern Ciscaucasia in the Kirgiz subprovince of the central Asian subregion and the Caucasus and Transcaucasia in the Caucasian subprovince of the eastern Mediterranean province of the Mediterranean subregion of the Palaearctic region.

The northern boundary of the Caucasian subprovince defined by Menzbir is in the foothills of the northern Caucasus on a line from Novorossiisk on the Black Sea coast to Khachmas on the Caspian. The southern boundary is drawn from Batumi to Yerevan around southern Talysh. The fauna of this subprovince, which includes the southern Crimea, is mixed Europaeo-Asian. According to Menzbir, the Caucasian fauna was affected by two faunal centers — the Mediterranean and the central Asian.

The boundaries of Menzbir's subprovinces coincide almost exactly with the broadly defined limits of the climatic and phytolandscape zones of the Recent. Clearly, Menzbir's work simply gives the faunal characteristics of the landscape zones of the Isthmus.

Puzanov's treatise (1938a) of the fauna and nature of the Caucasian Isthmus is based on broad knowledge of geographic facts and presents a concise, lucid discussion.

He places all of Transcaucasia in the Mediterranean subregion, grouping it with the Greek archipelago, Asia Minor and mountainous Crimea in the eastern Mediterranean province. The northern slopes of El'brus and Talysh are included in the Asterabad province, adjacent to the central Asian subregion.

Puzanov describes the Greater Caucasus as a "complex faunal knot in which Mediterranean forms predominate to the south, European forms to the north, and central Asian forms to the east. The nucleus of the fauna, however, is made up of an endemic alpine fauna of great antiquity."

Kuznetsov (1949, 1950), who was familiar with the extensive data compiled in Soviet time, proposed a special geographic zonation of the mammalian fauna of the Caucasian Isthmus. In his scheme of the Palaearctic region, the plains of Ciscaucasia and the eastern Transcaucasian plains are included in the zone of deserts and steppes, the foothills of Ciscaucasia
459 in the transitional forest-steppe zone, and the largest part of Transcaucasia in the Mediterranean province of the subregion of northern forests.

His delineations of six Caucasian districts and nine subdistricts were drawn on the basis of characteristic features of a fauna comprised of 113 species and on Bush's descriptions (1935) of the phytolandscape zones. Both of Kuznetsov's papers were hastily published and contain much erroneous data and many conflicting conclusions. Although he was correct in his understanding and interpretation of the Mediterranean subregion, which includes almost all of the Caucasian Isthmus, his treatment of the pattern of faunal development is inadequate, as can be seen in the following quotation: "The third group of species of Caucasian mammalian fauna consists of forms of definite Mediterranean (! ? — N. V.) origin." From this statement it would follow that the Caucasian, i.e., Mediterranean, forms originate within themselves. His discussion of the Armenian Highland is also vague, since the same area is referred to as the Armenian forest-upland region and the upland Armenian region. Talysh is incorrectly described as a forest-mountain area, although Satunin clearly distinguished both mountain-forest Indian types and upland-steppe Iranian types in the Talysh fauna.

Kuznetsov omitted the following forms from his list of species: the vespertilio bats (V. ognevi and V. bobrinskii), pocketed bat, Asia Minor field mouse, Caucasian snow vole, saiga, goitered gazelle, bison, and recently extinct forms, i.e., elk, kulan, tarpan. There are also many errors in his conclusions on the origin of the fauna, in the faunal characterizations of the districts, particularly in the zoning of the Caucasian district, and in the descriptions of boundaries.

The Azerbaidzhan district is an example. Its boundaries are described by Kuznetsov (1950) as follows: "From the town of Astara on the Iranian-Soviet international boundary near the eastern end (? — N. V.) of the Talysh Range, the boundary follows the foothills ridge (! ? — N. V.) in the southern marginal area of the Mugan, Mil'skaya and Karabakh steppes to Lake Sevan (! — N. V.) and farther through the town of Karaklis, south of Tbilisi, to the Surami pass. Here the boundary turns sharply to the east through the towns of Gori, Mtskheti, Lagodekhi, Zakataly and Nukha toward the eastern end of the Main Range and over the Kuban lowlands toward the Caspian coast" (p. 157). This description creates complete confusion since, according to it, the subdistrict of steppes and deserts includes both the Lenkoran, Alazan-Agrichai and Khachmas lowlands with almost subtropical forests and the northern slopes of the Shakh-Dag and Trialet ranges, surrounding Lake Sevan, with beech—hornbeam forests.

The marginal sections of the Kura-Araks lowlands were never covered by the waters of the Aral-Caspian basin in the Quaternary, rather than being covered "many times." And, therefore, rather than being a young fauna, as Kuznetsov maintains, the fauna is in fact so ancient that it contains such elements as Asia Minor hamster and mole (!).

In the mammals listed for this district, which Kuznetsov described as a plain with wormwood-steppes and floodplain forests, he included such species as the common and lesser shrews, harvest mouse, forest vole (! ? — N. V.), pine vole and common vole, which definitely do not occur in the Kura-Araks, Lenkoran and the greater part of the Alazan-Agrichai lowlands. And such characteristic species as pine marten, serotine vespertilio, Ognev's vespertilio, tiger polecat, panther and red deer are not included.

460 However, Kuznetsov's interpretation of the Mediterranean subregion is more accurate than interpretations of earlier authors.

In recent years the refinement of the ranges of rodents in western Transcaucasia has engaged the attention of Shidlovskii (1940c, 1941b, 1945, 1947, 1948, 1950, 1951). He established the great diversity of the faunal influences on the rodent fauna of Georgia and refined the district boundaries laid down by Satunin (Shidlovskii, 1941b). In distinguishing some species of rodents as immigrants to Georgia from the west, east and south and others as ancient relicts, he presents a correct zoogeographic position. Shidlovskii attempted to establish the geologic age and history of the ranges of some of the species which comprise the rodent fauna of Georgia. For example, he places the migration of the Asia Minor hamster to the Caucasian Isthmus at the end of the Miocene-Lower Pliocene, and relates the discontinuity in the range of Promethean vole on the Greater Caucasus and in Adzharia to the development of xerothermal conditions on the Dzirul'skii massif in postglacial time. Shidlovskii, at variance with Satunin, proposed designating the alpine zone of the Greater Caucasus as an independent zoogeographic unit, based on the presence of Promethean vole and Caucasian birch mouse.

Bobrinskii (1951) relates the fauna of the main part of Ciscaucasia to the fauna of the European-Kazakhstan steppes, the fauna of the northeastern section of Ciscaucasia to the fauna of the Aral-Caspian deserts, and the fauna of eastern Transcaucasia to the faunas of the Aral-Caspian deserts and the European-Kazakhstan steppes. The entire forest-mountain fauna of the Greater Caucasus, the northern slopes of the Lesser Caucasus and the eastern slopes of Talysh he relates to the fauna of the European broadleaf forests, and that of the alpine zone of the Bolshoi Range and Lesser Caucasus to the mountain fauna, like those of the Kopet-Dag, Tien Shan, Altai and the eastern Siberian ranges. Bobrinskii, quoting Satunin and making use of his map, repeats his error on the predominance of the Aral-Caspian fauna in Transcaucasia. His description of the fauna of the Lesser Caucasus uplands also abounds in error (p. 314), such as his statements on the absence of deer, pine marten, mole and Bezoar goat from that area.

Bobrinskii discussed the origin of the Caucasian fauna on the basis of modern geological data. He maintained that the migration of European animals to the Caucasus mainly followed the southwestern route via the Balkans and Asia Minor, and that the extension of the ranges of the European common vole and snow vole to the Caucasus was only possible through large-scale migrations.

In addition to these disputable statements, he made the strange statement that the isolation of Promethean vole, Caucasian black grouse, goat and snow partridge began at the time when the Main Range was still an island, when in fact the Caucasus was not an island in the Oligocene and in the Lower and Upper Miocene.

A very detailed zonation of the Armenian territory into ecological and landscape districts was made by Dal' (1954a), who compiled lists of land vertebrates from various natural, mainly phytolandscape, zones of the Armenian Highland and the middle Araks valley. The fact that he employs four vertebrate classes concurrently in his zoogeographic analysis of the region, and that he adheres to the theory of a Eurasian "faunal type",

creates considerable difficulty in ascertaining the origin and composition
461 of the mammalian fauna of Transcaucasia, even for the author. In his zonation of Transcaucasia, Dal', in the main, followed Kuznetsov's (1949) scheme.

This brief review of zoogeographic concepts of the Caucasian mammalian fauna of the Recent indicates, as did our paleontological data (Chapter III), that the ancient local focus of speciation and of faunal development in the mountainous parts of the Isthmus was under strong influence from mammalian complexes of adjacent areas.

In order to make a correct evaluation of these faunal influences and their distribution in time and space, it is necessary to discuss the age and origin of the local Caucasian and the neighboring faunal complexes. It is particularly important to understand the origin and the nature of the Mediterranean complexes — a subject on which there is no general agreement. Paleogeographers consider the Mediterranean littoral as the relict basin of the Tethys sea, or, at least, of the Sarmatian sea which extended from the Atlantic to the Transcaspian region. In the climatological sense, the Mediterranean is regarded as comprising southern Europe, north Africa, part of southwest Asia and even part of central Asia (see Berg, 1938).

Geobotanists Alekhin (1938) and Vul'f (1944) include the coastal areas of the Mediterranean and Black seas in the Mediterranean region of the Holarctic north Africa, Spain, Italy, Greece, Asia Minor and the Crimea. And Maleev (1946) and Grossgeim (1936, 1948) have repeatedly pointed out the genetic affinities, if not the identity, of Caucasian formations of maquis, garigue, phrygana and broadleaf forest with similar formations in the western Mediterranean, clearly establishing them in their view as one unit. Lavrenko recently published the opinion (1958) that the forest region of the Caucasus is similar in the phytogeographic sense to the broadleaf forests of Europe in its origin and ecology (climate), but not to the Mediterranean. Earlier zoogeographers often considered the Mediterranean region to include the coastal areas of the Mediterranean Sea, Asia Minor, northern Arabia and Transcaucasia (Wallace, the Sclaters, Severtsov, Kobelt).

Modern ornithologists like Serebrovskii (1928) regard southwest Asia (Sumer) as the area where the faunal elements of Africa, central Asia, India and Europe converge. According to Shtegman (1938) the Mediterranean type of fauna, apart from being found on the Mediterranean coasts, can also be found in the Sumer of Serebrovskii, but the fauna of Transcaucasia and the southern Crimea is characterized only by a tinge of the Mediterranean type.

Kashkarov and Korovin (1931) observed the Mediterranean influences in the flora and fauna of even the middle life-zones in Tien Shan. There is a recent tendency to regard the Caucasian and Hyrcanian fauna as a part of the province of broadleaf forests of Europe (Rustamov, 1945; Kuznetsov, 1950; Bobrinskii, 1951).

Geptner (1939, 1940, 1945) developed the idea that the centers of origin — he named four — of the mammalian desert-steppe fauna of the Palearctic all lay far to the south. He opposes (1945) the notions of an endemic origin of Mediterranean fauna and of a Mediterranean region on the assumption that there were no ancient and specific mammalian forms in the

Mediterranean, maintaining that the coasts of north Africa and southern Europe are inhabited only by immigrants from the north and the south.

462 These assumptions are invalid because no true comparison can be made between the landscapes and the diversity of biotopes in the deserts and in the Mediterranean.

Animal immigration to the Mediterranean was always more open than to the Sahara and Kara-Kum, but this does not detract from the importance of the Mediterranean as an ancient independent center of speciation and faunal evolution.

A correct interpretation of the concept "Mediterranean region" (and a resulting understanding of the Mediterranean type of fauna) can only be reached through an analysis of the natural changes which occurred in the Cenozoic in the Mediterranean geosyncline.

It is known that the Sarmatian sea, which extended from Gibraltar to the Transcaspian area, repeatedly formed in later — Pliocene and Pleistocene — time a chain of isolated basins, which were sometimes interconnected during periods of transgressions. Their separate coastal areas evolved under varying conditions. The Aral and northern Caspian coasts because of their relief and greater continentality early became deserts, which excludes them from the unique system of Mediterranean zonation.

The other coastal areas of this chain of Cenozoic basins, including the Caucasus, inherited a number of unique, primitive features of landscapes, flora and fauna, which originated in the Miocene. Therefore, the southern areas of Europe (including the southern Ukraine and the Crimea), north Africa, Asia Minor, the Caucasian Isthmus (excluding the Manych area) and the Talysh and El'brus ranges should be included by virtue of their paleogeographic identity in the Mediterranean region.

Differences in physiographic conditions resulted in differences in the development of landscapes and Cenozoic fauna between the western Mediterranean — Pyrenean-Balkan, and the eastern Mediterranean — Balkan-El'brus. Even in the Oligocene the southern part of the eastern Mediterranean was under the influence of the central Asian continental Indricotherium fauna. Later, the thermophilous faunal complexes persisted on the northern and southern coasts of the western Mediterranean until the beginning of the Pleistocene. These complexes consisted of primates, viverrids and hippopotami. It has only recently been established that hippopotami and primates lived in Transcaucasia in the Upper Pliocene-Lower Pleistocene. At that time, the Azov Sea area was inhabited by some thermophilous forms — elephant and antelope, but the complex, as a whole, was characteristic of savannah and forest-steppe landscapes on the margins of temperate and subtropical climatic belts.

The western Mediterranean in the Pleistocene was protected in the north by the high Alps and the Carpathian Range, whereas the eastern sections were exposed to masses of winter-cooled air from the Russian Plain. The landscapes and fauna of Spain, Italy and Greece were not as strongly affected by the glaciation of northern Europe as the landscape and fauna of the Caucasus and the Crimea.

During the maximum, Dnieper stage of glaciation, a number of taiga and tundra species of mammals extended their ranges over the Russian Plain as far as the southern coast of the Crimea. These northern forms did not migrate farther to the southeast, i.e., to the Caucasian Isthmus, because 463 the steppe zone of the Pleistocene on the Russian Plain made a sharp northward turn in the northeastern Azov area. In addition, the opening of the Manych strait during the Caspian transgressions (see Chapter II) also influenced the distribution of the fauna.

The Mediterranean-type landscape is often identified by biogeographers with the Recent landscapes of Spain, Sicily and Palestine, i.e., sun-burned, rocky, dry slopes, grazed by goats, grown here and there with olive groves, fig trees and orchards, supporting colonies of rabbits and stone martens and occasional relict mouflons and wild goats. Actually in both the eastern and western Mediterranean, relict landscapes of Tertiary coniferous and broadleaf forests and mesophytic meadows of alpine- and subalpine-type occur alongside xerophytic landscapes of garigue, phrygana and upland steppes (see Il'inskii, 1937). Such characteristic species of mammals as Asia Minor mouse, snow vole, Promethean vole, chamois, Spanish, Alpine and Caucasian goats and macaca evolved and survived in these mesophytic areas of the mountains. These species are probably as old as piebald shrew, jerboa, gerbil, Selevinia and other animals of the adjacent desert centers of speciation.

The highland landscapes of the Caucasus, like other mountain ranges of the Alpine folded system, formed in the Miocene. Even if some peneplanation subsequently occurred in the Pliocene, nevertheless some of the ranges retained their prominence.

The Holocene complex of Caucasian mountain-forest mammals has, therefore, many features in common with mountain-forest mammalian complexes of the Alpine ranges of the western Mediterranean. In the main, it evolved locally, rather than migrating as a unit, which accounts for its high degree of specific and subspecific endemism. In the east this type of fauna occurs in the forests of Talysh and on the southern slopes of the Elburz. During the hot, dry stages of the Pliocene, it was affected by southern faunal elements, and during the Pleistocene by influences from the northeast, northwest and southwest. Of these, the faunal ties with the south were the oldest, most extensive and most permanent.

The southwest Asian uplands are an independent center of evolution of two subtypes of mammalian complexes of Pliocene age: the upland-steppe and upland-desert complexes.

The differentiation within the southwest Asian complex of these two subtypes is observable in almost all orders of mammals, and is related to the sharply differentiated relief of the country and its climatic variability. At the same time when biocenoses of the upland-desert type evolved in broad intermontane valleys and narrow canyons, ecological assemblages of upland-steppes and even meadow-steppes evolved on neighboring high plateaus and ranges.

The influence of this southern complex on the Caucasian Isthmus was undoubtedly exerted in several stages, the oldest being the Miocene-Pliocene when the Hipparion fauna was dispersed over the Isthmus. It is probable that considerable influence from the south continued through the Upper Pliocene, but in the Pleistocene, particularly in the Upper Pleistocene, migration from south to north was probably impeded.

464 In the north, the Caucasian Isthmus joins the southern Russian Plain which, in the area of the Dnieper, Don and Volga watershed, has been dry

land since at least the Lower Miocene. The nucleus of the steppe flora and fauna of this area formed in the Pliocene, according to pollen analysis and paleofaunal data.

The early stages of settlement of the Ciscaucasian plains by immigrant species from the Eastern European and northern Kazakhstan steppes might have taken place in the Middle Pliocene. However, the large-scale migration to the Caucasian Isthmus of mammals belonging to this steppe complex undoubtedly occurred in the Pleistocene concomitantly with the southward shift of landscape zones. During the humid climatic phases of the Pleistocene, the mammalian complex of European and Asian broadleaf and taiga forests could also have influenced the Caucasian fauna. These forest mesophilous species could have dispersed along the valleys of the Don and Volga, through the Balkans and along the northern coast of Asia Minor.

The main features of the Transcaspian mammalian complex, i.e., the central Asian desert complex, had probably developed by the Lower Pliocene. The migration of representatives of the central Asian desert mammalian complex to the Caucasian Isthmus could have come partly from the northeast and southeast around the Caspian, and partly directly from the east.

The Pleistocene and Holocene immigrants from the semideserts and deserts of Turan to eastern Ciscaucasia — jerboa and gerbil — probably appeared during the regressions of the ancient Caspian. The late, Holocene, stage of immigration of a number of thermophilous southern mammals is apparent in their ranges of distribution.

In our systematic analysis of Holocene mammalian fauna of the Caucasian Isthmus we include, in addition to extant relict species, those species which became extinct in the historical epoch under direct and indirect anthropogenic influences. This approach gives a much more comprehensive list of Caucasian animals than those compiled by other investigators.

As previously mentioned, the analysis of the Recent fauna was intended to reveal two aspects of the distribution ranges: their origins and their ages, which is to say, both the historico-genetic and ecological identity of the species. Lacking paleontological data on some of the Caucasian species, their ages were estimated on the basis of comparisons between the antiquity and evolution of their preferred biotopes, on the one hand, and data on their ecology and migrational ability, on the other.

The review of Recent and restored distribution ranges of Quaternary mammals inhabiting the Caucasian Isthmus now or in the past (Maps 1-93) and a comparison of these with paleogeographic data resulted in considerable refinement of the scheme of genetic composition of the Caucasian Holocene fauna given in Chapter III. In its complete form, the scheme is as follows:

PALEOGEOGRAPHY AND ECOLOGY OF CAUCASIAN MAMMALS

I. Tertiary (Pliocene) :
   1) Caucasian, mesophilous, widely distributed;
   2) Southwest Asian, xerophilous and thermophilous;
   3) Eastern European, hydrophilous and steppe-type;
465 4) Turanian, desert-type.

II. Pleistocene:
  5) European, forest mesophilous;
  6) European-Asian, steppe-type;
  7) Turanian, semidesert- and desert-types.
III. Holocene:
  8) South Asian, thermophilous;
  9) Turanian, desert-type;
  10) accidentally introduced.

The principal types of ranges of some indicator species of these complexes are given in Figures 188-194.

The zoogeographic and chronological analysis of the Holocene fauna of the Caucasus is given by orders.

INSECTIVORA

The Caucasian Isthmus is one of the richest areas in Insectivora species in the U.S.S.R. We have identified 15 extant species from studies of 436 localities and 1,224 specimens (Maps 1-6). Modern compilations drawn from the Caucasus and neighboring areas (Ognev, 1928; Bobrinskii, Kuznetsov and Kuzyakin, 1944; Kuznetsov, 1950; Ellermann and Morrison-Scott, 1951; and others) do not reveal occurrences of Brandt's hedgehog of central Asia and Iran or of Diplomesodon or some white-toothed shrews of the western Mediterranean in the Caucasian fauna.

The nucleus of the Caucasian Insectivora is composed of local mesophilous species, such as the mole of the southern, Mediterranean type, Caucasian and lesser shrew and gray white-toothed shrew. It also includes such widely distributed species associated with mesophytic landscapes as European hedgehog and water shrew, whose origin on the Isthmus is obscured. Next in order of abundance is the group of species associated with the Tertiary steppe and semidesert landscapes of the eastern Mediterranean, e.g., the long-eared hedgehog, white-bellied white-toothed shrew and pygmy white-toothed shrew.

Among occurrences of relict Tertiary species of the Russian Plain are those of the Russian desman which is limited to the northwesternmost part of the Isthmus, the common shrew which is sparsely settled in the southeastern part, and the little white-toothed shrew which is rare in eastern Transcaucasia* and southwest Asia. These species migrated from the north to the Caucasus in the Pleistocene.

Table 97 sets forth our proposed scheme of the genetic composition of insectivores of the Caucasian Isthmus.**

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* In Transcaucasia, this form includes Crocidura dinniki Ogn., whose systematic position is not clear.

** Space cannot be devoted to a criticism of the classification of shrews given by Bobrinskii, Kuznetsov, Kuzyakin (1944) which was fully accepted by Ellermann and Morrison-Scott (1951). Peculiar misidentifications have been made of the gray white-toothed shrew. Ognev (1928) erroneously identified as gray white-toothed shrew an alcohol-preserved specimen of long-tailed white-toothed shrew from northern Iran (Mala-Kara), which is in the ZIN collections. Because of a semantic confusion (?!) Bobrinskii and Kuzyakin misidentified the Pontian Crocidura lasia Thos. as the Far Eastern C. lasiura Dobs.— an error which has resulted in a greatly confused nomenclature and has obscured discussions of the ranges of these two species.

466 TABLE 97. Genetic composition of Caucasian Insectivora

Species	Tertiary (Pliocene)				Pleistocene			Holocene		
	Caucasian, mesophilous and widely distributed	Southwest Asian, xerophilous and thermophilous	East European, hydrophilous and steppe-type	Turanian, desert-type	European, forest mesophilous	European-Asian, steppe-type	Turanian, semidesert- and desert-types	South Asian, thermophilous	Turanian, semidesert- and desert-types	Accidentally introduced
Erinaceus europaeus L.	+	—	—	—	—	—	—	—	—	—
Hemiechinus auritus Gmel.	—	+	—	—	—	—	—	—	—	—
Talpa orientalis Ogn. ,....	+	—	—	—	—	—	—	—	—	—
T. caucasica Sat.	+	—	—	—	—	—	—	—	—	—
Desmana moschata L.	—	—	+	—	—	—	—	—	—	—
Sorex minutus L.	+	—	—	—	—	—	—	—	—	—
S. araneus L.	—	—	—	—	+	—	—	—	—	—
S. raddei Sat.	+	—	—	—	—	—	—	—	—	—
Neomys fodiens Schr.	+	—	—	—	—	—	—	—	—	—
Crocidura suaveolens Pall.	—	—	—	—	—	+	—	—	—	—
C. leucodon Herm.	—	+	—	—	—	—	—	—	—	—
C. russula Herm.	+	—	—	—	—	—	—	—	—	—
C. lasia Thos.	+	—	—	—	—	—	—	—	—	—
C. zarudnyi Ogn.	—	+	—	—	—	—	—	—	—	—
Suncus etruscus Savi.	—	+	—	—	—	—	—	—	—	—

CHIROPTERA

We have identified 27 Holocene Chiroptera species from 785 specimens from 419 localities of the Caucasus (Maps 7-17). There are reasons to believe that the fauna was somewhat poorer in the Upper Pleistocene because of the southward retreat of the ranges of some thermophilous species caused by the cold phases. These ranges were restored to their former areas in the Holocene. It remains for future investigations to reveal new forms of bats, so far unknown on the Caucasus because of the difficulties of bat-collecting.

According to the compilations of Allen (1940), Tate (1942), Kuzyakin (1950) and Ellermann and Morrison-Scott (1951), the subtropical families Pteropidae, Rhinopomatidae, Embalonuridae, Nycteridae and Hipposiderinae, which are characteristic of the southern parts of southwest Asia, do not occur in the Caucasus. As a whole, however, the Caucasian bat fauna is much richer than that of Europe and Asia. The ranges of most of these Caucasian species belong in the Mediterranean region, sensu lato; viewed ecologically, they can be divided into those of relatively mesophilous forms and those of more xerophilous and thermophilous forms. The first occur in areas of broadleaf forests where the bats often build their nests in hollows. Their summer and winter habitats are mostly in marginal areas of the mountain formations of the Isthmus; the latter forms prefer the landscapes of low plateaus, foothills and hot lowlands.

467 TABLE 98. Genetic composition of Caucasian Chiroptera

Species	Tertiary (Pliocene)				Pleistocene			Holocene		
	Caucasian, mesophilous and widely distributed	Southwest Asian, xerophilous and thermophilous	East European, hydrophilous and steppe-type	Turanian, desert-type	European, forest mesophilous	European-Asian, steppe-type	Turanian, semidesert-and desert-types	South Asian, thermophilous	Turanian, semidesert-and desert-types	Accidentally introduced
Rhinolophus ferrum equinum Schr.	—	+	—	—	—	—	—	—	—	—
Rh. mehelyi Matsch.	—	+	—	—	—	—	—	—	—	—
Rh. euryale Blas.	—	+	—	—	—	—	—	—	—	—
Rh. hipposideros Bechst.	—	+	—	—	—	—	—	—	—	—
Rh. blasii Peters.	—	+	—	—	—	—	—	—	—	—
Myotis bechsteinii Kühl	—	+	—	—	—	—	—	—	—	—
M. emarginatus Geoffroy	—	+	—	—	—	—	—	—	—	—
M. oxygnathus Mont.	+	—	—	—	—	—	—	—	—	—
M. mystacinus Kühl	+	—	—	—	—	—	—	—	—	—
M. nattereri Kühl	+	—	—	—	—	—	—	—	—	—
Miniopterus schreibersii Kühl	+	—	—	—	—	—	—	—	—	—
Plecotus auritus L.	+	—	—	—	—	—	—	—	—	—
Barbastella darjelingensis Dobs.	—	—	—	+	—	—	—	—	—	—
B. barbastellus Schr.	—	+	—	—	—	—	—	—	—	—
Nyctalus leisleri Kühl	—	—	+	—	—	—	—	—	—	—
N. siculus Pall.	—	—	—	—	+	—	—	—	—	—
N. noctula Schr.	—	—	+	—	—	—	—	—	—	—
Vespertilio pipistrellus Schr.	+	—	—	—	—	—	—	—	—	—
V. nathusii Keys. et. Blas.	—	—	+	—	—	—	—	—	—	—
V. kühlii Kühl	—	+	—	—	—	—	—	—	—	—
V. savii Bonap.	+	—	—	—	—	—	—	—	—	—
V. murinus L.	+	—	—	—	—	—	—	—	—	—
V. bobrinskii Kuz.	—	—	—	+	—	—	—	—	—	—
V. nilssonii Keys. et. Blas.	—	—	—	—	+	—	—	—	—	—
V. serotinus Schr.	+	—	—	—	—	—	—	—	—	—
V. ognevi Bobr.	—	—	—	+	—	—	—	—	—	—
Tadarida taeniotis Raf.	+	—	—	—	—	—	—	—	—	—

The mesophilous group comprises most of the mouse-eared bats and vespertilids, including the serotine vespertilio, which occurs more often in beech forests, e.g., in Talysh, than on open plains.

The more xerophilous and thermophilous group consists primarily of the horseshoe bats, barbastels and the Mediterranean pipistrel. The extent of the influence exerted by European Chiroptera fauna is undetermined, but it was probably not significant, no more so than that of the central Asian desert fauna. Among the desert species, the distribution range of Ognev's great bat is highly characteristic of the Tertiary hills in the Kura lowlands of eastern Transcaucasia.

Only two species can be tentatively identified as Upper Pleistocene immigrants from Europe: the giant noctule and the northern vespertilio. Their appearance on the Caucasus at that time was possibly a second one caused by the end of the glaciation.

The complete list, divided into genetic groups, is given in Table 98, using the terminology of Ognev (1928) and Kuzyakin (1950).

468 Some species — Vespertilio bobrinskii Kuz. and V. ognevi Bobr. — require additional study. The first should be compared with V. (Eptesicus) nasutus Dobson, 1877, and the second with V. (Eptesicus) sodalis Barr. Hamilton, 1910.

CARNIVORA

The Carnivora fauna of the Caucasus in the Holocene is comprised of 25 species; it was probably no richer in the Upper Pleistocene. Of these, 22 species survived until recent time. We have had available a wealth of material for the zoogeographical analysis of this group (Maps 18-38): extensive collections of fossil remains from 92 localities, skulls and skins of extant species from 376 localities, observations and data from state fur stations covering 257 localities, and 417 specimens. In comparison with neighboring territories, the Caucasian Isthmus is rich in carnivores (Ognev, 1931, 1935; Bobrinskii, Kuznetsov and Kuzyakin, 1944; Ellermann and Morrison-Scott, 1951). The absence of Viverridae from the Caucasian fauna is noticeable, and is accounted for by the fact that the northern boundary of their range lies somewhat to the south in Iraq. The family of honey badgers (Mellivorinae) is also conspicuously missing, as they occur much farther to the south and east. The rest of the Palaearctic carnivore families are fairly well represented in the Caucasian fauna. The Caucasus lies outside the ranges of some of the Canidae, e.g., some foxes of southwest Asia (Vulpes ruppeli Schinz., V. cana Blanf., Fennecus zerda Zimm.). True feline desert species (Felis margarita Loche and F. caracal Schr.) do not occur in the Caucasus either. Most Caucasian carnivores belong to ubiquitous forms of uncertain origins, which have, nevertheless, been included by us in the group of Caucasian Mediterranean forms because of the occurrences on the Isthmus of closely related forms in the Middle and even in the Upper Pleistocene. These forms are wolf, fox, European brown bear, badger, and lynx.

(469) TABLE 99. Genetic composition of Caucasian Carnivora

Species	Tertiary (Pliocene)				Pleistocene			Holocene		
	Caucasian, mesophilous and widely distributed	Southwest Asian, xerophilous and thermophilous	East European, hydrophilous and steppe-type	Turanian, desert-type	European, forest mesophilous	European-Asian, steppe-type	Turanian, semidesert- and desert-types	South Asian, thermophilous	Turanian, semidesert- and desert-types	Accidentally introduced
Canis aureus L.	—	—	—	—	—	—	—	+	—	—
C. lupus L.	+	—	—	—	—	—	—	—	—	—
Vulpes vulpes L.	+	—	—	—	—	—	—	—	—	—
V. corsac L.	—	—	—	—	—	+	—	—	—	—
Hyaena hyaena L.	—	—	—	—	—	—	—	+	—	—
Ursus arctos L.	+	—	—	—	—	—	—	—	—	—
Martes martes L.	—	—	—	—	+	—	—	—	—	—
M. foina Erxl.	—	+	—	—	—	—	—	—	—	—
Vormela peregusna Güld.	—	+	—	—	—	—	—	—	—	—
? Putorius putorius L.	—	—	—	—	+	—	—	—	—	—
P. eversmanni Less.	—	—	—	—	—	+	—	—	—	—
Lutreola lutreola L.	—	—	—	—	+	—	—	—	—	—
Mustela nivalis L.	+	—	—	—	—	—	—	—	—	—
? M. erminea L.	—	—	—	—	+	—	—	—	—	—
Meles meles L.	+	—	—	—	—	—	—	—	—	—
Lutra lutra L.	+	—	—	—	—	—	—	—	—	—
* Panthera tigris L.	—	—	—	—	—	—	—	+	—	—
* P. leo L.	—	—	—	—	—	—	—	+	—	—
P. pardus L.	+	—	—	—	—	—	—	—	—	—
Felis lybica Forst.	—	+	—	—	—	—	—	—	—	—
F. silvestris Schr.	—	—	—	—	+	—	—	—	—	—
F. chaus Güld.	—	—	—	—	—	—	—	+	—	—
F. lynx L.	+	—	—	—	—	—	—	—	—	—
Otocolobus manul Pall.	—	—	—	+	—	—	—	—	—	—
* Acinonyx jubatus Schr.	—	+	—	—	—	—	—	—	—	—

Note. ? —species whose occurrence on the Isthmus has not been definitely established; * —species which became extinct in modern time.

The southern (southwest Asian-Mediterranean) species of steppe and desert landscapes are represented by pine marten, tiger polecat, African wildcat and cheetah).

The Pliocene eastern species (Turanian-Afghan) are represented by the manul.

The Pleistocene European immigrants from the north and southwest are easily recognized by the poor development of their ranges, which wedge out toward the southeast. These forms include pine marten, mink, European wildcat and, possibly, the "European-type" bear of the Greater Caucasus.

All the immigrant carnivores of the Holocene originated in the south and are relatively thermophilous. Their late appearance on the Isthmus is confirmed by modern ecological data, the development of their ranges and the absence of their remains in Pleistocene bituminous deposits on the Apsheron and in the caves on the upper Rion. The jackal, striped hyena, tiger, lion and jungle cat belong to this group; their origin on the Caucasus has been discussed in Chapter III.

Most of the nomenclature employed for the list of carnivores given in Table 99 follows the usage of Russian authors.

469 LAGOMORPHA

Two species of Lagomorpha emerged on the Caucasus in the Holocene — the European hare and the Armenian pika. Indications from Recent ecological data, from the characteristics of their ranges and from Cenozoic fossil hares and pikas, found on the southern Russian Plain and in Ciscaucasia, are that they were ancient Pliocene (Miocene) immigrants to the Isthmus, which evolved in the eastern Mediterranean xerothermic landscapes of the Tertiary. Of the more southern forms, the Arabian hare (Lepus arabicus Ehr.) does not occur on the Caucasus, and of the western Mediterranean forms, the rabbit (Oryctolagus cuniculus L.) is absent.

The Pleistocene migration of the blue hare and small pika from the north to the Caucasus has not been proven.

The two Holocene Caucasian species are Tertiary forms of eastern Mediterranean origin and their Recent ecology indicates their relatively xerophilous character (Table 100, p. 471).

470 RODENTIA

The Holocene fauna of the Caucasus includes no less than 50 species of rodents. The specific composition of the Caucasian rodent fauna can be regarded as completely known from the 10,623 specimens which we studied and from data from 1,770 collecting localities of extant forms. The Middle and Upper Pleistocene rodent fauna was probably not much richer than the postglacial fauna.

The variation of the zoogeographical and ecological composition of the rodent fauna and its considerable geological antiquity permit a number of reliable conclusions on the particular features and developmental patterns of this faunal group. Taking stock of the faunal complexes of neighboring territories and their potential influence on the Caucasian fauna, it becomes apparent that a number of rodent species do not occur on the Isthmus. This review and comparative study of rodent fauna are based on works by Ognev (1940, 1947, 1948, 1950), Bobrinskii, Kuznetsov and Kuzyakin (1944), and Ellermann and Morrison-Scott (1951).

The following species are missing from the Caucasian fauna: from the Eastern European steppe complex — marmot*, gray, big or red-cheeked suslik and Eversmann's hamster; from the European forest and mountain-forest complexes — common squirrel, dormice of the genera Eliomys and Muscardinus, the Balkan Dolomys, common vole, root vole and a number of other subterranean voles of the genus Pitymys; from the central Asian desert and southwest Asian upland-desert complexes — large-toothed suslik, long-clawed suslik or ground squirrel, jerboas of the genera Pygeretmus and Jaculus, mouse-like dormouse and Betpakdala dormouse, many species of gerbils of the genera Gerbillus, Psammomys. Tatera and subterranean rats of the genus Nesokia.

There are also some western Mediterranean species that do not occur on the Caucasus: African porcupine (Hystrix cristata L.), mouse (Lemniscomys barbarus L.), Arvicanthis niloticus Desm., Acomys cahirinus Desm., and other species.

Upper Tertiary (Pliocene) mesophilous species of the humid broadleaf-forest and mountain-meadow landscapes of the eastern Mediterranean comprise the largest group within the Caucasian rodent fauna:

Persian (Caucasian) squirrel
Fat dormouse
Forest dormouse
Black rat
House mouse
Caucasian yellow-spotted mouse
Common field mouse

Broad-toothed field mouse (Asia Minor mouse)
Promethean vole
Water vole
Caucasian snow vole
Long-tailed snow vole
Pine vole

The species referred to here as house mouse includes a number of wild forms, some associated with biotopes of the mountain, foothills and lowland-forest zones: Mus musculus formosovi Hept. and M. musculus abbotti Wat.; some associated with biotopes of the steppe and semidesert: M. musculus hortulanus Nordm. and M. musculus tataricus Sat. Those large Caucasian mice of the
471 Apodemus fulvipectus Ogn. type (A. flavicollis ponticus Svirid., A. f. saturatus Neuh., A. f. argiropuli Vin. et Arg.) which inhabit the forests of the Caucasus, and which grade into a smaller, lighter-colored form with a small spot on the neck which inhabits the semidesert zone of eastern and southern Transcaucasia (i.e., the A. arianus Blanf. type), are regarded as a polymorphic species of the eastern Mediterranean (Caucasian) yellow-spotted mouse.

The ancient xerophilous species of eastern Mediterranean origin include the following:

Asia Minor suslik
William's jerboa
Asia Minor hamster
Migratory hamster
Mouse-like hamster
Red-tailed Libyan gerbil

Asia Minor gerbil
Vinogradov's gerbil
Transcaucasian mole vole
Asia Minor snow vole
Lesser mole rat
Porcupine
Persian gerbil

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* It is possible that the bobak marmot inhabited the Ciscaucasian steppes in historical time.

The time of the emergence of these ancient species in different parts of the Isthmus and the characteristics of their dispersion vary, as the examples given in Chapter III show.

The European beaver and Ciscaucasian mole rat are representative of Eastern European Tertiary species, hydrophilous in nature and adapted to steppe ecology. Without pursuing the question of the origin of European beaver, it is assumed that the species inhabited the Caucasian Isthmus and Russian Plain as early as Pliocene time.

It is more difficult to place the origin and emergence of mole rat in Ciscaucasia. In the absence of fossil mole rats on the Isthmus and any proof of their migration from Asia Minor, they must be considered descendants of the Miocene-Pliocene mole rats which inhabited the southern Russian Plain. Immigration of the Russian mole rat and the giant Russian mole rat to the Isthmus could have taken place at the time of deposition of the Balakhan beds, i.e., in the Middle Pliocene, and they could have survived the subsequent marine transgressions in the Caucasian foothills.

The sole Caucasian representative of the ancient Turanian and Afghanistan desert species is the small five-toed jerboa. Its distribution range, which includes eastern Ciscaucasia and eastern and southern Transcaucasia, is an interesting example of the influence of the "Aral-Caspian fauna."

A fairly large group of Pleistocene immigrants of various ages and origins can be identified from a comparison of the ranges and palaeogeographic data.

There are at least seven generally mesophilous, "European" forest species:

Northern birch mouse
Harvest mouse
Striped field mouse
Yellow-necked field mouse
Common hamster
Common vole*
Common red-backed vole

The ranges of these species on the Isthmus are rather poorly developed. Where they penetrated deep into Transcaucasia, the ecological channels
472 of their dispersion were either the floodplain river marshes of the piedmont valleys or the mesophytic meadows and coniferous forests of the uplands. Their routes followed the Black and Caspian sea coasts, bypassing the Caucasian Range on the east and on the west. Examples are the harvest mouse, striped field mouse and common hamster. The range of the European yellow-necked field mouse of the Apodemus flavicollis samariensis type is confined to the tugai forests of the lower Terek and Sulak in eastern Ciscaucasia. Indeed a puzzling phenomenon of distribution.

Since it is doubtful that the species is endemic, it would seem that it could only have migrated to this region from the lower Volga. The most probable time would have been the Upper Pleistocene; the desert landscapes which formed in the northern Caspian area in later, postglacial, time could not have carried the migration of this species.

Immigration of three eastern xerophilous species of the southern Kazakhstan semidesert and of the central Asian desert complexes occurred in the Pleistocene: thick-tailed three-toed jerboa, northern three-toed jerboa and little earth hare.

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* Bones of this vole which have recently been found in Acheulean beds of Kudaro I cave indicate that the occurrence of this species on the Caucasus dates from ancient time.

(473) TABLE 100. Genetic composition of Caucasian Lagamorpha and Rodentia

Species	Tertiary (Pliocene)				Pleistocene			Holocene		
	Caucasian, mesophilous and widely distributed	Southwest Asian, xerophilous and thermophilous	East-European, hydrophilous and steppe-type	Turanian, desert-type	European, forest mesophilous	European-Asian, steppe-type	Turanian, semidesert- and desert-type	South Asian, thermophilous	Turanian, semidesert- and desert-types	Accidentally introduced
Lagomorpha										
Lepus europaeus Pall.	—	+	—	—	—	—	—	—	—	—
* Ochotona sp.	—	+	—	—	—	—	—	—	—	—
Rodentia										
Sciurus anomalus Güld.	+	—	—	—	—	—	—	—	—	—
Citellus pygmaeus Pall.	—	—	—	—	—	+	—	—	—	—
C. citellus L.	—	+	—	—	—	—	—	—	—	—
* Castor fiber L.	—	—	+	—	—	—	—	—	—	—
Glis glis L.	+	—	—	—	—	—	—	—	—	—
Dyromys nitedula Pall.	+	—	—	—	—	—	—	—	—	—
Sicista subtilis Pall.	—	—	—	—	—	+	—	—	—	—
S. betulina Pall.	—	—	—	—	+	—	—	—	—	—
S. caucasica Vin.	+	—	—	—	—	—	—	—	—	—
Allactaga elater Licht.	—	—	—	+	—	—	—	—	—	—
A. jaculus Pall.	—	—	—	—	—	+	—	—	—	—
A. williamsi Thos.	—	+	—	—	—	—	—	—	—	—
Alactagulus acontion Pall.	—	—	—	—	—	—	+	—	—	—
Scirtopoda telum Licht.	—	—	—	—	—	—	+	—	—	—
Dipus sagitta Pall.	—	—	—	—	—	—	+	—	—	—
Spalax microphthalmus Güld.	—	—	+	—	—	—	—	—	—	—
S. giganteus Nehr.	—	—	+	—	—	—	—	—	—	—
S. leucodon Nordm.	—	+	—	—	—	—	—	—	—	—
Rattus rattus L.	+	—	—	—	—	—	—	—	—	—
R. norvegicus Berken	—	—	—	—	—	—	—	—	—	+
Mus musculus L.	+	—	—	—	—	—	—	—	—	—
Micromys minutus Pall.	—	—	—	—	+	—	—	—	—	—
Apodemus agrarius Pall.	—	—	—	—	+	—	—	—	—	—
A. fulvipectus Ogn.	+	—	—	—	—	—	—	—	—	—
A. flavicollis Melch.	—	—	—	—	+	—	—	—	—	—
A. sylvaticus L.	+	—	—	—	—	—	—	—	—	—
A. mystacinus Danf. et Alst.	+	—	—	—	—	—	—	—	—	—
Mesocricetus auratus Water.	—	+	—	—	—	—	—	—	—	—
Cricetus cricetus L.	—	—	—	—	+	+	—	—	—	—
Cricetus migratorius Pall.	—	+	—	—	—	—	—	—	—	—
Calomyscus bailwardi Thos.	—	+	—	—	—	—	—	—	—	—
* Rhombomys opimus	—	—	—	—	—	—	—	—	+	—
Meriones meridianus Pall.	—	—	—	—	—	—	—	—	+	—
M. erythrourus Gray	—	+	—	—	—	—	—	—	—	—
M. persicus Blanf.	—	+	—	—	—	—	—	—	—	—
M. tamariscinus Pall.	—	—	—	—	—	—	—	—	+	—

Note. Asterisk indicates species which became extinct in historical time.

TABLE 100 (continued)

Species	Tertiary (Pliocene)				Pleistocene			Holocene		
	Caucasian, mesophilous and widely distributed	Southwest Asian, xerophilous and thermophilous	East European, hydrophilous and steppe-type	Turanian, desert-type	European, forest mesophilous	European-Asian, steppe-type	Turanian, semidesert- and desert-types	South Asian, thermophilous	Turanian, semidesert- and desert-types	Accidentally introduced
M. blackleri Thos.	–	+	–	–	–	–	–	–	–	–
M. vinogradovi Hept.	–	+	–	–	–	–	–	–	–	–
Meriones sp.	–	+	–	–	–	–	–	–	–	–
Lagurus lagurus Pall.	–	–	–	–	–	+	–	–	–	–
Ellobius talpinus Pall.	–	–	–	–	–	+	–	–	–	–
E. lutescens Thos.	–	+	–	–	–	–	–	–	–	–
Prometheomys schaposchnikovi Sat.	+	–	–	–	–	–	–	–	–	–
(474) Arvicola terrestris L.	+	–	–	–	–	–	–	–	–	–
Microtus nivalis Mart.	–	+	–	–	–	–	–	–	–	–
M. gud Sat.	+	–	–	–	–	–	–	–	–	–
M. roberti Thos.	+	–	–	–	–	–	–	–	–	–
M. majori Thos.	+	–	–	–	–	–	–	–	–	–
M. arvalis Pall.	–	–	–	–	+	–	–	–	–	–
M. socialis Pall.	–	+	–	–	–	–	–	–	–	–
Clethrionomys glareolus Schr.	–	–	–	–	+	–	–	–	–	–
Hystrix leucura Sykes	–	+	–	–	–	–	–	–	–	–

Their Pleistocene age is evident from the Upper Pleistocene occurrence of their remains on the lower Don, indicating that these species migrated from the Transcaspian deserts far to the west no later than the time of the post-Khazar sea regression. Partial survival of the Khvalynsk transgression was possible on the southern shores of the Terek bay. Again in the Holocene there was another wave of immigration of these species and of Turanian desert species to the Terek-Kuma semidesert and the Manych area. The great, midday and tamarisk gerbils are representative of these Holocene immigrants from the central Asian deserts, as shown by the absence of their remains from Quaternary alluvial beds of the lower Don and by the sparseness of their Recent distribution. The great gerbil became extinct in Ciscaucasia in historical time.

One would expect that new southern rodents would have emerged during the xerothermal postglacial epoch in the southeastern part of the Isthmus, in addition to this second wave of immigration of desert species to the northeast. However, no such instances are known with the possible exception of the distribution of Asia Minor gerbil on the Kura-Araks lowlands and the local dispersion of Persian gerbil, steppe vole and some other species caused by anthropogenic changes in the landscape.

The Norway rat is the only accidentally introduced species which has inhabited the Isthmus in historical time; this species and black rat are widely distributed over railroad, water and air routes. The penetration of house mouse of the northern type into the Caucasus continues.

The complete genetic composition of the rodent fauna is given in Table 100, employing the basic nomenclature accepted by Russian authors. Thus, the great jerboa is referred to as Allactaga jaculus Pallas, and not as A. major Kerr.; the thick-tailed three-toed jerboa* as Alactagulus acontion Pallas, and not as A. pumilio Kerr.; the red-tailed Libyan gerbil as Meriones erythrourus Gray, and not as M. lybicus Licht.; the porcupine as Hystrix leucura Sykes, and not as Hystrix indica Kerr., etc.

474 PERISSODACTYLA

According to collection material and data drawn from ancient historical sources, two or three species of horse lived in the Caucasus in postglacial time. The origin of tarpan remains obscured by unanswered questions on the morphology and evolution of horses of the Old World. Adopting the generally accepted view, we have included it in the group of Pleistocene immigrants from the northern steppes. The kulan is considered a Holocene immigrant from the south. It seems likely that postglacial evolution of horses proceeded differently in the north and in the south. Ciscaucasia was inhabited by horses of the Eastern European plains, feru
whereas Transcaucasia was inhabited by southwest Asian horses. pumpelli

As is the case with some rodents and carnivores, perissodactyls occurring in different parts of the Caucasus had different origins. Examples are the kulan and the southwest Asian horse, which in southern Transcaucasia must be regarded as local Tertiary species, but which in eastern Transcaucasia and Ciscaucasia must be regarded as Holocene immigrants.

Table 101 shows the different positions occupied by Caucasian perissodactyls in our scheme.

ARTIODACTYLA

The Caucasian Isthmus occupies first place in the U.S.S.R. in the number of artiodactyl species and individuals per unit area. It is a large center of speciation and development of this order.

There has been no migration of the arctic forms, reindeer and musk ox, to the Caucasus. And the ranges of southern thermophilous species (such
475 as Asia Minor and Mesopotamian fallow deer belonging to the genus Dama) and of a number of southwest Asian gazelle species (Gazella dorcas L., G. gazella Pall., G. leptoceros Cuv.) do not extend to the Caucasus in Recent time.

Of the mountain forms of central Asia, no markhor [Capra falconeri Wagner] occurs in the Caucasian fauna; and of the Western European forms no Ammotragus lervia Pall., Capra sinaitica Ehr,, C. ibex L., or C. pyrenaica Schinz. are found either.

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* [This is the correct translation for the Russian "emuranchik," but the author apparently meant "little earth hare" ("zemlyanoi zaichik") ... see Table 103.]

TABLE 101. Genetic composition of Caucasian Perissodactyla and Artiodactyla

Species	Tertiary (Pliocene)				Pleistocene			Holocene		
	Caucasian, mesophilous and widely distributed	Southwest Asian, xerophilous and thermophilous	East European, hydrophilous and steppe-type	Turanian, desert-type	European, forest mesophilous	European-Asian, steppe-type	Turanian, semidesert- and desert-types	South Asian, thermophilous	Turanian, semidesert- and desert-types	Accidentally introduced
Perissodactyla										
* Equus hemionus Pall.	—	—	—	—	—	—	—	+	—	—
* E. caballus ferus gmelini Ant.	—	—	—	—	—	+	—	—	—	—
* E. caballus L. (subsp.) pumpelli	—	+	—	—	—	—	—	—	—	—
Artiodactyla										
Sus scrofa L.	+	—	—	—	—	—	—	—	—	—
Cervus elaphus L.	+	—	—	—	—	—	—	—	—	—
* Alces alces L.	—	—	—	—	+	—	—	—	—	—
Capreolus capreolus L.	+	—	—	—	—	—	—	—	—	—
Saiga tatarica L.	—	—	—	—	—	+	—	—	—	—
Gazella subgutturosa Güld.	—	—	—	—	—	—	—	+	—	—
Rupicapra rupicapra L.	+	—	—	—	—	—	—	—	—	—
Capra caucasica Güld.	+	—	—	—	—	—	—	—	—	—
C. cylindricornis Blyth.	+	—	—	—	—	—	—	—	—	—
C. aegagrus Erxl.	—	+	—	—	—	—	—	—	—	—
Ovis gmelini Blyth.	—	+	—	—	—	—	—	—	—	—
* Bison bonasus L.	+	—	—	—	—	—	—	—	—	—
* Bos primigenius Boj.	+	—	—	—	—	—	—	—	—	—

Note. Asterisk indicates species which became extinct in historical time.

There was a gradual impoverishment in Artiodactyla on the Isthmus in the Quaternary, in spite of immigration of new species from without. Fifteen to sixteen species existed there in the Pleistocene, but by the Holocene, there were only thirteen, of which only eleven survived into recent time. Most of the Caucasian artiodactyls are local mountain-forest, often endemic, forms. The endemic forms include the Caucasian chamois and the east Caucasian and the west Caucasian goat. The group of widely distributed, generally somewhat mesophilous forest species is comprised of boar, red deer, roe deer, bison and primitive bull. It is possible that elk should also be included in this group, once its southern origin has been established.

The southwest Asian xerophilous species, which are mainly associated with upland-steppe landscapes, are represented by Bezoar goat and Asia Minor mouflon.

476 The Pleistocene immigrant group includes the northern-type elk, which may have made a second appearance in the forests of the Caucasus, and the saiga. The latter species reached the maximum development of its distribution on the Isthmus in the Middle Pleistocene. This group should probably also include the large form of roe deer which occurs in Ciscaucasia.

The goitered gazelle is the only late — postglacial — immigrant; it penetrated eastern Transcaucasia from the south, and eastern Ciscaucasia possibly from the east.

The genetic composition of Holocene artiodactyls of the Caucasus is given in Table 101.

The results of this paleogeographic and zoogeographic analysis of the Holocene mammalian fauna of the Caucasus can be summarized as follows:

1. The Holocene mammalian fauna of the Caucasian Isthmus consisted of 136 species of Insectivora, Chiroptera, Carnivora, Lagomorpha, Rodentia, Perissodactyla and Artiodactyla, of which 124 species survived into recent time.

2. The nucleus of the fauna — up to 36 % of the species — consists of local (predominantly mesophilous) and widely distributed forms of Pliocene age, They subsequently evolved on the Caucasian Isthmus and in adjacent areas of the eastern Mediterranean where the landscape retained its original (mesophytic) character because of proximity to the sea, warm climate and a particular relief.

TABLE 102. Genetic composition (number of species by type of origin) of the Recent (Holocene) mammalian fauna of the Caucasus, by orders

Orders		Tertiary (Pliocene)				Pleistocene			Holocene			Total number of species
		Caucasian, mesiphilous and widely distributed	Southwest Asian, xerophilous and thermophilous	East European, hydrophilous and steppe-type	Turanian, desert-type	European, forest mesophilous	European-Asian steppe-type	Turanian, semidesert- and desert-types	South Asian, thermophilous	Turanian, semidesert- and desert-types	Accidentally introduced	
Insectivora		8	4	1	—	1	1	—	—	—	—	15
Chiroptera		10	9	3	3	2	—	—	—	—	—	27
Carnivora		8	4	—	1	4	2	—	5	—	—	24
Lagomorpha		—	2	—	—	—	—	—	—	—	—	2
Rodentia		14	15	3	1	7	5	3	—	3	1	52
Perissodactyla		—	1	—	—	—	1	—	1	—	—	3
Artiodactyla		8	2	—	—	1	1	—	1	—	—	13
Total	absolute	48	37	7	5	15	10	3	7	3	1	136
	%	35.7	27.2	5.1	3.6	11.0	7.3	2.2	5.0	2.2	0.7	

(477)

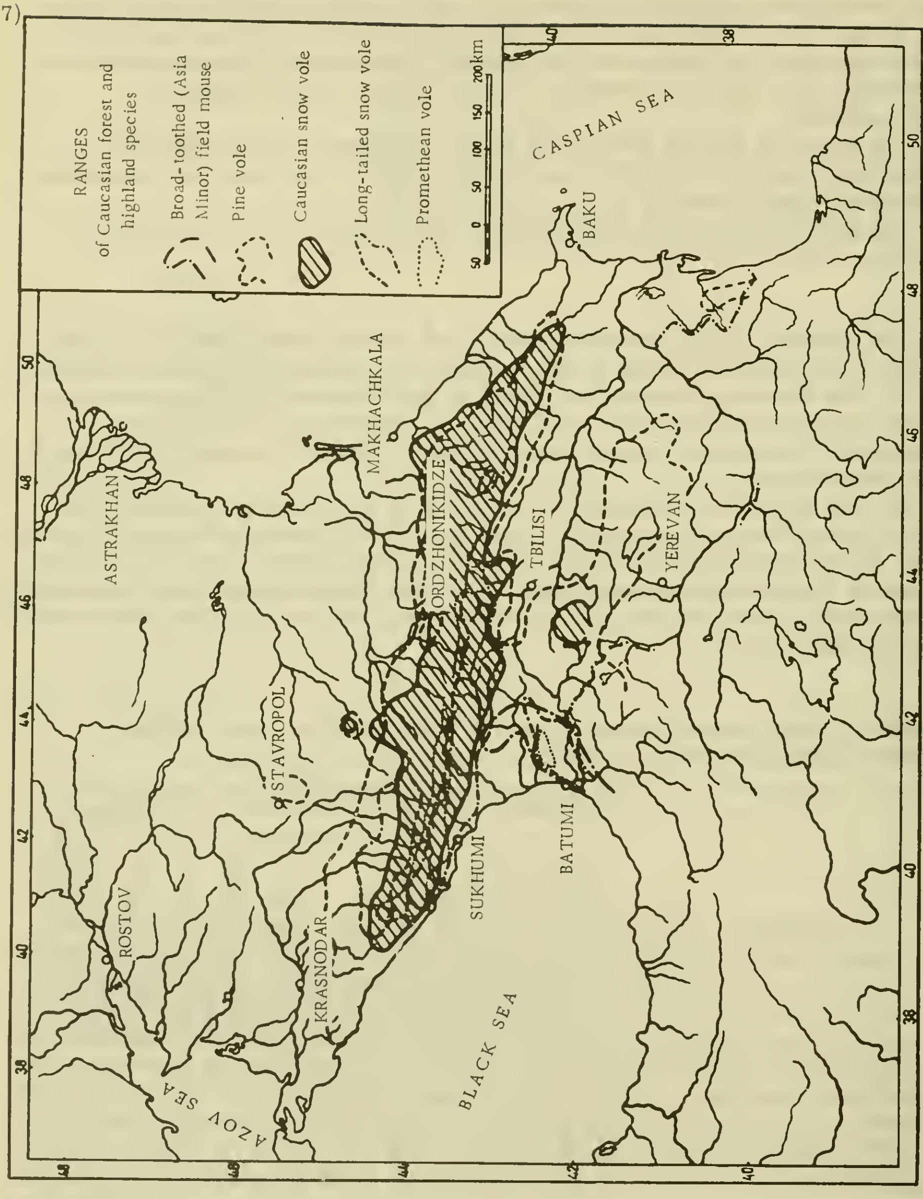

FIGURE 188


RANGES
of southwest Asian
upland-steppe species
Asia Minor suslik
Lesser mole rat
Asia Minor hamster
Bezoar goat
Mouflon
50 0 50 100 150 200 km
ROSTOV
ASTRAKHAN
AZOV SEA
STAVROPOL
KRASNODAR
MAKHACHKALA
ORDZHONIKIDZE
BLACK SEA
SUKHUMI
TBILISI
BATUMI
BAKU
CASPIAN SEA
YEREVAN
38
40
42
44
46
48
50

FIGURE 189


RANGES
of southwest Asian
upland-desert species
Asia Minor gerbil
Persian gerbil
Vinogradov's gerbil
Mouse-like hamster
Transcaucasian mole vole
50 0 50 100 150 200 km
ASTRAKHAN
ROSTOV
AZOV SEA
STAVROPOL
KRASNODAR
MAKHACHKALA
ORDZHONIKIDZE
BLACK SEA
SUKHUMI
TBILISI
BATUMI
BAKU
CASPIAN SEA
YEREVAN
38
40
42
44
46
48
50

FIGURE 190

(479)

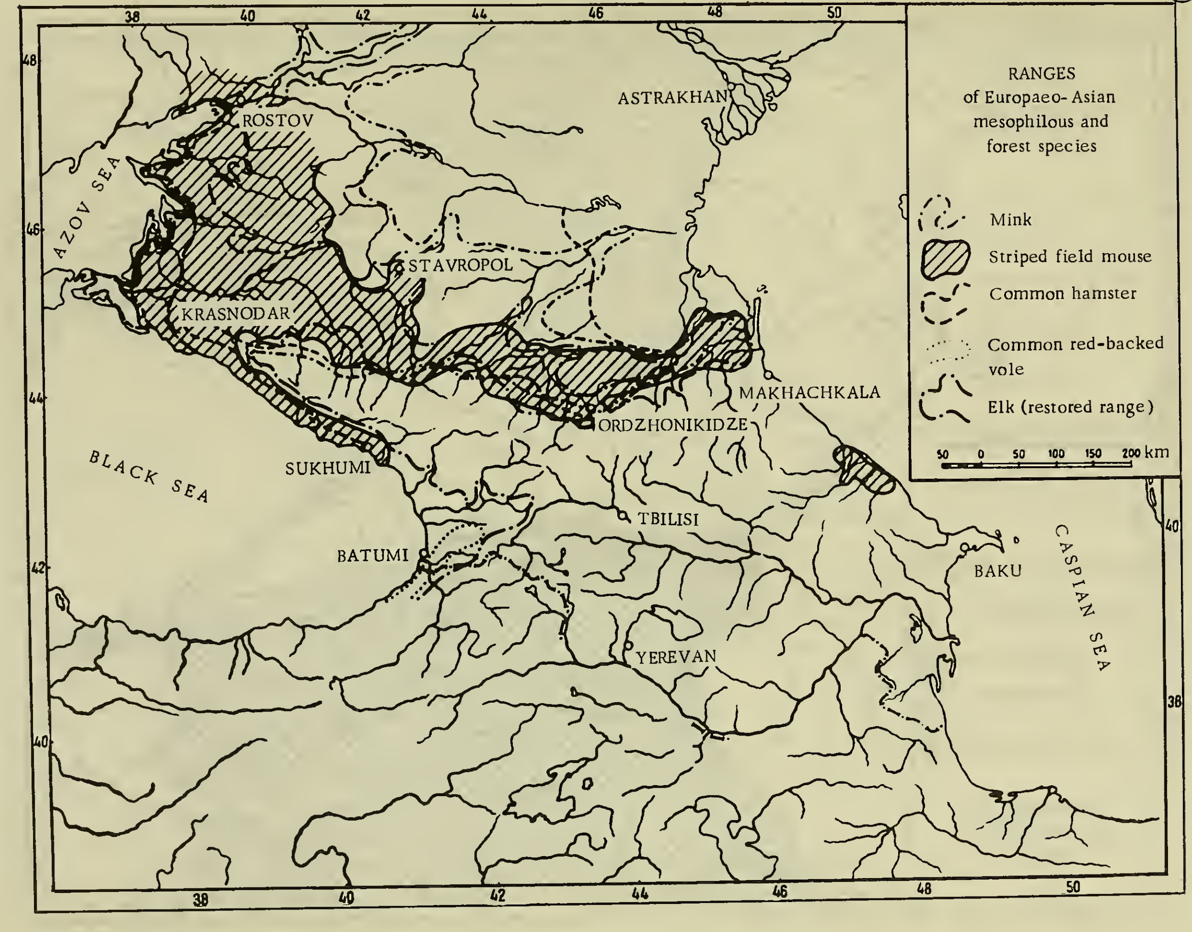

FIGURE 191

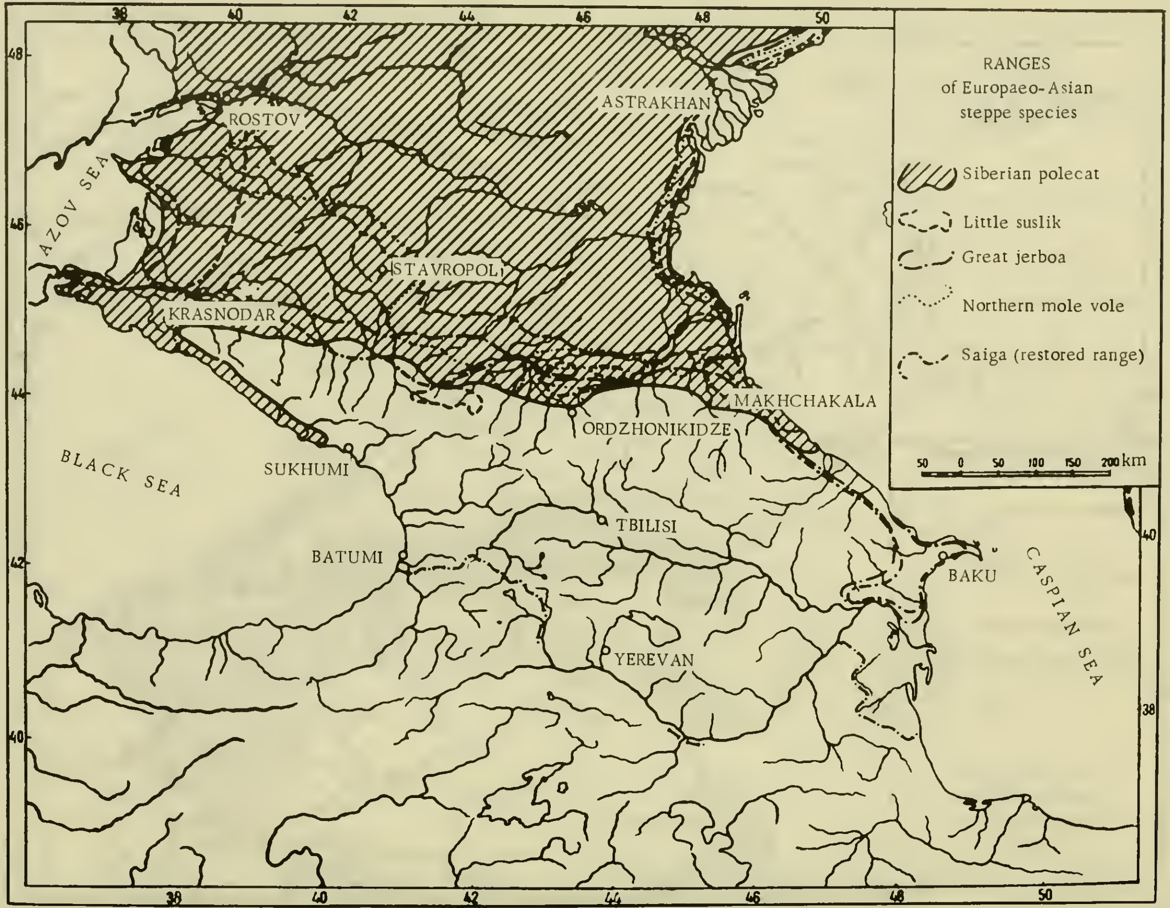
RANGES
of Europaeo-Asian
steppe species
Siberian polecat
Little suslik
Great jerboa
Northern mole vole
Saiga (restored range)
50 0 50 100 150 200 km
ROSTOV
ASTRAKHAN
AZOV SEA
STAVROPOL
KRASNODAR
MAKHCHAKALA
ORDZHONIKIDZE
BLACK SEA
SUKHUMI
TBILISI
BATUMI
BAKU
CASPIAN SEA
YEREVAN
38
40
42
44
46
48
50

FIGURE 192

(480)

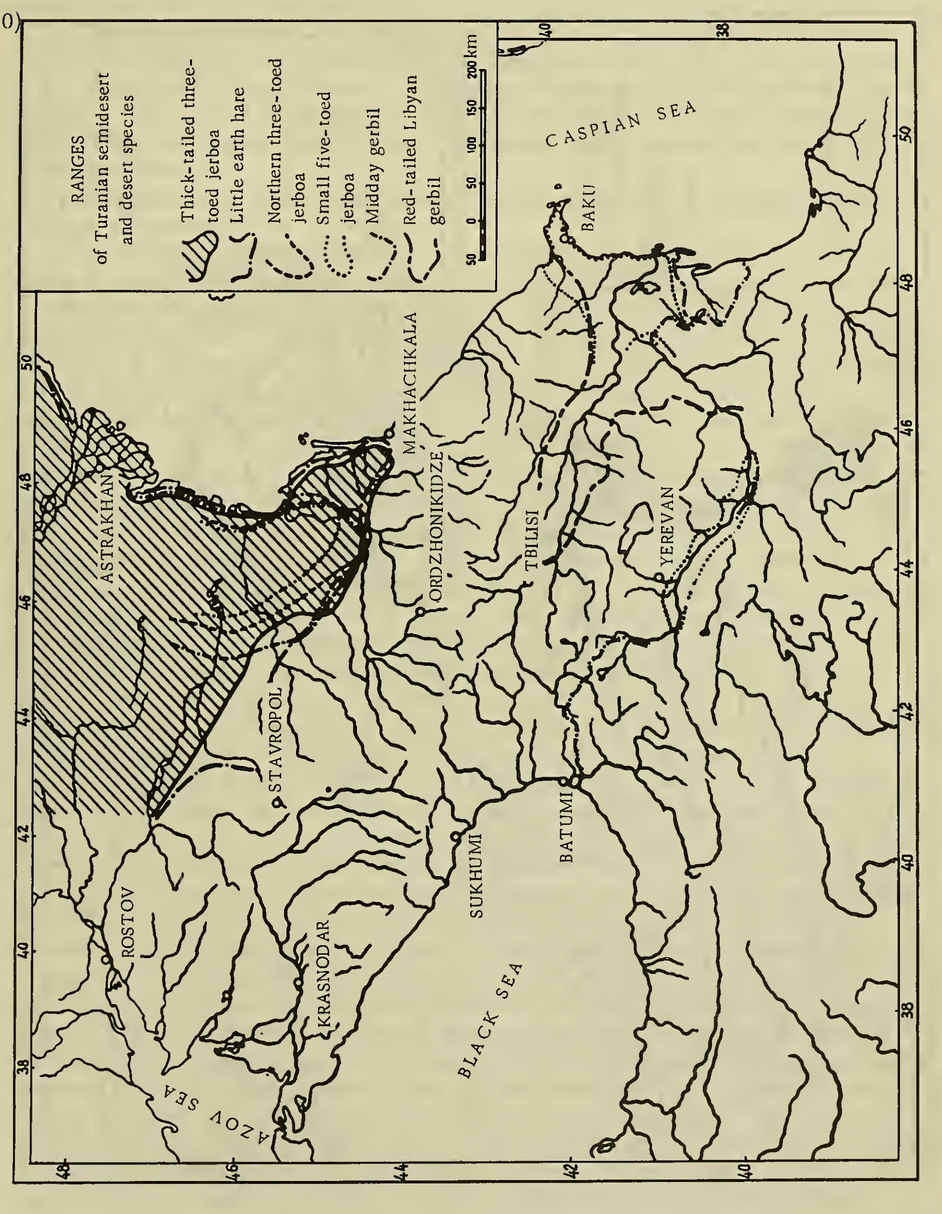

FIGURE 193

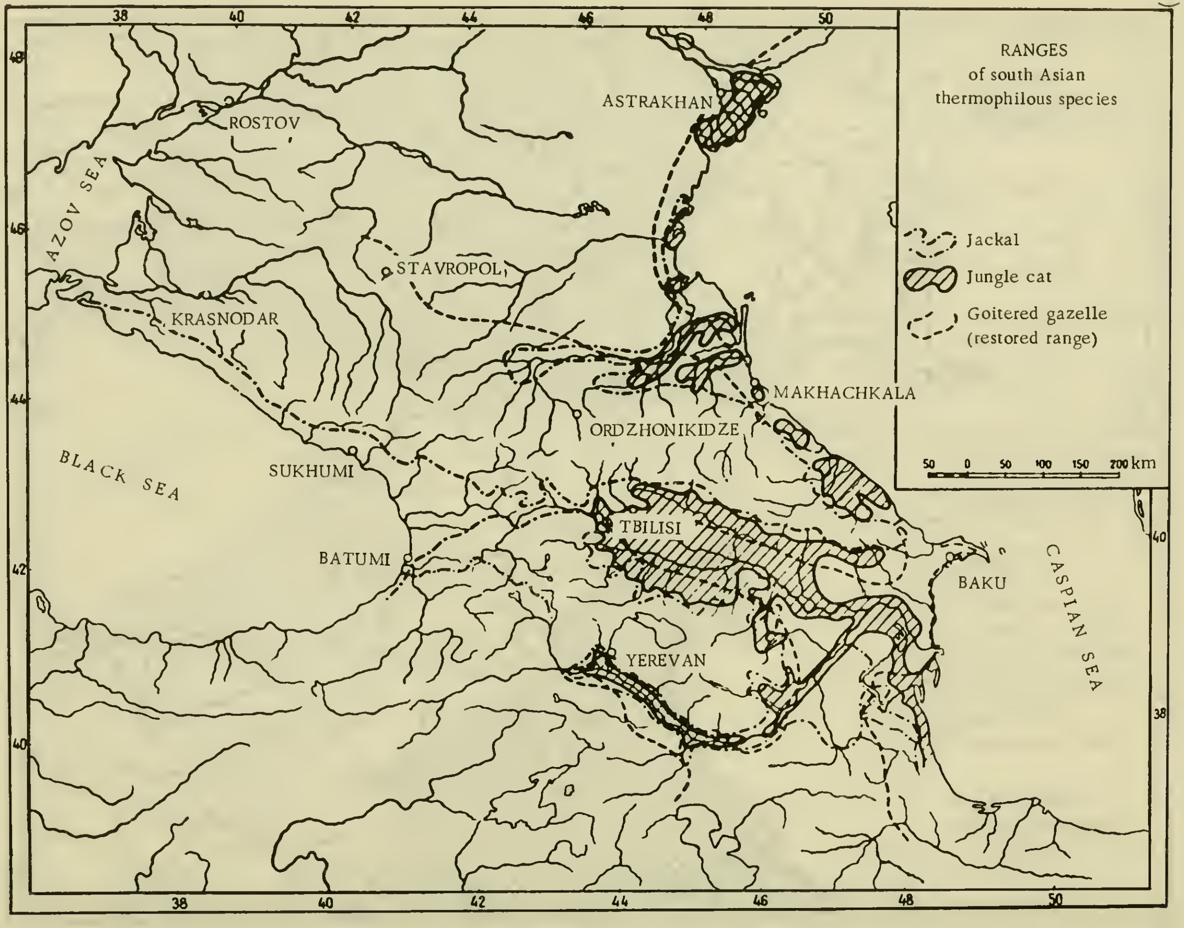
RANGES
of south Asian
thermophilous species
Jackal
Jungle cat
Goitered gazelle
(restored range)
50 0 50 100 150 200 km
ASTRAKHAN
ROSTOV
AZOV SEA
STAVROPOL
KRASNODAR
MAKHACHKALA
ORDZHONIKIDZE
BLACK SEA
SUKHUMI
TBILISI
BATUMI
BAKU
CASPIAN SEA
YEREVAN
38
40
42
44
46
48
50

FIGURE 194

3. The next largest group — up to 27% of the species — is that of southwest Asian xerophilous immigrants of Tertiary age.

4. Eastern European steppe and hydrophilous forms, some of which migrated to the Caucasus in the Pliocene and some in the Pleistocene, account for 12.5% of the species.

5. European mesophilous and forest species, which appeared on the Caucasus mainly in the Pleistocene, constitute up to 11% of the species.

477 6. Postglacial immigrants, consisting of thermophilous species which could not live under conditions of deep snow cover, and which migrated from the east and the south (central and southwest Asia), comprise up to 7% of the species.

7. Accidentally introduced species which appeared in historical time amount to less than 1%.

All of these data, which differ considerably from the opinion of other authors, have been summarized in Table 102. (p. 475).

The proposed scheme of geographical zonation of the mammals of the Caucasian Isthmus is based on the results of the zoogeographical mapping and the analysis of the mammalian fauna given in this chapter and Chapter III.

The generalized contours of the ranges of indicator mammalian complexes, both those that are relatively stenotopic to the Caucasus and those that were introduced, were employed to delineate districts, subdistricts and sectors (Figures 188-194). In preparing the zonation, the paleogeographical significance of territories and species was considered first, rather than the simple numerical preponderance of animals in one or another zoogeographic group. Thus, for example, the Caucasian mountain-forest district includes, in addition to the Greater and Lesser Caucasus, the eastern slopes of Talysh and the northern slopes of Elburz, even though only four clearly autochthonous species of the ancient mammalian complex of the Caucasus remain in the latter two sectors. The rest are Pleistocene and Holocene forms. The entire steppe area and part of the forest-steppes of Ciscaucasia belong to the Eastern European steppe subregion of Pleistocene immigrant fauna, inasmuch as no
481 autochthonous Caucasian elements of Pliocene age remain in the Holocene fauna of this area. Our subdivision of the territory is not based on as many units as the zonation schemes of other zoogeographers, who based their schemes more on geomorphology and geobotany, rather than on the zoological material. Nevertheless, the boundaries of the phytolandscapes figure significantly in our scheme because of the importance of the relationships between index species of mammals and the phytolandscapes.

In view of the fact that the greater part of the Caucasian Isthmus belongs in the eastern half of the Mediterranean region of the Palaearctic (i.e., the eastern Mediterranean subregion), we include the northern part of the Ciscaucasian plains in the Ciscaucasian subdistrict of the subregion of Eastern European and northern Kazakhstan steppes, and the northwestern corner of eastern Ciscaucasia in the Terek-Kuma sector of the central Asian desert subregion. The entire Greater Caucasus, the northern slopes of the Lesser Caucasus and the eastern slopes of Talysh are included in the Caucasian district, which is further divided into the Asterabad or Talysh-El'brus and the Dagestan subdistricts. The Lesser Caucasus uplands (the Armenian Highland) is included in the Sevan subdistrict, and the semideserts and steppes of eastern Transcaucasia are included in the Kura subdistrict of the southwest Asian district of the same eastern Mediterranean subregion. The Talysh upland-steppe and the middle Araks valley are regarded as the main sectors of the southwest Asian district. The general scheme, the historico-geological characteristics of the districts, subdistricts and sectors and of their mammalian complexes, are given below and summarized in Table 103 (p. 500) and Figure 195 (p. 515).

EASTERN MEDITERRANEAN SUBREGION

CAUCASIAN DISTRICT

(District of mole and pine vole)

The definition of the Caucasian district is based on the distribution ranges of some index species of the Caucasian mammalian complex. These ranges almost entirely cover the mountain forests, upland meadows and rocky passes, the wooded parts of the inclined piedmont plains of Ciscaucasia, and the lowland forests of Transcaucasia. The northern boundary of the district is in the area of the inclined piedmont plains.

In the Ciscaucasian steppes there are two isolated sectors which belong to this district — Stavropol and Pyatigor'e (Figure 195). In eastern Transcaucasia the southern boundary of the district runs along the latitude of Shemakha and Ivanovka in the Agri-Chai and Alazan valleys and near the Kakhetian Range at Telavi. In Kartalinia and South Ossetia, the boundary is on the northern edge of the dry Gori depression. It passes at the foot of the Surami Range where it turns sharply east to the foot of the Trialet Range, continues above Tbilisi and on through the lower Khram valley at the foot of the Shakh-Dag, south of Shamkhor and Kirovabad. In the southeast, the boundary bypasses Karabakh at altitudes of 600-700 m near Martuni, and encompasses Karyagino and part of the Okhchi-Chai basin. It takes a turn to the north and northwest, passing east and northeast of the high steppes and meadow-steppes of the Armenian (Sevan) Highland. The southern boundary of the Lesser Caucasus subdistrict of the Caucasian district follows the divides of the Shakh-Dag and Pambak ranges in a 482 westerly direction, passing somewhat south of Kirovakan, and, skirting northern Dzhavakhetia, enters eastern Turkey along the divide of the Adzhar-Imeretian ridge. Its western boundary extends from Trabzon to Sukhumi along the Black Sea coast; shifting slightly to the east, it coincides with the boundary of the Ciscaucasian subdistrict of immigrant steppe species.

The Caucasian district includes the isolated Asterabad Talysh-El'brus sector which lies in the far southeastern part of Transcaucasia. The boundaries of this sector almost completely coincide with the contours of the forest zone on the eastern slopes of Talysh and the northern slopes of Elburz.

The main massif of the Caucasian district encompasses the Dagestan subdistrict, located between the mesophytic landscapes of the marginal ridges of the eastern Caucasus (Figure 195).

It should be noted that where the boundary of the Caucasian district passes at the foot of ranges and foothill plains certain parts of it comprise a broad, transitional zone where animals of the steppe plains and of the mountain-forest landscapes coexist sympatrically. Contrary to Kuznetsov's opinion (1950), this zone, even in Ciscaucasia, has little in common with the forest-steppe of the Russian Plain.

Most of the district has been dry land at least since the Oligocene, gradually increasing in size on the periphery. Large mountain ranges formed in the Miocene. The central parts of the Greater Caucasus mountain system are composed of Jurassic slates and volcanic rock. The diluvium and soil cover are well developed only on the high plateaus; in the canyons the bedrock is exposed as rocky cliffs and talus. The marginal ranges are composed mainly of sandstones and limestones, which in the foothills are overlain by deposits of the Cenozoic seas and alluvial-diluvial boulder trains.

The Lesser Caucasus and Talysh present similar geologic phenomena but calcareous deposits occur more rarely in these areas. As the orogenesis of the Pliocene and post-Pliocene waned, stages of peneplanation of the ranges alternated with mountain-building and glacial cycles.

The contemporary types of vegetation in the Caucasian district date from the Lower Pliocene at least. The Recent zonation of climate and altitudinal vegetation zones were formed by the first half of the Quaternary.

The contemporary landscapes of the Caucasian district which were formed in the Holocene are not homogeneous over its vast area. In the west, the Trans-Kuban piedmont plain is somewhat hilly in places and is dissected by numerous, almost completely non-meandering streams.

The upper half of this plain is covered by oak and smoothleaf-elm forests alternating with wide sections of steppe meadows. This type of landscape does not occur in central Ciscaucasia; it reappears on the Terek-Sunzha inclined plain, and finally disappears in the east near Sulak, east of Gudermes.

In Transcaucasia — Colchis, Alazan-Agrichai, Khachmas and the Lenkoran piedmont lowlands — lowland forests of a special type have developed in which oak, Caucasian wingnut and smoothleaf elm covered with thorny liana predominate. The marshy areas are characterized by European alder. The abundance of nut shrubs and trees on these lowlands favors the existence of rodents, ungulates and carnivores.

483 The slopes of the Chernye Gory, the northernmost ridge of the Greater Caucasus, are covered with humid beech—hornbeam forests. Relict grassy steppe vegetation covers some of the calcareous rock outcrops.

The next ridge, the Skalistyi, is characterized by subalpine meadows in mountain passes and by mountain pine forests which replace the beech forests on the southern slopes. Sections of mountain xerophytic vegetation occur in the valley bottoms of the Kuban, Teberda and other rivers, particularly in the longitudinal-latitudinal valleys between the El'brus and central Dagestan.

Most of the mountain slopes of the lower and middle belts of the southern slope of the Greater Caucasus, of the northern slopes of the Lesser Caucasus and of eastern Talysh are covered with beech and hornbeam forests, which provide seasonal food for forest rodents and ungulates.

Fir and pine forests are developed in the upper mountain-forest belt of the western Caucasus, and fir—maple forests on the southern slopes. The well-defined rocky relief is a favorable habitat for snow vole and chamois, which are plentiful in the area. As a rule, the upper edge of the forests is characterized by high-mountain oak and birch. Caucasian rhododendron which wedges into the upland-meadow zone is also typical.

The alpine zone proper is completely developed in the western and central parts of the Greater Caucasus and on the highest ridges of the Lesser Caucasus with mesophytic meadows, taluses and rocky passes, and glaciers at altitudes of 2,800-3,500 m. In the uplands of Talysh the upper edge of the forest lies on the boundary of upland-steppe and upland-xerophytic vegetation formations. In the eastern part of the Greater Caucasus the subalpine meadows usually grade into areas of dense bunchgrass formations, particularly sheep's fescue and matgrass, which are typical for eastern alpine meadow formations. The steppe development is even more pronounced on the median-altitude plateaus of Dagestan where low precipitation and physiological dryness of the thin soil layer prevail, and where upland-steppe meadows and meadow-steppes with low grasses became the predominant formations. The turf-covered sections and slopes of the plateau, which have a plentiful food supply of grasses and a rapid run-off of rain- and snow-water, are particularly favorable environments for subterranean rodents such as hamster and vole. The main food resources of highland ungulates are also located in this zone.

The Recent mammalian complex of the Caucasian district mainly consists of local Tertiary mesophilous forms which are associated with highland meadows and mountain and lowland forests. This mammalian complex and the ranges of its components developed out of local speciation and biocenotic-forming processes which occurred in the Neogene and the Quaternary.

Immigration of animals from adjacent territories to this district, mainly to the piedmont transitional belt, took place during the Quaternary.

The Holocene mammalian complex of the Caucasian district consists of 88 species, most of which belong to genetic group 1 (see p. 462). There is little representation from group 2, but somewhat more from group 3. No Turanian forms, i.e., representatives of group 4, appear in the complex. The nucleus of group 5 is fairly strongly developed, but group 7 is completely unrepresented. There are a few occurrences of species from groups 8 and 10 (Table 103, p. 500).

The index species are local representatives of group 1·
484 mesophilous Pliocene species comprising the Caucasian faunal nucleus and the widely distributed forms, totalling at least 48 species and accounting for more than one half of the total number of animals of the district (Table 103).

Seem from the genetic and ecological points of view, this is not a homogeneous group. It includes animals associated with the mesophytic forests and meadows, which are fairly widely distributed in the broadleaf forests of Europe, such as lesser shrew, fat dormouse, roe deer and red deer. The list of endemic Caucasian highland species associated with alpine mesophytic meadows is more specific. Caucasian birch mouse, Promethean vole, long-tailed snow vole and Caucasian snow vole are characterized by their mountainous ranges. In addition to these rodents, the larger, more dynamic, but still stenotopic, species which are associated with mountain relief, rocks, alpine meadows and mountain forests (Caucasian goat and chamois) are also indicative of the Caucasian complex of mammals.

In the Stavropol and Pyatigor'e sectors and the Dagestan and Asterabad subdistricts, the species of group 1 are poorly represented and have not permeated the complex, mainly because of anthropogenic influences and postglacial changes in climate and landscape. As examples, there are no deer, goat, chamois, Promethean vole or long-tailed snow vole in the Stavropol, Pyatigor'e and Talysh sectors; Promethean vole does not occur in the Dagestan sector, etc.

Among the species in this group, European beaver and Caucasian mountain marmot recently became extinct, but the black rat has survived.

Xerophilous and thermophilous Pliocene species (group 2) are represented by Chiroptera, Carnivora, Rodentia and Ungulata which migrated to certain landscape areas.

Since a number of species in this group could cross the ecological barriers on the periphery of the mountain system, these species could also inhabit some areas in the interior of the mountain system, such as the longitudinal valleys of Svanetia, Kabarda and Digoria.

There are at least 16 extant species, of which the most common are horseshoe bat, pine marten, European hare, Dagestan hamster, porcupine and Bezoar goat.

The group of forest and mesophilous forms is comprised of Pleistocene immigrants of northern (European) origin (group 5). For the most part their occurrences are confined to the zones of mountain forest and highland meadows of the Greater Caucasus. The habitat of the common shrew is an example. Other species are more widely distributed, e.g., the Caucasian [subspecies of the European] wildcat and pine marten, which, however, do not occur in central Dagestan and Talysh. The pine marten is also absent from the eastern part of the Lesser Caucasus. Ciscaucasian subspecies of mink and field mouse occur in the district only in the foothills of the northwestern Caucasus. The distribution of the common vole and the Pontian common red-backed vole is somewhat peculiar: the range of the first is primarily connected with the highland meadows, but does not extend to western Transcaucasia; the partial range of the latter extends from Asia Minor to the northern slopes of the Adzhar-Imeretian ridge. The distribution of Caucasian elk, which became extinct in the last century, was probably limited in the Pleistocene to Ciscaucasia and western Transcaucasia.

485 It is exceptional that the little suslik, a representative species of group 6, should occur in this district; it inhabits the dry longitudinal valleys of the northern slopes of the Bolshoi Range along with Caucasian snow vole and Caucasian goat.

The occurrences of Recent southern thermophilous immigrants (group 8) — jackal, tiger and hyena which inhabit the periphery of the district — are noteworthy.

The sole species from group 10, the Norway rat, inhabits the lower mountain-forest belt of Ciscaucasia and the lowland forests of eastern and western Transcaucasia. The species is particularly numerous in the marshes of Colchis and Asterabad. It is possible that several races of house mice (Mus musculus subsp.), which have been introduced into the Caucasus from the north, should be included in this group.

The Caucasian district is a climatic and landscape refuge for all the mesophilous species, but its particular importance lies in the shelter it provides for large game animals which have been displaced by man from woodless piedmont plains, lowlands and high plateaus. It is a large natural reserve in which many of the large animals have survived, and which may in the future serve a variety of practical and scientific purposes.

The protective qualities of the mountain relief and forest vegetation account for the great variety and high rate of survival of carnivore and ungulate species and individuals since the Pleistocene in this region, in contrast with the adjacent woodless plain areas.

If measures were taken to control human intervention and to develop suitable landscapes, they would undoubtedly promote the expansion of the Recent ranges of mountain [Caucasian] wildcat, panther, mountain boar, deer, roe deer and bison into the surrounding plains, thereby making the Caucasus a new species-dispersion center.

On the basis of studies of the mammalian fauna, it is difficult to justify any segregation of a highland, or alpine, complex and subdistrict. There is not a single mammal connected in one way or another with the subalpine and mountain-forest zones which does not also occur in the highland zone of the Caucasus. The so-called alpine species — Promethean vole and Caucasian birch mouse — occur both in alpine meadows and in the subalpine and meadow areas of the middle mountain-forest zone. Caucasian goat, chamois and Caucasian snow vole attain their maximum population in this forest zone. And so one can only speak of an alpine ecological assemblage. The true alpine species do not occur as far downslope as the lower mountain-forest belt or in the piedmont lowlands. This distribution pattern creates the transitional phytolandscape and geomorphological characteristics mentioned above.

The ecological assemblage of animals of the highland zone of the Greater Caucasus is relatively poor in species: 3 insectivore, 8 carnivore (of which 5 inhabit the region only in summer), 1 lagomorph, 8 rodent and 5 ungulate, of which 2 migrate to this zone only in summer.

In view of the Miocene age of the Greater Caucasus relief and the Upper Miocene age of the Caucasian mountain vegetation zones, the isolation of these forms must have begun in the Lower Pliocene. Evidently the known morpho-physiological adaptations of highland mammals also date from the Lower Pliocene, and reflect to some extent the orogenic and other associated physical processes.

486 Caucasian highland mammals are characterized by the usual adaptations to lower atmospheric pressure and temperature, such as higher rate of metabolism, red blood cell count and blood hemoglobin, enlarged heart, etc. In the jagged topography and rock debris of their environment, the fossorial habits of goats, chamois and snow voles were weakened, and they acquired the habits of walking and climbing on ledges and inclined rock faces. Boar, roe deer, deer, goat and chamois developed diurnal and seasonal migratory habits, both vertical and horizontal, in the face of such environmental factors as bloodsucking diptera, the distribution of mineral springs and seasonal food deficiencies which followed snowfalls. The snow vole's habit of stocking hay undoubtedly developed because of the plentiful shelters available in rocks where food remains dry in spite of the heavy atmospheric precipitation.

The occurrences of some endemic highland fossorial rodents (pine vole and Promethean vole), which feed on rhizomes, came about because of the disappearance of tree and bush vegetation and the development of areas of humid meadows, meadow-steppes and bare soil in the orogenic process.

The relatively poor specific composition of the highland fauna of the Greater Caucasus, which is easily seen upon comparison with the fauna of the steppe plateau of the neighboring Lesser Caucasus, can be accounted for, in our opinion, by four factors:

1. The accelerated orogenesis which probably caused the extinction of many specialized species of the Miocene mountain-forest faunal complex.
2. The lack of other nearby mountain centers of speciation, i.e., the relatively early isolation of the area and the difficulties of new immigration.
3. The space limitations of the highland life zone imposed by the sharp relief of the terrain: steep slopes and no plateaus suitable for carrying animal migrations. (These features probably account for the contemporary absence of mountain mouflon and marmot.)
4. The inability of the taiga-arctic species to colonize the Caucasian highlands, so that the area did not benefit from migrations caused by the European glaciation.

The vertical boundaries in the Quaternary ranges of Caucasian mammals underwent relatively minor shifts, which were caused by the advances and retreats of glaciers with concomitant shifts in the phytolandscape zones. The segregation of the ranges of the endemic species mentioned above into two sections — Caucasian and Lesser Caucasian — occurred primarily in post-glacial time, as xerophytic vegetation developed on the Surami Range.

The Caucasian type of mountain-forest mammalian complex reached its maximum development on the ridges and slopes surrounding the Colchis (Rion) lowlands. This saturation of the western Caucasus with Caucasian endemic forms cannot be linked to the Pliocene and Quaternary Pontian landmass in the Recent Black Sea basin, as some investigators have done. To the east, over the Greater and Lesser Caucasus, the ranges of these ancient autochthonous elements and later Pleistocene forms, connected with highland meadows and mountain, broadleaf forests, gradually decline;
487 their distribution becomes discontinuous and even shifts into other zones and zoogeographic districts.

At present, the species composition of the mammalian fauna of the Colchis lowlands is impoverished, particularly in rodents and ungulates. The periodically flooded habitats are unsuitable for burrowing rodents and paleontological and historical evidence shows that many hoofed mammals have been exterminated by man in the present epoch.

The Caucasian district can therefore be subdivided into the western and eastern sectors of the Greater Caucasus subdistrict (approximately on the longitude of Tiflis and Kazbek) and the Lesser Caucasus subdistrict, based upon the degree of saturation of the Caucasian mammalian complex. The Lesser Caucasus is somewhat poorer in species than the Greater Caucasus, e.g., at present, there are no Caucasian goats in this area, the distribution range of the pine marten is narrower, etc.

Inner Dagestan and the mountain-forest area of Talysh are characterized by the greatest faunal peculiarity. In origin, the fauna undoubtedly belong to the Caucasian district, but, because of the pronounced changes which took place in the original Quaternary complex, they should be categorized in separate subdistricts.

Dagestan Subdistrict

(Subdistrict of Dagestan hamster and Bezoar goat)

This subdistrict includes the basins of the Argun, Andi Koisu, Avar Koisu and Samur. Its northern boundary follows the Chernye Gory on a line between Shatyr and Buinaksk which in the west is drawn near the upper Iora and the Krestovyi pass. The southern boundary extends from the upper Iora along the divide to Mount Baba-Dag, and the eastern boundary is a line drawn from Buinaksk to Mount Baba-Dag. In the Quaternary this area was subject to uplift, and was sharply dissected by river erosion. The presence of solpugids and scorpions may indicate that the landscapes were dry throughout the Cenozoic and that the fauna was linked with the southern landmasses. The phytolandscape of this subdistrict is characterized by mountain-steppe meadows and meadow-steppes; birch groves and subalpine steppe-meadows occur on the high plateaus. The bottoms and southern slopes of the ravines are typically grown with wormwood formations with an admixture of xerophilous bushes — Christ's thorn and barberry. Mountain pine and beech forests are well developed in the upper reaches of the Argun and Andi Koisu.

The Caucasian mammalian complex of the Dagestan subdistrict, an area of mountain relief with a poorly developed forest vegetation, subject to drought, is impoverished in the ancient forest and highland species. Of 22 species of bats known in the Caucasian district, only 6 are recorded for inner Dagestan: 2 barbastels, 1 pipistrel and 3 noctules. There are no moles, Promethean voles or roe deer; long-tailed snow vole occurs only along the upper Avar Koisu, and deer occur only occasionally during the summer season. Chamois is not numerous, occurring only near the marginal ridges in forest-covered areas, although east Caucasian goat is abundant. The extinction of mouflon probably took place recently.

However, the occurrences of southwest Asian mountain xerophilous forms — Bezoar goat and Dagestan hamster, both larger local races existing in isolated canyons — are evidence of early (Upper Pliocene,
488 Middle Pleistocene) connections with southern Transcaucasia. Small races of voles are also characteristic: Caucasian snow vole and water vole, which, like the Transcaucasian mole vole, inhabit dry, irrigated areas.

Asterabad Subdistrict

(Subdistrict of Talysh mole and fat dormouse)

This subdistrict encompasses the low coastal areas of the southwestern and southern Caspian, the eastern slopes of Talysh and the northern slopes of El'brus. On the Isthmus, the Lenkoran lowlands and the mountain forests of Talysh are incorporated into a further subdivision — the Talysh sector of this subdistrict.

The northern boundary of the Talysh sector starts at southern Mugan (at the village of Masally) and the spurs of the Talysh near Astrakhan-Bazar. The eastern boundary follows the seacoast from the mouth of the Vilyazh-Chai, and the western boundary coincides with the lower boundary of the upland steppes at an altitude of 1,700-1,800 m. The Lenkoran lowlands are the youngest area geologically. They are formed of marine sediments and sediments deposited by the rivers of the Talysh, and are marsh-covered in winter. The phytolandscapes of the lowland and of the mountain slopes consist of dense broadleaf, lowland and mountain forest with some thermophilous endemic Tertiary forms, e.g., silk tree, Russian pea-shrub and thorny liana.

Geobotanists and zoogeographers generally tend to segregate the southern Caspian coast as a district — Asterabad — because of its Recent isolation and peculiar features. From the standpoint of the mammalian fauna and the paleogeography, however, the Talysh-El'brus mountain massif belongs in the Caucasian district for the following reasons.

Even in the Lower Miocene the northern spurs of El'brus, Talysh, the Lesser Caucasus and eastern Taurus formed a continuous coast of the Miocene basin. The landscapes of these areas were, therefore, similar, in spite of the influence of the Poltava flora from the east and their isolation beginning with the Upper Miocene (Sarmatian). The common landscape features have survived into the present. As an example, the alder swamp forests and mountain beech forests of Asterabad are very like, and often indistinguishable from, the corresponding formations of Colchis.

The Talysh sector is characterized by a specific climatic and soil regime. The mountain slopes and coastal lowland become extremely dry in summer, although the winters bring heavy precipitation. There is practically no subalpine zone in this sector. The upper margins of the broadleaf forests of Talysh (oak and fruit-bearing Rosales) grade into xerophytic, tall, herbaceous vegetation and into upland steppe or thorny astragali formations. Because of summer drought, the compacted zheltozem soil and lack of meadow-growth in the lowlands, there are no moles, common field mice or pine voles. Water vole occurs only in some marshes which are relicts of marine bays and never dry up. There are no occurrences of common and snow vole in the forest zone; their habitat is confined to the highest parts of the upland steppe.

As a whole, the subdistrict contains only a few survivors of the Miocene-Pliocene Mediterranean mammals, representing the southeasternmost limit of their distribution.

489 The Talysh sector is characterized by an extreme impoverishment in Caucasian mammals, there being no occurrences of Caucasian [Persian] squirrel, Caucasian birch mouse, Promethean vole, Caucasian snow vole, broad-toothed field mouse, Caucasian goat or chamois. It is possible, however, that some of these species may still be discovered on the El'brus.

In addition to relict species of the ancient Tertiary faunal nucleus and the widespread species of group 1 of our scheme, the Holocene mammalian complex of the subdistrict consists of representatives of groups 2, 8 and 10.

Of group 1, the dark long-tailed white-toothed shrew is abundant in the subdistrict, and mole and lesser shrew inhabit the upper, more humid part of the mountain forest zone.

Chiroptera are very abundant in Talysh, occurring mainly on the lowland near buildings and hollows. The specific composition of the bats of the southern Caspian coast, however, is inadequately known.

The distribution pattern of carnivores in Talysh presents no new features: fox is extremely rare in the mountain forests, as elsewhere on the

Caucasus; small southern bear is seldom found, but otter is particularly abundant along quiet rivers where fish are plentiful.

Rodentia are primarily represented by arboreal forms. Fat dormouse is especially numerous from the upper margins of the forest to the seacoast. Black rat occurs only on the lowland, and common field mouse only in mountain forest. Pine vole, a rare species, lives only in the upper third of the mountain forest. Beaver is not known in the area at present, but might have inhabited the lowland in the Holocene. The most numerous of the ungulates is boar. Deer were exterminated in Talysh at the beginning of this century, but still survive in the forests of Gilan and Mazandaran. The possibility of occurrences of bison and primitive bull has been discussed in Chapter III.

The southern (southwest Asian) species of xerophilous landscapes (group 2) are not numerous in the subdistrict. They include stone marten, hare and steppe vole, immigrants from the Mugan Steppe and highland steppes, and porcupine, which occurs from sea level to the Talysh mountain passes.

Bezoar goats do not occur in the Talysh sector, but probably lived there in the past. The species currently inhabits the El'brus.

For historical reasons and because of specific ecological features, the Asterabad subdistrict cannot be expected to contain any European or Eastern European hydrophilous, forest or steppe species of Pliocene-Pleistocene age, or any Turanian-Afghan desert forms.

Second in importance are the Holocene immigrants to the Isthmus (group 8), of which none are definitely known among insectivores and bats, although they probably occur, since Talysh and El'brus were affected by the Pleistocene cooling. Reports on the Recent occurrences of jackal, striped hyena, tiger and, possibly, lion are more reliable.

Of the accidentally introduced species (group 10), there is the Norway rat, which at present inhabits the lowland marshes and mountain forests.

The characteristic mammalian fauna of the Asterabad subdistrict clearly indicates that this area is typical of the mesophytic eastern Mediterranean, and that all of its "Indian" elements are later additions.

490 The early independent development of the Caucasian mountain-forest mammalian complex logically suggests questions on the extent of its influence on neighboring mammalian complexes, i.e., of the southern Russian Plain, the Transcaspian deserts and the southwest Asian highlands. The nature and scope of this influence were determined by the high degree of specialization of the component species of the Caucasian complex.

Their adaptations to their mountainous, humid-forest and meadow habitats precluded most of them from migrating to the northern steppes and northeastern deserts, and resulted in a distribution pattern which began to develop as early as the Middle Pliocene. At that time, the extensive landmasses formed during the regression of the Pontian basin probably became desert under the hot, arid climatic conditions of the period of the productive beds. Even in the Pleistocene (the period of glaciation) the mountain-forest species migrated only as far as the inclined piedmont plains of Ciscaucasia, or at the farthest to the Stavropol Plateau.

The southern, southwestern and southeastern migration routes were more feasible for the Caucasian mammals, and the influence of the

Caucasian highland assemblage on the alpine zone of the Armenian Highland and eastern Turkey was quite pronounced.

Common vole, Caucasian snow vole, Caucasian birch mouse, Caucasian deer, roe deer and even Caucasian goat could have migrated south, possibly on a considerable scale during the major cooling epochs. Later, in the Holocene, the effects of these migrations were blurred and in places completely obliterated by the climate warming and the development of xerothermal landscapes.

Of more significance was the role played by the mountain-forest area of the Caucasian district as a transitional area on the eastward migration routes of the European forest species. Pine marten, common red-backed vole, common dormouse and possibly elk migrated from Europe via the Balkans over the northern wooded slopes of the Taurus.

SOUTHWEST ASIAN DISTRICT

(District of Asia Minor hamster and gerbil)

The southwest Asian district, as understood here, implies the eastern Mediterranean province of other authors, but excludes the Greater Caucasus and the Crimea. It encompasses Asia Minor, northwestern Iran, the Armenian Highland and the lowlands of eastern Transcaucasia.

The animals characteristic of this district belong to two subcomplexes — the upland-desert and upland-steppe. These ranges replace each other in some places, sometimes in a mosaic pattern, sometimes in altitudinal zones. The upland-steppe variant has no clear boundaries on the Isthmus because its representative species ("medium" hamster [? Asia Minor (golden) hamster], William's jerboa, Bezoar goat and other more specialized species) migrated far to the north in the course of their evolution, following suitable landscapes (Figure 189).

The upland-desert variant consists of narrowly specialized desert species, which accounts for the more conservative nature of this subcomplex and its clearly developed northern boundary. The range of the gerbils (Persian, Asia Minor and Vinogradov's) presents the best developed
491 northern boundary of the upland-desert subcomplex distribution. The boundary is more or less clearly delineated, cutting at some places into the Sevan subdistrict along ravines and river valleys, following mountain slopes and zones of xerophytic vegetation (Figure 190).

Most of the district is at least of Oligocene age. Remains of Oligocene plants are known from a locality in the middle Araks valley, a deposit of Oligocene mammals from a locality near Alkhaltsykh, Upper Miocene mammals from the vicinity of Lake Urmia, and Pliocene mammals from the Zanga ravine. The periphery of the district (e.g., the Kura lowlands) is considerably younger — Upper Pliocene and Quaternary.

The predominant Recent types of landscape of the northwestern Iranian uplands, eastern Turkey and the middle Araks valley are sun-burned ridges of volcanic and sedimentary rocks, alternating with valleys and narrow ravines. The mountain slopes are covered with astragali formations with small xerothermal shrubs, buckthorn, almond and ephedra. Sparse juniper forests with groupings of silver hawthorn and willowleaf pear have survived in some places. The hot broad valleys are characterized by tree-like mountain saltwort and wormwort, and the river banks are covered by tugai thickets of poplar (Populus diversifolia), oleaster, buckthorn and tamarisk.

Upland-steppe formations with sheep's fescue predominating and some loose-bunch grasses cover the altitudinal ranges of the plateaus from 1,600-1,900 m. Alpine-type meadows occur at altitudes no lower than 2,000 m, e.g., in the region of Khvoy and Bayazet. Small tracts of mountain pine and occasional oak forests survived in eastern Turkey in the region of Van, Kars and Kagizman, and some oak forests were preserved on the Armenian Highland.

The mammalian complex of the district consists of species from genetic groups 1, 2, 4, 5, and 8.

It should be noted that most of the species of group 7 [? group 8], which, further north on the Isthmus, are postglacial immigrants, in this district are either endemics or immigrants from the south in much earlier times. In other words, part of group 8 can be eliminated for this district, and included in group 2.

In that part of the district that is within the U.S.S.R., the typical mammalian complex appears in only two small sectors. The district also includes two large sectors with mammalian complexes which underwent considerable change.

The general characteristics and mammalian geographic features of the sectors in Soviet territory are given below and in Table 103.

West Iranian Subdistrict

ARAKS SECTOR

(Sector of Persian gerbil and mouse-like hamster)

The northern boundary of this sector extends from the Kagizman area in the west, follows the southern slope of the Armenian Highland and Karabakh, crossing the Araks in the east, and enters the Iranian part of Mugan in the vicinity of the mouth of the Akera. The southern boundary is conditionally drawn along the Araks. This sector can be seen to include the entire left half of the middle Araks valley with its characteristic rocky
492 elevations: Alindzha-Dag, Ilyanlu-Dag, Darry-Dag and Negram-Dag. The main type of vegetation is saltwort—wormwort formations and grasses. In the Holocene tugai vegetation grew along the river banks, but later this was partly destroyed and partly replaced by planted groves of plane tree and walnut.

The Holocene mammalian complex of the Araks sector consists of almost all the species of the upland-desert variant of the southwest Asian type.

Group 1 is composed entirely of widespread species; there are no occurrences of mesophilous Caucasian species. The predominant forms are noctules, pipistrels, carnivores and mouse-like rodents.

Most of the species of this group inhabit either the relict wooded areas or biotopes of the cultivated landscape, i.e., gardens and settlements.

The faunal background is provided by 34 representative species of groups 2 and 8 (considered as one group): long-eared hedgehog and little white-toothed shrew among the Insectivora; horseshoe bats among the Chiroptera; hyena, stone marten, tiger polecat and other forms among the Carnivora; hamster and gerbil among the Rodentia; kulan, Bezoar goat, mouflon and goitered gazelle among the Ungulata. The index species are Persian gerbil, Transcaucasian mole vole and mouse-like hamster.

The number of species which recently became extinct is considerable: kulan, horse, deer, goitered gazelle and dromedary (?). Their extinction was caused by the early occupation of the area by cattle-raising tribes and the terrain advantages of an intermontane valley for easy extermination of large animals. The central Asian or Turanian-Afghan elements (group 4) are poorly represented. These species include manul, Aralykh small five-toed jerboa and, possibly, the Arazdayan gerbil. The region of the middle Araks is the northwestern limit of their present distribution.

The postglacial group (8) includes tiger, jungle cat and jackal. Tigers still occurred occasionally in the last century and jungle cat still inhabits the tugai and reedlands of the Araks valley, but jackals are exceedingly rare there. The migration of a number of Chiroptera species from the south during the postglacial warming of the climate seems a possibility. These species are identified as ancient Mediterranean forms. Of the latest, casually introduced species (group 10), Norway rat is noteworthy.

UPLAND TALYSH STEPPE SECTOT

(Sector of Persian gerbil and migratory hamster)

This sector occupies the plateau in the upper reaches of the Vilyazh-Chai, and the Zuvanda depression in the upper reaches of the Vasharu-Chai and Vassaru-Chai near Kel'vyaz and Kelakhan. The lower boundary of this sector coincides with the upper boundary of the forest and xerothermal high-grass lands on the western, northern and eastern slopes of the Talysh Range at altitudes of 1,700-1,800 m. The landscape of the plateau is composed of gentle slopes and level ground of chestnut soil with a thin cover of low loose-bunch grasses (brome, mouse barley and other forms) alternating with thorny astragali and Acantholimon. The landscape
493 is prominently marked by the isolated peaks of Kyz-Yurda, Mount Kelakhan and other mountains with fields of volcanic rocks.

The Holocene mammalian complex mainly consists of species of genetic groups 2 and 5. The common species are: among insectivores, long-tailed white-toothed shrew and long-eared hedgehog; among carnivores, fox, wolf and badger; among rodents, William's jerboa, steppe vole, Transcaucasian mole vole, Persian gerbil, migratory hamster and Asia Minor hamster. Asia Minor snow vole occurs on Mount Kelakhan, which is obviously a relict habitat. The common vole occurs on the higher parts of the plateau in areas planted to rye. European hare is characteristically plentiful.

There are no hoofed mammals in the sector; however, kulan, mouflon and Bezoar goat undoubtedly inhabited the area in the recent past.

Sevan subdistrict

(Subdistrict of Asia Minor snow vole and Asia Minor hamster)

The Sevan subdistrict includes the steppe uplands of the Lesser Caucasus.

The northern boundary of the subdistrict follows the mountain passes of the Adzhar-Imeretian ridge and curves around the northern part of the Dzhavakhetia highland, including the Mokrye Gory, Somkhetskii and Bezobdal'skii ridges. Farther east the boundary follows the divide of the Pambak ridge, passing north of Lake Sevan, and part of the steppe uplands of Karabakh. The southern boundary lies along the southern slope of the Karabakh, Zangezur and Daralagez ridges at altitudes of 1,500-1,700 m. To the west it passes beyond Yerevan on the southern slope of Alagez, entering Turkey in the vicinity of Kagyzman.

The Sevan subdistrict landscape is high-plateau with ridges of gentle relief and isolated peaks; the lower areas are covered by steppe with sheep's fescue and loose-bunch grasses predominating. Canyons, fields covered with broken rock and sunlit areas are typically grown with astragali and dry, sparse forests of juniper, willowleaf pear and silver hawthorn, which have been partially destroyed. Rare oak forests have been preserved on the northern slopes of the canyons. The higher sections, upwards of 2,000 m, are characterized by steppe meadows, and true mesophytic meadows are developed at still higher altitudes.

The Sevan subdistrict was an area of contest between the central southwest Asian (xerophytic mountain desert) landscape and the Caucasian (mesophytic forest) landscape, a contest which was reflected in the Holocene mammalian complex. The complex has no original features, but consists of a Caucasian-southwest Asian species combination.

The boundaries of the subdistrict are best delineated by the distribution of relatively xerophilous species of rodents, which inhabit upland-steppe and steppe-meadow landscapes. At high altitudes their ranges extend into Iran and eastern Turkey.

The mammalian complex of the subdistrict comprises representatives of groups 1, 2, 5, 8 and 10; the total number of extant forms is 43.

The most completely represented groups are 1 and 2; there are no occurrences of species of the early European forest and Eastern European steppe fauna (groups 3 and 6). Nor are there any Turanian forms in the complex (groups 4 and 9).

494 The ancient Caucasian and widely distributed species (group 1) are poorly represented as compared with the composition of the same group in the Caucasian district. In the Sevan subdistrict they consist of Transcaucasian hedgehog, Caucasian mole, Caucasian shrew, pocketed bats, noctules, southern bear, Caucasian birch mouse, Caucasian snow vole and roe deer.

Up to the present time in the Holocene, 5 species of hoofed mammals have become extinct: boar, deer, chamois, bison and primitive bull. Some of these always inhabited the subdistrict, some migrated from the forest zone of the northern slopes of the Lesser Caucasus.

With the exception of bats and carnivores, the species listed were, and still are, inhabitants of the most mesophytic, even hydrophytic, biotopes on elevated parts of the subdistrict: the banks of streams, springs, marshes and relict broadleaf forests. Lynx and bear inhabit relict oak forests.

Of the ancient Pliocene species of Iranian-Asia Minor or eastern Mediterranean origin (group 2), it is those which are associated with upland-steppe biotopes which inhabit the Sevan subdistrict. There is a poor representation of upland-desert species: long-eared hedgehog, Persian white-toothed shrew, horseshoe bats, stone marten, European hare and pika (now extinct), William's jerboa, Asia Minor suslik, lesser mole rat, Asia Minor hamster, Asia Minor snow vole, Shidlovskii's steppe vole, Bezoar goat and mouflon. The horse and possibly the dromedary became extinct in the Holocene.

The Asia Minor suslik and lesser mole rat now inhabit only the western part of the subdistrict although their distribution on the plateau has fluctuated considerably throughout the Holocene.

In some parts of the subdistrict, the ranges of species of groups 1 and 2 form a mosaic pattern which is caused by the mountainous relief.

There are no occurrences of early European forest, steppe and hydrophilous forms and central Asian desert and semidesert species. The subdistrict is inhabited by some species of northern (European?) origin which migrated there only in the Pleistocene (group 5). These species include the common vole (?), which inhabits the subalpine meadows, and the Caucasian wildcat, which inhabits the relict forests. At the present stage, it is difficult to identify any species which can be considered postglacial immigrants (group 8), although there were probably some belonging to various orders. It seems particularly probable that some bats resettled in the Armenian Highland following the Upper Pleistocene cooling, and that some southern carnivores (striped hyena, lion, tiger) began to migrate there seasonally.

The desert ungulates — kulan and goitered gazelle — probably also migrated from time to time to the gently sloped steppe sections of the plateau from the middle Araks valley.

Of the latest synanthropic immigrants, it is worth noting the Norway rat and house mouse.

The development of the ecological assemblages and mammalian complex of the Sevan subdistrict in the Quaternary proceeded under intensive orogenic conditions, accompanied by faulting and extensive lava flows which covered the western part of the country in various directions.

The Pleistocene glaciation of the highlands was not extensive and did not figure significantly in the development of the local mammalian complex. Man's settlement, which began in the Acheulean and developed through the Bronze and Iron Ages, was the chief reason for the disappearance of large mammals from the subdistrict.

495 Within the Sevan subdistrict an isolated sector can be distinguished in the cold Akhalkalaki highland — Satunin's "district of the sources of the Kura River." This sector differs from the rest of the subdistrict in the presence of lesser mole rat and of Caucasian snow vole and Caucasian birch mouse in the Mokrye Gory mountains, which form the northeastern boundary of the sector. The cold climate and the availability of spring water on the Dzhavakhetian Plateau created conditions favorable for the development of such species as water shrew and common vole. Conversely these reasons are also accountable for the absence of steppe vole. The naturally treeless landscape and low relief of the plateau hastened the early displacement of large carnivores and ungulates by man.

Kura subdistrict

(Subdistrict of steppe vole and red-tailed Libyan gerbil)

The Kura subdistrict is located between the eastern parts of the Caucasian district and most of it coincides with the areas of wormwood—saltwort semidesert and beard-grass steppes in the lowlands of eastern Transcaucasia. It is shaped like a wedge extending to the foot of the Surami ridge and bounded by the Caspian in the east.

Between Karabakh and Talysh it grades into the western Iranian subdistrict of the southwest Asian district.

The various parts of the subdistrict differ in geologic age. The eastern part at 20 m below sea level was probably covered by the Holocene sea; areas lying 30-40 m above sea level were covered by the Khvalynsk, Khazar and Baku seas. The foothills and piedmont plains of the Lesser and Greater Caucasus and the entire valley of the middle Kura, from Mingechaur to Gori, are of Late Tertiary age.

The landscape and geobotanical zones can be described as follows: level areas of saltwort—wormwood semidesert; ephemeretum and beard-grass steppes; tugai forests on the Kura, Araks and their tributaries; reed vegetation around lakes and in floodplains; and pistachio-juniper forests on the eroded clayey ridges ("bozdags") of the northern slopes. The age of this landscape is at least Lower Pleistocene, and its early stages of formation were probably in the Upper Pliocene.

The Kura subdistrict cannot be rated as impoverished and undersaturated in species, as zoogeographers have sometimes done because of the young age of the Kura-Araks lowlands and their recent emergence from the sea waters. Only the group of mammals of the southwest Asian uplands, which was the ancient core of the developing local complex, can be considered poor in species. And only the biotope of the open plain semidesert, particularly the Shirvan steppe, can be regarded as undersaturated in species. The mammalian complex consists of representatives of genetic groups 1, 2, 4, 8 and 10.

There are at least 25 species of the Caucasian mesophilous and widely distributed species (group 1) in the subdistrict. The most characteristic are: Caucasian mole, black rat, boar and deer which occur in relict mesophytic habitats (tugai, oases, reed marshes, etc.). The carnivores are represented by widely distributed forms: wolf, little fox, weasel, badger, otter and bear.

496 The nucleus of this subdistrict comprises up to 22 species of Pliocene age (group 2).

The ranges of most of these species extend south, southeast and southwest thereby corroborating our delineation of this subdistrict. The index insectivore species (long-eared hedgehog, long-tailed white-toothed shrew and lesser shrew) are characteristic of the dry biotopes of the open semidesert.

The index Chiroptera (up to 9 species) inhabit caves and buildings and feed in tugai areas and the margins of oases. The most commonly occurring species in the Kura subdistrict are horseshoe bats, Mediterranean (Kühl's) vespertilio, tiger polecat and African wildcat, whose ranges penetrate the Caucasian Isthmus from the south in this part of eastern Transcaucasia. Cheetah recently became extinct.

The characteristic ranges of the southwest Asian rodents (up to 6 species) are either relicts (as in the case of Asia Minor [William's] jerboa and Transcaucasian hamster) or poorly developed (as in the case of Asia Minor gerbil). The most numerous of these species are migratory hamster, red-tailed Libyan gerbil and steppe vole.

There is a possibility that the subdistrict was still inhabited in the Holocene by horses of the perissodactyls, and by argali of the artiodactyls.

There are no representatives of group 3 (European) in the subdistrict.

Species of Pliocene age — eastern, Turanian and Turanian-Afghan (groups 4 and 9) — are not numerous. In this respect the mammalian complex in this area evidently differs significantly from the insect complex, particularly the beetle complex (see Semenov-Tyan-Shanskii, 1936). Neither ancient nor younger Turanian species of insectivores, lagomorphs, perissodactyls and artiodactyls occur in the subdistrict.

The small five-toed jerboa, which mainly inhabits the ephemeretum semidesert of the Apsheron and Kabristan, may be the only representative of the early immigrants originating in Turan.

It will be recalled that some of the species of the Russian Plain (corsac fox, great jerboa, saiga) migrated to this area in the Middle Pleistocene.

There are only 6-7 of the southern thermophilous species which migrated to the Isthmus in postglacial time (group 8). It is possible that this group should include some small insectivores and bats which we have categorized as Pliocene immigrants.

The late appearance of jackal, stripped hyena, goitered gazelle, tiger, lion and kulan is beyond doubt; of these, the last three are completely extinct. The accidentally introduced species which have inhabited the area during the historical epoch include Norway rat, a contemporary inhabitant of lake and marsh environs and of all large population centers.

Present-day agricultural activity promotes further saturation of this subdistrict with small Caucasian species.

SUBREGION OF EASTERN EUROPE AND NORTH KAZAKHSTAN

EASTERN EUROPEAN DISTRICT

Ciscaucasian subdistrict

(Subdistrict of common hamster and striped field mouse)

The ranges of the index species of this subdistrict developed from the north, and we have, therefore, drawn a purely conditional northern
497 boundary along the Manych. The western boundary follows the seacoast from the lower Don to the mouth of the Kodor. In western Transcaucasia, only the narrow belt of the coastal terraces over which some Eastern European species migrated from the south falls into this subdistrict. The southern boundary coincides at all points with the northern boundary of the Caucasian district. The eastern boundary, starting from the lower Kalaus in the north, follows the middle Kuma to the Terek near Mozdok, bypassing the lower reaches of the Terek on the north and terminating at

(498) TABLE 103. Species and geographic distribution of Holocene mammals on the Caucasian Isthmus

<table>
<tr><th rowspan="4">Species</th><th colspan="4">Eastern Mediterranean</th></tr>
<tr><th colspan="4">Caucasian district</th></tr>
<tr><th rowspan="2">Greater Caucasus subdistrict</th><th rowspan="2">Dagestan subdistrict</th><th rowspan="2">Lesser Caucasus subdistrict</th><th>Asterabad subdistrict</th></tr>
<tr><th>Talysh forest sector</th></tr>
<tr><td>European (common) hedgehog — Erinaceus europaeus L.</td><td>concolor Martin</td><td>rumanicus Barr. et Ham.</td><td colspan="2">transcaucasicus Sat.</td></tr>
<tr><td>Long-eared hedgehog — Hemiechinus auritus Gm.</td><td>—</td><td>—</td><td>—</td><td>—</td></tr>
<tr><td>Eastern mole — Talpa orientalis Ogn.</td><td>orientalis Ogn.</td><td>—</td><td>transcaucasica Dahl.</td><td>talyschensis N. Ver.</td></tr>
<tr><td>Caucasian mole — Talpa caucasica Sat.</td><td>caucasica Sat., ognevi Strog.</td><td>—</td><td>ognevi Strog.</td><td>—</td></tr>
<tr><td>Common desman — Desmana moschata L.</td><td>—</td><td>—</td><td>—</td><td>—</td></tr>
<tr><td>Lesser shrew — Sorex minutus L.</td><td colspan="4">volnuchini Ogn.</td></tr>
<tr><td>Common shrew — Sorex araneus L.</td><td colspan="3">caucasicus Sat.</td><td>—</td></tr>
<tr><td>Caucasian shrew — Sorex raddei Sat.</td><td colspan="3">raddei Sat.</td><td>—</td></tr>
<tr><td>Water shrew — Neomys fodiens Schr.</td><td>balearicus Ogn., schelkovnikovi Sat.</td><td>dagestanicus Hept. et Form.</td><td>leptodactylus Sat.</td><td>—</td></tr>
<tr><td>Little white-toothed shrew — Crocidura suaveolens Pall.</td><td>—</td><td>dinnicki Ogn.</td><td>—</td><td>—</td></tr>
<tr><td>White-bellied white-toothed shrew — Crocidura leucodon Herm.</td><td>+</td><td>—</td><td>+</td><td>—</td></tr>
<tr><td>Long-tailed white-toothed — shrew — Crocidura russula Herm.</td><td>monacha Thos.</td><td colspan="2">güldenstaedti Pall.</td><td>caspica Thos.</td></tr>
<tr><td>Gray white-toothed shrew — Crocidura lasia Thos.</td><td>lasia Thos.</td><td>—</td><td>lasia Thos.</td><td>—</td></tr>
<tr><td>Persian white-toothed shrew — Crocidura zarudnyi Ogn.</td><td>—</td><td>—</td><td>—</td><td>—</td></tr>
<tr><td>Pygmy white-toothed shrew — suncus etruscus Savi</td><td>—</td><td>—</td><td>—</td><td>—</td></tr>
<tr><td>Great horseshoe bat — Rhinolophus ferrum-equinum Schr.</td><td>+</td><td>—</td><td>+</td><td>+</td></tr>
<tr><td>Mehely's horseshoe bat — Rhinolophus mehelyi Matschi</td><td>—</td><td>—</td><td>+</td><td>—</td></tr>
<tr><td>Southern horseshoe bat — Rhinolophus euryale Blas.</td><td>nordmanni Sat.</td><td>—</td><td>+</td><td>—</td></tr>
</table>

Note: Asterisk (*) indicates species which became extinct during the last centuries and decades of the present

subregion				Eastern European steppe subregion	Central Asian desert subregion
Southwest Asian district				Eastern European district	Western district
Western Iranian subdistrict		Sevan subdistrict	Kura subdistrict	Ciscaucasian subdistrict	Northern Caspian subdistrict
Araks sector	Upland Talysh steppe sector				Terek-Kuma sector
transcaucasicus Sat.				rumanicus Barr. et Ham.	
calligoni Sat.		brachyotis Sat.		auritus Gmel.	
—	—	transcaucasica Dahl.	—	—	—
—	—	—	caucasicus Sat.		—
—	—	—	—	+	—
—	—	—	—	—	—
—	—	—	—	caucasicus Sat.	—
—	—	raddei Sat.	—	—	—
—	—	leptodactylus Sat.		balearicus Ogn.	—
—	—	—	—	dinnicki Ogn.	suaveolens Pall.
persica Thos.				+	+
güldenstaedti Pall.				—	—
—	—	—	—	—	—
zarudnyi Ogn.		—	—	—	—
—	—	—	+	—	—
+	—	—	+	+	—
—	—	+	+	+	—
+	—	—	+	—	—

era. Plus sign (+) indicates nominal forms and forms not identified closer.

(500) TABLE 103 (continued)

Species	Eastern Mediterranean			
	Caucasian district			
	Greater Caucasus subdistrict	Dagestan subdistrict	Lesser Caucasus subdistrict	Asterabad subdistrict
				Talysh forest sector
Small horseshoe bat — Rhinolophus hipposideros Bechst.	+	—	—	+
Blasius' horseshoe bat — Rhinolophus blasii Peters.	—	—	—	—
Bechstein's mouse-eared bat — Myotis bechsteinii Kühl	+	—	—	—
Tricolor mouse-eared bat — Myotis emarginatus Geoffr.	+	—	—	—
Sharp-eared mouse-eared bat — Myotis oxygnathus Mont.	+	+	+	—
Whiskered mouse-eared bat — Myotis mystacinus Kühl	+	—	+	+
Natterer's mouse-eared bat — Myotis nattereri Kühl	+	+	—	—
Long-winged bat — Miniopterus schreibersii Kühl	+	—	+	—
Long-eared bat — Plecotus auritus L.	wardi Thos.	—	+	—
Asiatic barbastel — Barbastella darjelingensis Dobs.	—	+	—	—
European barbastel — Barbastella barbastellus Schr.	+	+	+	—
Leisler's noctule — Nyctalus leisleri Kühl	+	—	—	—
Giant noctule — Nyctalus siculus Palumbo	+	—	+	—
Common noctule — Nyctalus noctula Schr.	+	—	+	—
Pipistrel — Vespertilio pipistrellus Schr.	+	+	+	+
Nathusius' vespertilio — Vespertilio nathusii Keys. et Blas.	+	—	+	+
Kühl's vespertilio — Vespertilio kühlii Kühl	—	—	—	—
Savi's vespertilio — Vespertilio savii Bonap.	caucasicus Sat.	—	—	—
Bicolor vespertilio — Vespertilio murinus L	+	—	+	+
Bobrinskii's vespertilio — Vespertilio bobrinskii Kuz.	—	—	—	—
Northern vespertilio — Vespertilio nilssonii Keys. et Blas.	—	—	—	—

subregion				Eastern European steppe subregion	Central Asian desert subregion
Southwest Asian district				Eastern European district	Western district
Western Iranian district		Sevan subdistrict	Kura subdistrict	Ciscaucasian subdistrict	Northern Caspian subdistrict
Araks sector	Upland Talysh steppe sector				Terek-Kuma sector
+	−	−	+	+	−
+	−	−	+	−	−
−	−	−	−	−	−
−	−	−	+	−	−
+	−	+	+	+	−
+	−	+	+	+	−
araxenus Dahl	−	+	−	−	−
+	−	−	+	−	−
+	−	+	+	−	−
−	−	+	+	−	−
−	−	+	+	−	−
−	−	−	−	+	−
−	−	−	−	−	−
+	−	−	+	+	−
+	−	+	+	+	−
+	−	−	+	−	−
+	−	−	+	−	−
−	−	−	caucasicus Sat.	−	−
+	−	−	+	+	−
−	−	−	−	+	−
−	−	−	+	−	−

TABLE 103 (continued)

Species	Eastern Mediterranean			
	Caucasian district			
	Greater Caucasus subdistrict	Dagestan subdistrict	Lesser Caucasus subdistrict	Asterabad subdistrict
				Talysh forest sector
Serotine vespertilio — Vespertilio serotinus Schr.	+	+	+	+
Ognev's vespertilio — Vespertilio ognevi Bobr.	–	–	–	–
Pocketed bat — Tadarida taeniotis Raf.	–	–	+	–
Jackal — Canis aureus L.	+	–	+	+
Wolf — Canis lupus L.	cubanensis Ogn.	+	+	+
Fox — Vulpes vulpes L.	caucasica Dinn.		alticola Ogn.	+
Corsac fox — Vulpes corsac L.	–	–	–	–
Striped hyena — Hyaena hyaena L	–	–	–	–
European brown bear — Ursus arctos L.	caucasicus Smirn., arctos L.		meridionalis Midd.	
Pine marten — Martes martes L.	lorenzi Ogn.	–	lorenzi Ogn.	–
Stone marten — Martes foina Erxl.	nehringi Sat.			
Tiger polecat — Vormela peregusna Güld.	–	–	–	–
Polecat — Putorius putorius L.	–	–	–	–
Siberian polecat — Putorius eversmanni Less.	–	–	–	–
Mink — Lutreola lutreola L.	turovi Kuzn. et Nov.	–	–	–
Weasel — Mustela nivalis L.	caucasica Barr. et Ham.			
Ermine — Mustela erminea L.	+?	–	–	–
Badger — Meles meles L.	caucasicus Ogn.		canescens Blanf.	
Otter — Lutra lutra L.	+	+	+	+
* Tiger — Panthera tigris L.	–	–	–	septentrionalis Sat.
* Lion — Panthera leo L	–	–	–	–
Panther — Panthera pardus L.	ciscaucasicus Sat.		tullianus Valenc.	
African wildcat — Felis lybica Forst.	–	–	–	–
European wildcat — Felis silvestris Schr.	caucasicus Sat.			–
Manul — Otocolobus manul Pall.	–	–	–	–

subregion				Eastern European steppe subregion	Central Asian desert subregion
Southwest Asian district				Eastern European district	Western district
Western Iranian subdistrict		Sevan subdistrict	Kura subdistrict	Ciscaucasian subdistrict	Northern Caspian subdistrict
Araks sector	Upland Talysh steppe sector				Terek-Kuma sector
+	—	—	+	+	+
+	—	—	+	—	—
—	—	—	—	+	—
+	—	—	+	+	+
+	+	hajastanicus Dahl.	+	+	+
alpherakyi Sat.	+	kurdistanica Sat.	alpherakyi Sat.	stepensis Braun, caucasica Dinn.	karagan Erxl.
—	—	—	—	kalmykorum Ogn.	
*	—	—	satunini Matschi	*	—
—	—	meridionalis Midd.		* arctos L.	—
—	—	—	—	—	—
nehringi Sat.				nehringi Sat.	—
+	+	+	+	+	+
—	—	—	—	+?	—
—	—	—	—	+	+
—	—	—	—	turovi Kuzn. et Nov.	—
caucasica Barr. et Ham.				dinniki Sat.	
—	—	—	—	+?	+?
minor Sat.				caucasicus Ogn.	heptneri Ogn.
+	—	+	+	+	+
—	—	—	—	—	—
*	—	—	*	—	—
tullianus Valenc.				*	—
+	—	—	+	—	—
—	—	—	—	caucasicus Sat.	—
		*			
+	—	—	—	—	—

TABLE 103 (continued)
(504)

Species	Eastern Mediterranean			
	Caucasian district			
	Greater Caucasus subdistrict	Dagestan subdistrict	Lesser Caucasus subdistrict	Asterabad subdistrict
				Talysh forest sector
Jungle cat — Felis chaus Güld.	+	—	+	+
Lynx — Felis lynx L.	orientalis Sat.			
• Cheetah — Acinonyx jubatus Schr.	—	—	—	—
European hare — Lepus europaeus L.	caucasicus Ogn.		cyrensis Sat.	
• Armenian pika — Ochotona sp.	—	—	—	—
Persian (Caucasian) squirrel — Sciurus anomalus Güld.	+	—	+	—
Little suslik — Citellus pygmaeus Pall.	musicus Men.	—	—	—
Asia Minor suslik — Citellus citellus L.	—	—	—	—
• European beaver — Castor fiber L.	•	—	—	—
Fat dormouse — Glis glis L.	tschetschenicus Sat.		+	persius Erxl.
Forest dormouse — Dyromys nitedula Pall.	caucasica Ogn. et Turov	ognevi Hept. et Form.	pictus Blanf.	
Southern birch mouse — Sicista subtilis Pall.	—	—	—	—
Northern birch mouse — Sicista betulina Pall.	strandi Form.	—	—	—
Caucasian birch mouse — Sicista caucasica Vinogr.	+	+	+	—
Small five-toed jerboa — Allactaga elater Licht.	—	—	—	—
Great jerboa — Allactaga jaculus Pall.	—	—	—	—
William's (mountain) jerboa — Allactaga williamsi Thos.	—	—	—	—
Little earth hare — Alactagulus acontion Pall.	—	—	—	—
Thick-tailed three-toed jerboa — Scirtopoda telum Licht.	—	—	—	—
Northern three-toed jerboa — Dipus sagitta Pall.	—	—	—	—
Russian mole rat — Spalax microphthalmus Güld.	—	—	—	—

subregion				Eastern European steppe subregion	Central Asian desert subregion
Southwest Asian district				Eastern European district	Western district
Western Iranian subdistrict		Sevan subdistrict	Kura subdistrict	Ciscaucasian subdistrict	Northern Caspian subdistrict
Araks sectors	Upland Talysh steppe sector				Terek-Kuma sector
+	—	—	+	+	—
—	—	orientalis Sat.	—	* orientalis (?) Sat.	—
*	—	—	*	—	—
cyrensis Sat.				caucasicus Ogn.	
—	—	*	—	—	—
—	—	—	—	—	—
—	—	—	—	kalabuchovi Ogn., satunini Svirid., boehmi Krass.	planicola Sat.
xanthoprymnus Benn.	—	xanthoprymus Benn.	—	—	—
—	—	—	*	*	—
—	—	—	—	+	—
pictus Blanf.			tichomirovi Sat.	daghestanicus Ogn. et Turov.	—
—	—	—	—	nordmanni Keys. et Blas.	—
—	—	—	—	—	—
—	—	—	—	—	—
aralychensis Sat.	—	—	caucasicus Nehr.	—	kizljaricus Sat.
—	—	—	—	jaculus Pall., fuscus Ogn.	fuscus Ogn.
—	williamsi Thos.		schmidti Sat.	—	—
—	—	—	—	dinniki Sat.	—
—	—	—	—	turovi Hept.	
—	—	—	—	nogai Sat.	
—	—	—	—	+	—

TABLE 103 (continued)

Species	Eastern Mediterranean			
	Caucasian district			
	Greater Caucasus subdistrict	Dagestan subdistrict	Lesser Caucasus subdistrict	Asterabad subdistrict
				Talysh forest sector
Giant Russian mole rat — Spalax giganteus Nehr.	—	—	—	—
Lesser mole rat — Spalax leucodon Nordm.	—	—	—	—
Black rat — Rattus rattus L.	+	—	+	+
Norway rat — Rattus norvegicus Berck.	colchicus Lvov	+	+	+
House mouse — Mus musculus L.	formosovi Heptn., abbotti Waterh.		abbotti Waterh.	tataricus Sat.
Harvest mouse — Micromys minutus Pall.	—	—	—	—
Striped field mouse — Apodemus agrarius Pall.	caucasicus Duk.	—	—	—
Caucasian yellow-spotted mouse — Apodemus fulvipectus Ogn.	ponticus Svirid.	saxatilis Krass.	argiropuli Vin. et Arg.	—
Yellow-necked field mouse — Apodemus flavicollis Melch.	—	—	—	—
Common field mouse — Apodemus sylvaticus L.	ciscaucasicus Ogn.		arianus Blanf.	
Broad-toothed field mouse (Asia Minor mouse) — Apodemus mystacinus Danf. et Alst.	euxinus G. Allen	—	euxinus G. Allen	—
Asia Minor (golden) hamster — Mesocricetus auratus Waterh.	koenigi Sat.	raddei Nehr., avaricus Ogn. et Heptn.	brandti Nehr.	—
Common hamster — Cricetus cricetus L.	+	—	—	—
Migratory (gray) hamster — Cricetulus migratorius Pall.	pulcher Ogn.		+	—
Mouse-like hamster — Calomyscus bailwardi Thos.	—	—	—	—
Great gerbil — Rhombomys opimus Licht.	—	—	—	—
Midday gerbil — Meriones meridianus Pall.	—	—	—	—
Red-tailed Libyan gerbil — Meriones erythrourus Gray	—	—	—	—
Persian gerbil — Meriones persicus Blanf.	—	—	—	—

subregion				Eastern European steppe subregion	Central Asian desert subregion
Southwest Asian district				Eastern European district	Western district
Western Iranian subdistrict		Sevan subdistrict	Kura subdistrict	Ciscaucasian subdistrict	Northern Caspian subdistrict
Araks sector	Upland Talysh steppe sector				Terek-Kuma sector
–	–	–	–	+	–
–	–	armeniaca Mehely, nehringi Sat.	–	–	–
–	–	–	+	+	+
+	+	+	+	+	+
tataricus Sat.		abbotti Waterh.	tataricus Sat.	hortulanus Nordm.	wagneri Eversm., nogaiorum Heptn.
–	–	–	–	+	+
–	–	–	–	caucasicus Duk.	–
–	–	–	–	planicola Svirid.	–
–	–	–	–	samariensis Ogn.	
arianus Blanf.				ciscaucasicus Ogn.	–
–	–	–	–	–	–
–	brandti Nehr.			nigriculus Nehr.	–
–	–	–	–	stavropolicus Sat.	–
+	+	+	+	pulcher Ogn.	phaeus Pall.
+	–	–	–	–	–
–	–	–	–	–	*
–	–	–	–	–	nogaiorum Heptn.
+	–	–	caucasicus Brandt.	–	–
rossicus Heptn.		–	–	–	–

(508) TABLE 103 (continued)

Species	Eastern Mediterranean			
	Caucasian district			
	Greater Caucasus subdistrict	Dagestan subdistrict	Lesser Caucasus subdistrict	Asterabad subdistrict
				Talysh forest sector
Tamarisk gerbil — Meriones tamariscinus Pall.	—	—	—	—
Asia Minor gerbil — Meriones blackleri Thos.	—	—	—	—
Vinogradov's gerbil — Meriones vinogradovi Heptn.	—	—	—	—
Arazdayan gerbil — Meriones sp.	—	—	—	—
Steppe lemming — Lagurus lagurus Pall.	—	—	—	—
Northern mole vole — Ellobius talpinus Pall.	+	—	—	—
Transcaucasian mole vole — Ellobius lutescens Thos.	—	—	—	—
Promethean vole (long-clawed mole vole — Prometheomys schaposchnikovi Sat.	+	—	+	—
Water vole — Arvicola terrestris L.	ognevi Tur., rufescens Sat., turovi Ogn.	djukovi Ogn. et Form., kuruschi Heptn. et Form.	persicus de Fil.	
Asia Minor snow vole — Microtus nivalis Mart.	loginovi Ogn.	—	trialetcus Schidl.	—
Caucasian snow vole — Microtus gud Sat.	nenjukovi Form., gud Sat.	lghesicus Schidl., oseticus Schidl.	+	—
Long-tailed snow vole — Microtus roberti Thos.	personatus Ogn.	+	+	—
Pine vole — Microtus majori Thos.	colchicus Schidl., ciscaucasicus Ogn.	daghestanicus Schidl.	intermedius Schidl.	schelkovnikovi Sat.
Common vole — Microtus arvalis Pall.	macrocranius Ogn., gudauricus Ogn.		transcaucasicus Ogn.	—
Steppe vole — Microtus socialis Pall.	—	—	—	+
Common red-backed vole — Clethrionomys glareolus Schr.	* ponticus Thos.	—	—	—
Porcupine — Hystrix leucura Sykes	—	—	hirsutirostris Brandt	
* Kulan (Asiatic wild ass) — Equus hemionus Pall.	—	—	—	—
* Tarpan — Equus caballus gmelini Ant.	—	—	—	—

subregion				Eastern European steppe subregion	Central Asian desert subregion
Southwest Asian district				Eastern European district	Western district
Western Iranian subdistrict		Sevan subdistrict	Kura subdistrict	Ciscaucasian subdistrict	Northern Caspian subdistrict
Araks sector	Upland Talysh steppe sector				Terek-Kuma sector
–	–	–	–	–	ciscaucasicus Sat.
bogdanovi Heptn.		–	bogdanovi Heptn.	–	+
+	–	–	–	–	–
+	–	–	–	–	–
–	–	–	–	+	–
–	–	–	–	+	+
+	+	–	–	–	–
–	–	–	–	–	–
persicus de Fil.				caucasicus Ogn., cubanensis Ogn.	+
–	–	satunini Schidl.	–	–	–
–	–	–	–	–	–
–	–	–	–	–	–
–	–	–	–	–	–
–	mystacinus de Fil.	transcaucasicus Ogn.	–	macrocranius Ogn.	
+	+	schidlovskii Arg.	binominatus Ellerm.	parvus Sat.	
–	–	–	–	–	–
–	–	–	–	–	–
*	*	*	*	*	*
–	–	–	–	*	*

(510) TABLE 103 (continued)

Species	Eastern Mediterranean			
	Caucasian district			
	Greater Caucasus subdistrict	Dagestan subdistrict	Lesser Caucasus subdistrict	Asterabad subdistrict
				Talysh forest sector
* Southwest Asian horse — Equus caballus L (subsp.)	—	—	—	—
Boar — Sus scrofa L.	attila Thos.			
Red deer — Cervus elaphus L.	maral Ogilby			*
* Elk — Alces alces L.	* caucasicus N. Ver.	—	—	—
Roe deer — Capreolus capreolus L.	capreolus L., pygargus Lyd.		capreolus L.	
Saiga — Saiga tatarica L.	—	—	—	—
Goitered gazelle — Gazella subgutturosa Güld.	—	—	—	—
Chamois — Rupicapra rupicapra L.	caucasica Lyd.			—
West Caucasian goat — Capra caucasica Güld.	caucasica Güld., severtzovi Menzb., dinniki Sat.	—	—	—
East Caucasian goat — Capra cylindricornis Blyth	+	+	—	—
Bezoar goat (wild goat or ibex) — Capra aegagrus Erxl.	+	+	+	—
Armenian mouflon — Ovis gmelini Blyth	—	*	—	—
* Caucasian bison — Bison bonasus L.	caucasicus Sat.	*	—	—
* Primitive bull — Bos primigenius Boj.	—	—	—	—

the Caspian coast near Makhachkala (Figure 195).

The various sections of the subdistrict differ in geologic age. The youngest are the Kuban and Manych plains and the lower reaches of the Terek and Sulak; the oldest are the Stavropol Plateau and the sloping piedmont plains, which are made up of Maikop (Oligocene), Upper Sarmatian (Miocene), Apsheron (Pliocene) and Quaternary formations.

The primeval postglacial landscapes are diversified in their features and in their origins. To the north in the Manych area, sheep's fescue and wormwood steppes predominate; the piedmont plains in the western area are characterized by steppe meadows, mesophytic meadows and forest steppe with islands of broadleaf forest and tugai-type forest growing along

(511)

subregion				Eastern European steppe subregion	Central Asian desert subregion
Southwestn Asian district				Eastern European district	Western district
Western Iranian subdistrict		Sevan subdistrict	Kura subdistrict	Ciscaucasian subdistrict	Northern Caspian subdistrict
Araks sector	Upland Talysh steppe sector				Terek-Kuma sector
*	*	*	?	—	—
		attila Thos.			attila Thos.
—	—	*	maral Ogilby		
—	—	*	—	* caucasicus N. Ver.	—
—	—	capreolus L.	—	* pygargus Lyd.	—
—	—	—	—	+	+
*	*	—	+	*	*
—	—	—	—	—	—
—	—	—	—	—	—
—	—	—	—	—	—
+	*	+	—	—	—
armeniana Nas.			—	—	—
—	*	—	—	—	—
—	—	*	—	*	—

the river floodplains. Steppes developed on a considerable scale on the Trans-Kuban and Terek-Sunzha plains during the xerothermal phase of the Holocene. At the beginning of the present epoch, forests began to cover the steppe areas (Zakharov, 1935). The typical landscape of the southeastern area is dry wormwood steppe which grades into saltwort semidesert. Thickets of reed, narrowleaf cattail and bulrush grow on the shores of the estuaries along the Azov and Caspian coasts and on the floodplains of the lower Kuban, Chelbas, Yeya, Terek and Sulak. These swampy areas are separated by sand spits covered with dry steppe vegetation and inhabited by jerboas, hamsters and hares. Tugai forests, alternating with plumegrass and licorice, remained intact only along the lower Terek and Sulak.

The mammalian complex of the subdistrict is not homogeneous: it comprises elements of genetic groups 1, 2, 3, 5, 6 and 8, of which groups 5 and 6 furnish the foundation of the complex.

The Caucasian Pliocene group is poor in species, consisting of European (common) hedgehog, Caucasian mole, lesser shrew, noctules and vespertilios, widely distributed carnivores, small rodents and ungulates (of which the only survivor is the boar). Caucasian bear, European beaver, Caucasian deer [maral: subspecies of red deer] and Caucasian bison became extinct in historical time.

There are 15 southern species, i.e., group 2, originating in southwest Asia: long-eared hedgehog, white-bellied white-toothed shrew, horseshoe bat; stone marten and tiger polecat among the carnivores; and a number of xerophilous rodents — medium hamster, steppe vole and others. Most of the species of this group inhabit the xerophytic biotopes of the foothills zone.

The ancient Eastern European species (group 3) are rare; they include desman and mole rat.

All the other extant species are later — Pleistocene and Holocene — immigrants to Ciscaucasia, primarily from the north: from the forests of Western Europe and the steppes of Eastern Europe.

Group 5 consists of 9-11 Pleistocene-age species of northern origin and characteristically of forest and mesophilous biotopes: Caucasian shrew,
510 mink, Caucasian wildcat, harvest mouse, striped field mouse, Samarian subspecies of yellow-necked field mouse, common hamster. Of those species which became extinct in historical time, the following are noteworthy: European brown bear, Caucasian elk, Caucasian large roe deer and, possibly, primitive bull.

The ranges of most of these species are close to the Caucasian foothills. The principal proof of their Pleistocene age on the Isthmus rests on their poorly-developed southeastern distribution, geological data and the history of the phytolandscapes. Since all of these species are inhabitants of relatively cold environments, it is doubtful that they could have migrated to the hot, arid south in pre-Baku time. The distribution of the Eastern European subspecies of yellow-necked mouse, which, so far as is known, is confined to the tugai sections of the Sulak, is somewhat enigmatic.

The steppe species of Eastern Europe (group 6) migrated to the subdistrict mainly during the Pleistocene. They are: lesser shrew, corsac fox, Siberian polecat, little suslik, southern birch mouse, great jerboa, northern three-toed jerboa, thick-tailed three-toed jerboa, steppe lemming and northern mole vole.

511 Marmot and tarpan are among the recently extinct species.

Some of these species (e.g., little suslik) invaded the upland steppes on the northern slope of the Caucasus; others (great jerboa and saiga) migrated in the Middle Pleistocene by way of the Caspian coast as far as eastern Transcaucasia.

The postglacial immigrants (group 8) comprise carnivores, perissodactyls and artiodacyls, and include jackal, jungle cat and such recently extinct forms as striped hyena, kulan and goitered gazelle. It is possible that lion, panther and cheetah inhabited the subdistrict in historical time.

The ranges of jackal and jungle cat within the subdistrict form a narrow strip along the river valleys and foothills of eastern Ciscaucasia.

FIGURE 195.

ZOOGEOGRAPHIC ZONATION OF THE CAUCASIAN ISTHMUS

Mammalia

The accidentally introduced species of the historical epoch are represented by Norway rat, which inhabits the floodplains of the Don, Kuban, Sulak and Terek, and is rapidly invading every settlement.

To the east and northeast, the subdistrict adjoins the semideserts and deserts of central Asia which are characterized by a mammalian complex better adapted to xerothermal conditions.

512 SUBREGION OF CENTRAL ASIAN DESERTS

WESTERN DISTRICT

North Caspian subdistrict

TEREK-KUMA SECTOR

(Sector of tamarisk gerbil and midday gerbil)

This sector encompasses the semideserts and deserts of the lower Kuma-Terek-Sulak interfluve. Its western boundary starts in the north at the Manych-Sarykamysh divide and continues southeasterly to the mouth of the Sunzha. The southern boundary crosses the lower Terek and Sulak and terminates on the Caspian coast near Makhachkala. The sector corresponds to that part of the Isthmus which was covered by the sea during the last major Khvalynsk transgression. Its northern half is made up of marine sediments of glacial time and is a level sandy-clayey semidesert. The southwestern third is in sandhills; the southeastern is composed of alluvial loams and clays of postglacial time. The youngest areas geologically are the northern half and the southeastern third, which were partly covered by the sea even during the minor transgressions of the Caspian in historical time. Most of the Terek-Kuma semidesert and desert is covered by wormwood—saltwort vegetation; the sandhills are covered by lopsided oat, wormwood and sweet clover; and the coasts of the Caspian estuaries are covered with reed thickets alternating with weeds on low elevations.

The nucleus of the Holocene mammalian complex of the sector is formed by group-6 and group-7 species; the complex is completed by species of groups 1, 2, 4, 8 and 9.

Group 1 is represented only by Palaearctic ubiquists which inhabit the interzonal biotopes; mesophilous Caucasian species of group 1 do not occur at all in this sector. Common hedgehog, wolf, weasel, badger, steppe mouse and boar inhabit reed-grown areas and hollows between sandhills. These species play no significant role in the biocenoses of this sector, however,

The only eastern Mediterranean xerophilous mammals (group 2) are the widely adapted species: long-eared hedgehog, white-bellied white-toothed shrew, tiger polecat, European hare, migratory hamster and steppe vole. The Russian mole rat has been replaced by giant Russian mole rat which occurs in isolated colonies in hollows between dunes. Small five-toed jerboa represents the ancient central Asian species (group 4).

The Eastern European steppe species (group 6) and Turanian species (groups 7 and 9), which inhabited the sector during the Pleistocene regressions of the ancient Caspian and in the Holocene, are represented by corsac fox, little suslik, jerboas and midday and tamarisk gerbils. Great gerbil, manul and tarpan became extinct in historical time, but saiga has survived in this sector.

The central Asian elements in this complex are comprised essentially of gerbils. Tarpan inhabited this sector longer than the Ciscaucasian subdistrict.

The southern, postglacial species (group 8) probably penetrated this sector from the south, and those from the northeast from central Asia. It can be assumed that the sector was inhabited in the Holocene by almost all the group-8 species which occurred in the Ciscaucasian subdistrict. Of these, only jackal and jungle cat survived until recent time.

513 A study of the mammalian fauna of the Terek-Kuma sector shows that it is essentially a part of the Aral-Caspian (central Asian) deserts, and not a part of the Caucasus zone. The animal assemblages of the sandhills in particular resemble the central Asian assemblages, e.g., the assemblage on the phenomenal Kumtorkala barchan* in the foothills of Dagestan.

The fluctuations in the sea level of the Quaternary Caspian affected the development of the mammalian complex of this sector more than that of any other Caspian area. This factor, as well as the bifurcation of the lower Volga, strongly influenced the migration of hibernating species from the east in the Quaternary.

This study of the faunal influences of adjacent territories and of the characteristics of the districts, subdistricts and sectors of the Caucasian Isthmus, based on the history of species distribution and paleogeographic data, reveals only a small part of the biological processes which took place during a time of complex change in the Cenozoic terrestrial environments around the Black and Caspian seas.

The geochronological continuity of the faunal influences, which we have noted, will certainly be better understood as paleontological data is accumulated and processes of speciation are analyzed. Nevertheless, the scheme presented here is justifiable at the present stage of zoogeographic knowledge.

The characteristics of the mammalian fauna given for each zonation also show the degree of its saturation with species. This opens avenues leading to new deductions on the restoration and enrichment of the fauna. The complete list of species (and subspecies) of the Holocene mammalian fauna of the Caucasian Isthmus is given in Table 103.(p. 500).

The effects of both casual and purposeful anthropogenic influence on the latest evolutionary patterns of mammalian ecological assemblages of the Isthmus, and on the changes in boundaries of the faunal complexes, are discussed in the next chapter.

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* [A symmetric dune with crescentic ground plan; gentler slope facing the wind on the convex side, and steeper slope on the concave or leeward side.]

ANTHROPOGENIC CHANGES IN MAMMALIAN ECOLOGICAL ASSEMBLAGES AND RANGES IN VARIOUS ZONES

Man's influence on the mammalian fauna of the Caucasus can be traced from Acheulean time by means of the kitchen middens of primitive tribes Here, as in other regions, the Paleolithic tribes were largely responsible for the extinction of a number of mammals and the reduction in range of others. The extent of the human influence on different species is difficult to gauge. The game of prehistoric hunters consisted largely of the widely distributed and most accessible species. For example, the chief game of Paleolithic tribes on the Trans-Kuban Plain was bison, followed by horse, mammoth, red and giant deer and cave hyena. On the Black Sea coast and and in central Transcaucasia, cave bear was the chief game, followed by boar and red deer. Bison and horse were hunted in the Lesser Caucasus highlands. Over the millennia, the species and their proportions in the game of Paleolithic hunters probably changed considerably from season to season. Many species of small animals, birds, reptiles and fish used for food may not be preserved in the paleontological record; they may well have been consumed immediately at the hunting site or at temporary camps.

Some of the animal species used for food by primitive Upper Pleistocene tribes in various parts of the Caucasus are given in Table 104. The proportions given probably relate more to the type of landscape than to the age of the site.

TABLE 104. Number of remains (in %) of predominating species of mammals at various Paleolithic sites in the Caucasus

Species	Northwestern Caucasus (Il'skaya)	Black Sea coast (Akhshtyrskaya)	Colchis (Sakazhia)	Lesser Caucasus upland (Zurtaketi)
Cave bear	2.6	57.3	5.0	–
Horse	6.5	–	2.5	50.0
Red deer	5.2	5.9	7.6	–
Primitive bison	56.0	2.9	26.5	16.6

515 In post-Paleolithic times, man's influence on the Caucasian mammals and their assemblages assumed many aspects:

1) direct extermination of game species by unrestricted hunting;

2) indirect influence on single species, their assemblages and ranges through changes in landscape, macro- and microclimate, soil and other ecological features caused by industrial and agricultural activity;

3) accidental introduction of synanthropic species;

4) planned changes in ecological assemblages effected by introducing and raising new species under natural conditions, breeding and protecting selected species and exterminating harmful species.

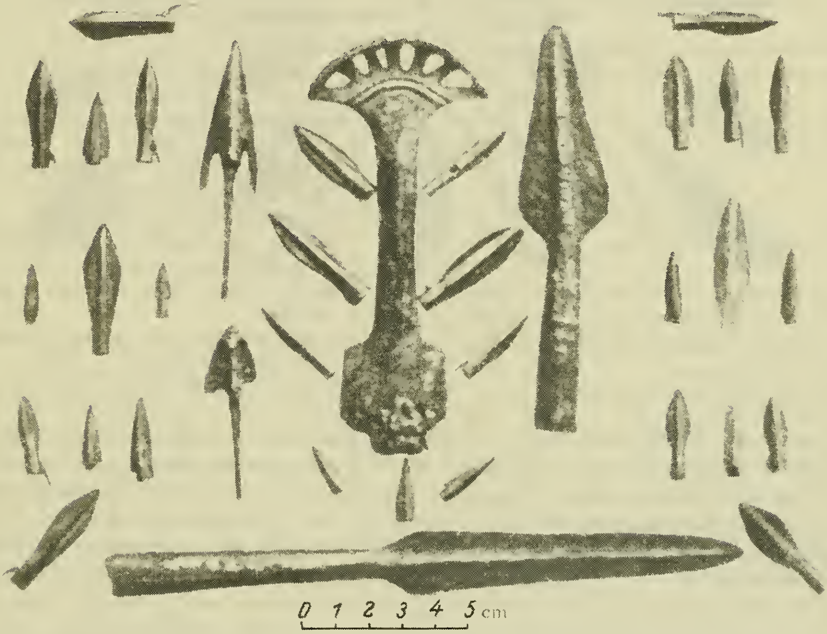


FIGURE 196. Bronze arrowheads and darts used in hunting and war from Late Bronze Age (darts) and Scythian-Sarmatian culture (Caucasian Museum collection)

As human population and dispersal areas grew and culture developed in post-Paleolithic time, the direct influence of man on the large wild mammals of the Caucasus increased rapidly.

The emergence of domesticated animals could not offset the magnitude of these effects. The decrease in the number of remains of wild animals which can be observed in post-Paleolithic cultural layers from Early to Recent is essentially the result of the development of animal husbandry, which is not to say that wild animals were hunted on any smaller scale (Table 105).

516 The direct extermination and population decrease of a number of game animals of the Caucasus during the last millennia was closely related to the history of the Caucasian tribes and peoples, their migrations and wars, and the development of their material culture, particularly weaponry.

TABLE 105. Number of bones of wild and domestic animals in post-Paleolithic localities, settlements and ritual sites of the Caucasus and the Russian Plain *

Monument and its age	Percentage of animal bones		Description
	wild	domestic	
Dzuars of North Ossetia. Digorized cave, 14th-19th centuries A.D.	18.95	81.05	Developed cattle raising; abundance of mountain-forest animals, killed with spears, bows and arrows, firearms.
Khazar fortress Belaya Vezha (Sarkel) on the Don, 8th-13th centuries A.D.	26.0**	74.0	Abundance of domestic cattle and wild steppe and forest animals, killed in safari-type hunt and by individual hunters.
Settlement near Baku Bay on the Apsheron, 9th-13th centuries A.D.	20.6	79.4	Abundance of domestic cattle, goitered gazelle, seals, migratory birds; developed hunting of goitered gazelle and kulan in game drives; seal hunting.
Ancient town of Semibratnoe, Kuban estuary, 4th century B.C. - 1st century A. D.	7.4	92.6	Developed raising of low-grade cattle; hunting more important as the town declined at the beginning of the present era.
Mud-hut settlements near Tsimlyanskaya on the Don, first millennium B.C.	20.0 28.9	71.1 80.0	Primitive cattle-raising; abundance of steppe ungulates.
Settlement near Kayakent in Dagestan, second millennium B.C.	16.2	83.8	Developed cattle-raising; hunting, including seal hunt, important.
Mud-hut settlements near Gelendzhik Bay, third millennium B.C.	34.2	65.8	Developed dolphin hunting; cattle-raising and hunting of forest animals.
Akhshtyrskaya cave, hunting site, Neolithic and later beds	46.3	53.7	Abundance of large forest animals in the vicinity of the cave.

* Unpublished author's materials.

** Percentage of bones of wild animals from Sarkel was artificially increased in the process of sorting for final identification.

Although we have plentiful archaeological and documentary materials on the Caucasus, it is difficult to trace the details in the evolution of hunting from the Paleolithic to the Recent. Ancient drawings on rocks in Kabristan and drawings on vessels from the Trialet and Maikop burials indicate that bows were widely used in the second and first millennia B.C.

517 Spears and bows were the chief weapons in the big-game hunting of the Koban, Colchis and later tribes (Figure 196). It is characteristic of medieval weaponry in the northern Caucasus that the iron arrowheads and darts used in combat and the hunt show remarkable variations in type (Figure 197).

The horse-mounted big-game drive was the principal hunting method used by the nomads of the Isthmus plains during the last three millennia, sometimes with either permanent or temporary fences or traps placed across gulleys and river valleys.

In addition to group hunting, individual game hunting was widely practiced in the forests and mountains.

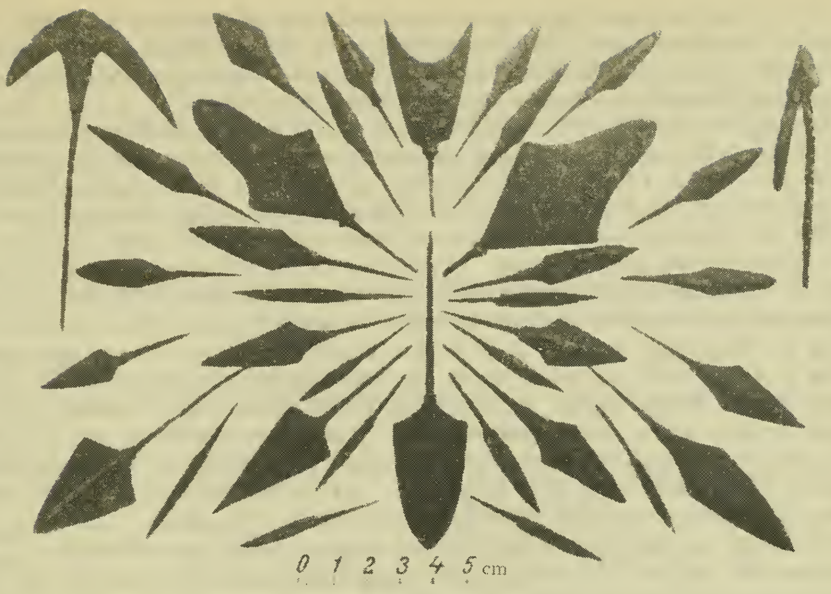


FIGURE 197. Iron arrowheads and darts from the Middle Ages — 7th-9th centuries A.D. (Caucasian Museum collection)

The sharp decrease in the large-animal population on the Caucasus undoubtedly occurred during the Middle Ages when the techniques of bow-manufacturing and forest and mountain hunting were at a very high level.

Large-scale hunting into late medieval time was made possibly by the conditions of a feudal society and by the existence of large bands of free armed men which provided the necessary manpower.

Rashid ad-Din, the Iranian chronicler of the 14th century (1946 edition), records a story of the expedition to Aladagh made by the "king of Islam," Ghazan-Khan (one of the Mongolian rulers of Iran). In the winter of 1301-02, Ghazan-Khan camped at Belesuvar (in the southern Kura-Araks lowland) and Khamashakhre, and from there he hunted in the mountain district en route to Talysh and Ispakhbad.

518 "Ghazan-Khan ordered the construction of two wooden fences in the mountains, each fence the length of one day's travel, which together would form a wedge fifty gyaz wide at the narrow end and one day's travel apart at the wide end. At the dead end the fences were to be closed off as a corral. After this the warriors drove the game — mountain buffalos, dzhurs, wild goats and asses, jackals, foxes, wolves, bears and other various wild and predatory beasts — between the fences until all were in the corral. The king of Islam was seated with Bulugan-Khatun on the stage which was built in the middle, and enjoyed the sight of the animals. Some were killed and some set free" (pp. 188-189).

From the latest Iranian chronicles, studied by Petrushevskii (1949, pp. 292-293), it is known that in the 16th-17th centuries in Iran, peasants were often called for a hunting duty — "shikari."

"Hunter-emirs assembled on the Shah's orders with the gentry ("mulyadzins") and men-at-arms ("nukers"), often as many as ten thousands or more. They enclosed the large area selected for the hunt to prevent the animals from escaping. The circumference of the enclosure gradually became smaller as the hunters moved into the area. The circumscribing line was called "dzherke," "negre" or "komarga" (p. 292).

"During the Shah's hunt in Mian-Kaleh in the forests of Mazandaran in 1028 (1618 A.D. — N. V.) the ring surrounding the animals was 3 farsangs (18–20 km — N. V.) long and 2/3 farsang (4–4.5 km — N. V.) wide. Before the beginning of the big hunt, the animals were driven for several days into the encircling ring. Hundreds and even thousands of large animals were killed during such hunting. In addition to the mounted warriors, foot soldiers were used to drive the animals. During the Shah's big hunt in the forests and thickets of Gilan (southern Caspian coast — N. V.) in the spring of 1002 (1564 A.D. — N. V.) nearly 10,000 peasants from among the people of Gilan were called to drive the animals into the dzherke" (p. 293).

During the Middle Ages, kulan and goitered gazelle were hunted in the middle Araks valley, and forest animals in northern Armenia and Georgia on a similarly grandiose scale, as described by Ananiah of Shirak in the "Book of Problems" (see Ter-Pogosyan, 1947), in Rustaveli's (1937) and Nizami's (1940) poems and in Prince Vakhusti's "Geography" (1904).

The large population of ungulates had already been considerably decreased by primitive hunting by the time firearms were discovered, introduced and perfected in the Caucasus.

The perpetual wars between small tribes and feudal lords occupying separate canyons and the local custom of blood revenge greatly accelerated the distribution of firearms, making them also generally available for hunting purposes during the last centuries.

With the decline in the animal population toward the 18th-19th centuries, large-scale hunting with fences and corrals was no longer feasible. But the introduction of small-gauge flint and percussion-type shotguns and rifles created new possibilities for individual hunting.

The Caucasian wars of the 19th century also contributed to the decimation of large animals.

The final stage in this development was the introduction of the four-
519 barreled Berdan rifle and, later, of the Mosin rifle — the Russian three-barreled rifle. The latter model created almost unlimited possibilities for shooting mountain ungulates from great distances. Cattle-herding from one pasture region to another, the arming of shepherds, and the shipment of large quantities of arms into the mountains during the Civil War (1917-1922) brought about the final stage in the destruction of the Caucasian populations of deer and bison.

The evolution of the distribution ranges of individual species of Caucasian mammals which is reviewed in Chapter IV shows the contributory role of man in the extinction of at least 9 species in the last thousand years (Table 106).

In addition to the forms mentioned above, deer, roe deer, goitered gazelle, saiga and other species have declined in population and distribution range (Vereshchagin, 1947).

Human activity indirectly affected the fauna of the Caucasian Isthmus in very complex and diversified ways through:

1) destruction of tugai, foothill and mountain forests by cutting, fires, cattle grazing and cultivation;

2) plowing and cultivation of steppes and semideserts, accompanied by irrigation and planting of groves, gardens and shelterbelts;

3) cattle driving which resulted in large-scale thinning of forests, mountain slope erosion and changes in the plant formations of mountain meadows, steppes, semideserts and deserts;

4) construction activity and development of mud-hut settlements, villages and larger towns with buildings of various types;

5) building of roads and railroads.

TABLE 106. Chronological order of disappearance (extinction) of some Caucasian mammals

Species	Probable time of disappearance	Area of last habitat
Lion	10th century	Eastern Transcaucasia
Primitive bull	12th century	Western Ciscaucasia
Kulan	13th century	Eastern Transcaucasia and (until the 18th century) eastern Ciscaucasia
Cheetah	13th century	Eastern Transcaucasia
Beaver	End of 19th century	Colchis and Trans-Kuban Plain
Elk	Beginning of 19th century	Ciscaucasia
Tarpan	1880's	Eastern Ciscaucasia
Bison	1920's	Western Caucasus
Tiger	1930's	Talysh

The formation of the secondary, or cultivated , man-made landscape caused the animals to develop new behavioral patterns and new assemblages adapted to the new conditions. These changes in the fauna followed the development of tribal economic life, cattle-raising, agricultural technology and industrialization. The relationships between species numbers within small-mammal assemblages (rodents and insectivores) were affected by particularly complex factors: the population dynamics from season to season and over long periods as they related to changes in biotopes brought
520 about by a variety of agricultural techniques, e.g., crop rotation, etc. (see Obolenskii, 1935; Polyakov, 1950, and others).

The direct and indirect effects of human activity on individual species, their ecological assemblages and faunal complexes is discussed below by geomorphological and phytolandscape districts with examples.

STEPPES AND SEMIDESERTS OF CISCAUCASIA

The typical primeval postglacial landscape of the Kuban Plain, lower Don, Manych area and steppe margins of the Stavropol area was one of motley-grasses—sheep's fescue—feathergrass and sheep's fescue—feathergrass steppes of the northern and southern type (Shiffers, 1953). The river valleys and steppe gulleys were developed with shrubs and leafy forests.

From the time of the Neolithic, the floodplain terraces were steadily settled by cattle-raising tribes. Mud-hut settlements and towns were quite common along the rivers in the Bronze and Iron ages (see Gorodtsov, 1935; Pokrovskii and Anfimov, 1937; Artamonov, 1937; Goretskii, 1948).

The spurs of the Taman Peninsula were widely colonized by the Greeks as early as the 6th century B.C. (Kallistov, 1949). The postglacial mammalian assemblages of the Ciscaucasian steppes were rich in species. The floodplain forests and reed thickets on the Don and Kuban were inhabited by wolf, bear, otter, European wildcat, panther, beaver, water rat, boar, roe deer, deer, elk, tur and bison. The steppe proper was inhabited by tarpan, kulan, saiga and goitered gazelle. The small-mammal assemblage of the virgin steppes of the Manych region included common and long-eared hedgehog, fox, corsac fox, Siberian polecat, marmot, little suslik, hamster, jerboa and mole rat.

It can be inferred from a comparison with the Recent and from historical data for adjacent regions (Barbaro, 1836 edition; Mikhail Litvin, 1890; Beauplan, 1832) that the disappearance and displacement of wild horse, kulan, saiga, tur and bison from the Ciscaucasian steppes were well advanced as early as the Middle Ages, brought about by domestic cattle herding and game drives by thousands of mounted Khazars, Polovtsy [Cumans] and Mongolians.

Bear, beaver, boar, deer, roe deer and elk were displaced from the lower Don, the Kuban, the Terek and the Sulak by the heavy deforestation by man during the last centuries (Kondrat'ev, 1885-86; Bogachev, 1918; Flerov and Balandin, 1931).

It is known that extensive forests existed on the right bank of the Kuban as late as the 18th century (Mishchenko, 1928; Rogovskii, 1928; Zakharov, 1935).

Rogovskii's map indicates nine isolated forest islands on the right bank of the Kuban where according to the 1775-76 map of the Kuban region an almost continuous zone of forests and bush extended from the source of the Protoka to the mouth of the Laba.

Flood control in the deltas of the Kuban, Terek and Sulak (building of embankments and filling the gaps in the banks) have noticeably affected the landscape since the middle of the last century. These measures only drained the marshes temporarily, since the river levels continued to rise.

The planned drainage and reclamation for wheat and rice cultivation of the Kuban plavni only began in the 1930's and brought about the greatest changes in the assemblages of rodents and carnivores.

521 Mink, otter, European wildcat and water rat were displaced from vast areas of drained swamps and lakes during reclamation, and their habitats were occupied by polecat, hare, common vole, steppe mouse, common hamster and jerboa.

Military considerations originally prompted the burning and cutting of the tugai forests on the Kuma, Terek and Sulak which began in the second half of the 18th century during the construction of the Caucasian fortifications (Popko, 1880; Potto, 1912). The establishment of Cossack settlements and posts brought about a rapid extermination of large animals, since the Cossacks were mainly engaged in hunting and fishing. During the reign of Anna Ioanovna, it was the duty of the Grebenskie Cossacks to supply live boars, deer, ibex ("steinboks") and bison to the menageries of the capital.

The destruction of "bairak" [small-gulley] forests scattered on the northern slopes of hills and in the gulleys of the Ciscaucasian plains was similar to the process described for the steppes of the Russian Plain (Kuznetsov, 1896; Tanfil'ev, 1896; Lavrenko, 1939). Cattle breeding and agriculture on the Ciscaucasian plains played an important part in the formation of the ranges, populations and assemblages of small mammals and completed the process of displacement of corsac fox, kulan, tarpan and saiga which began in the first half of the last century during the building of the Cossack settlements. The extermination of the bairak forests brought about a decrease in the area of the habitats of mesophilous insectivores (shrews, moles), small carnivores (stone marten, badger), and forest rodents (forest dormouse, common and striped field mouse). The distribution of these species on the Ciscaucasian plains gradually split into small isolated colonies.

Examples of the residual, disrupted ranges of these species can be observed in the Petrovskoe and Aleksandrovskoe Districts of the Stavropol Region, on the middle and upper Kalaus and on the Stavropol Plateau.

The depletion of wolves, susliks and mouse-like rodents in the Ciscaucasian steppes dates from the early 20th century, but planned extermination has been carried out only under the Soviet regime. The 20th century also marks the beginning of the latest phase of development of the cultural landscape, which is well presented in the extensive statistics of the collection "The Northern Caucasus after Districting" (1925).

During recent decades the introduction of new crops and irrigation and melioration projects (e.g., construction of canals on the left banks of the Malka and Kura, diversion of the Kuban waters to the Yegorlyk, and drainage of the Kuban plavni) resulted in accelerated agriculture and an increase in cultivated areas. Planting of shelterbelts started in the 1920's, at first along the railroads and later, in the 1930's, in the vast croplands. The largest shelterbelts are in Krasnodar, Tikhoretskaya and Salsk, where they are many hundreds of kilometers in length.

The highly diversified ecological features and potential adaptations of various species to new conditions is readily seen in the nature of the relationships which developed between the mammals and the biotopes of the cultural landscape.

The animal world of this region was affected by cattle raising for a longer time than by agriculture. The destruction of the steppe-grass stand by
522 cattle over the centuries resulted in the replacement of motley-grass—sheep's fescue—feathergrass steppe formations by sheep's fescue—feathergrass vegetation, and later by sheep's fescue—wormwood vegetation. Concomitant with this process, weed groupings developed near resting and watering places, along the routes of cattle drives and around settlements. As early as the 1880's extensive grain farming began to replace the fine-wooled-sheep breeding of Ciscaucasia, from the virgin mixed-grass steppes of the Kuban and Terek and the Stavropol area to the zone of sheep's fescue—feathergrass steppes of the Kuma basin (Rozhdaev, 1925). Cattle grazing of virgin vegetation cover and overgrazing and manuring promoted the rapid expansion of suslik and jerboa ranges. The extension of the suslik range southward from the Manych area was also promoted by plowing of the steppe, construction of bridges over canals and rivers and established

routing of cattle drives (Sviridenko, 1927; Formozov, 1929). The overgrazed, manured areas gave susliks and jerboas the advantages of a good field of vision, fresh green food, consisting of mixed weeds and grasses, fast movement and protection from predators. Both abandoned and occupied cattle stations were concentration sites for white-bellied white-toothed and lesser shrews and steppe voles.

Recent complexes of small-mammal habitats in the cultural landscape of the Ciscaucasian steppes — Obolenskii's permanent or temporary "farm habitats" (1935) — typically consist of pastures, roads of various types, cultivated lands and settlements.

Each of these categories comprises a number of biotopes, determined by the agricultural and construction methods of man and also by the ecological adaptability of the mammal species.

Pastures. When the cattle load is light, the pastures preserve almost all the natural biotopes of the primitive ecological assemblage consisting of little suslik, small five-toed and great jerboas, little earth hare, common mole rat, steppe vole, steppe lemming and mole vole. Pastures located near settlements, particularly if the soil is somewhat humid, are covered by vegetation that is unsuitable for cattle forage, and are inhabited by suslik, great jerboa, steppe mouse, common vole and mole rat.

Roads. The right-of-way zones along rail and major automotive roads are characterized by a mammalian assemblage similar to that of the pastures.

These zones of virgin land are inhabited by little white-toothed shrew, black hamster [Mesocricetus auratus nigriculus], common hamster, great jerboa, southern birch mouse, mole vole, mole rat and little suslik. The weeds and ditches along the railroads are attractive to long-eared hedgehog, tiger polecat, Siberian polecat, weasel, steppe mouse, striped field mouse, common vole and migratory hamster.

Cultivated areas. The composition of the mammalian assemblages in cultivated areas depends upon the routine agricultural techniques, crop rotation and the size of the arable areas. Usually large areas in cereal crops are inhabited only by common vole and steppe mouse. The margins of the planted areas are inhabited by little suslik, hamster, migratory hamster, mole vole and mole rat (Obolenskii, 1935).

The habitation of the fields by hare is contingent upon the state of the crop and the method of crop treatment. If rodents and insects are available, the fox is also a field inhabitant. Thus, for example, when snow cover is thin in the winter, the European hare feeds on winter crops but rests during
523 the day in fall-plowed fields. In such a winter foxes will concentrate in winter-crop and stubble fields which are inhabited by rodents. The most varied ecological assemblages occur in areas where the plantings of various crops alternate with sections of virgin land in a mosaic-like pattern. Perennial crops of alfalfa and other fodder plants are habitats of hamster, vole, steppe mouse and mole rat. Large plowed fields planted to grain and regularly worked are characterized by very impoverished assemblages consisting of fox, European hare, common vole and steppe mouse.

The specific composition of the rodent fauna changes with each year that land lies fallow. The first year, the stubble may be inhabited by steppe mouse and common vole, rarely by common and striped field mouse, and even more rarely by birch mouse and migratory hamster, "Aging" of the fallow land and development of weed cover (green bristlegrass, saltbush, wormwort) rapidly increases the stability of the rodent populations. The resulting assemblage consists of long-eared and common hedgehog, fox, hare, common hamster, mole vole and mole rat. Lands which have been fallow for many years are usually inhabited by suslik, jerboa and steppe lemming; this assemblage is similar to the original assemblage.

Field camps, silos and haystacks are inhabited by white-bellied and little white-toothed shrews, steppe mouse and common vole.

Settlements. The settlements of the Ciscaucasian steppes are characterized by a fairly large number of biotopes: limestone walls around estates, ditches overgrown with weeds, gardens, vegetable plots, farm buildings and stacked sunflower, corn and Italian millet stems (used for firewood) and invariably inhabited by white-toothed shrew, weasel, Siberian polecat, house mouse, Norway rat, common hamster and vole. Migratory hamsters live in non-residential structures. Common field mouse and forest dormouse inhabit overgrown gardens, particularly those adjoining exposed rock or groves in valleys and bairaks. Banks of dammed rivers (reservoirs) are inhabited by water vole. Residences and churches in settlements are the habitats of common noctules and serotine vespertilio, and more rarely bicolor vespertilio and sharp-eared mouse-eared bat. House mouse, either native or introduced, always occurs in residential buildings in settlements and at field stations. All the large settlements connected with the Don by rail or automobile roads were inhabited by Norway rat by the 1930's.

By now the synanthropic assemblage of small mammals in the settlements of the Ciscaucasian steppes can be considered fully developed, as is the assemblage of field and house pests (see also Stal'makova, 1935).

The spontaneous development of game hunting in the first half of the 20th century continued to decimate the saiga, corsac fox and, later, the white [Siberian] polecat populations. Since 1925-27, the hunting of the so-called "summer" fur species has developed rapidly and affected the populations of little suslik, common and black hamster and great jerboa (B. Kuznetsov, 1932).

Large-scale exterminating operations against harmful rodents were begun in Ciscaucasia early in the 20th century. Pest control of little suslik on the Ciscaucasian steppes was initiated to protect the peasants' crops. Later the great epidemiological threat presented by this species was
524 discovered and the boundaries of the endemic plague source area were drawn.

Organized extermination of suslik and mouse-like rodents has been carried out in Ciscaucasia only in Soviet time. The areas treated each year with chloropicrin and poisoned food increased from approximately 100,000 ha in 1923 to 3,000,000 ha in 1935. Tens and hundreds of thousands of haystacks were surrounded by special ditches, and silos were gas-treated (Sviridenko, 1925; Vinogradov and Obolenskii, 1926; Fal'kenshtein, 1933; B. Kuznetsov, 1932).

The scale of the pest control measures undertaken in the 1920's and 1930's only varied with the fluctuations in population of mouse-like rodents and the occurrences of epizootics in susliks. The present program is aimed toward the complete extermination of suslik in the Ciscaucasian steppes.

It has not been possible to bring this about by currently available techniques even with concentration of effort and large expenditures of resources and labor just within the Ciscaucasian endemic focus.

The operations, however, have resulted in a large decrease in population and density each year. While there have been no reports of successful extermination of widely distributed species of mouse-like rodents either, sudden rises in their populations have been prevented experimentally following Satunin's (1912a) advice on applying extermination methods in habitats suitable for survival in those years when they are least abundant, particularly in the early spring (Naumov, 1946).

Introduction of crop rotation, planting of shelterbelts and trapping susliks for their pelts has had a much greater effect on the distribution ranges of susliks and mouse-like rodents than pest control measures.

When fall plowing was introduced in the mid-thirties, it resulted in an abrupt population decline in mouse-like rodents over large areas. The plowing of the Salsk steppes and planting of shelterbelts also formed ecological barriers which prevented the susliks from invading the Kuban Plain. The continued development of shelterbelts and the construction of large water reservoirs near Stavropol, Novo-Troitskoe and other centers will create a more humid climate. Dispersion of common and striped field mouse and forest dormouse is currently taking place and will continued in the planted forests connecting the bairak and valley shrubs and forests. Concominantly, the ranges of steppe and common field mouse, common vole and hamsters will probably extend eastward into the semidesert zone. The ranges of small five-toed jerboa, thick-tailed three-toed jerboa, northern three-toed jerboa, little earth hare and midday gerbil will probably decrease. The development of hunting will promote the population expansion of European hare and fox.

The introduction of new species of fur animals onto the Ciscaucasian plains was associated with the landscapes of the lower Kuban, Terek and Sulak.

Forty-five raccoon dogs (Nyctereutes procyonoides Gray — Figure 198) were released in 1934 in the tugai forests on the Terek near Kizlyar. In subsequent years the raccoon dogs became widely distributed in the tugai and reedlands on the Terek and Sulak, migrating far north through the reed thickets on the coasts of the Caspian estuaries. The range of this Terek-based population soon touched the range of the Volga population
525 which had grown from the introduction of the species along the lower Volga in 1936 and 1939 (Map 94). Hunting of these animals in the Grozny area and in northern Dagestan commenced in 1943-44 and the next year the yield from the lower Terek was nearly 1,000 specimens (Map 7; also see Lavrov, 1946).

Attempts at introducing some exotic rodents were also fairly successful. In 1932 the South American nutria (Myocastor coypus Mol.) was introduced onto the plavni of the lower Kuban in the vicinity of Grivenskaya (43 specimens) and near Lake Shaitan-Kazak, an oxbow of the Sulak (22 specimens). The success of this experiment was hampered by the freezing of the water bodies in severe winters when the nutrias, dying on the ice of cold and hunger, fell prey to foxes, dogs and predatory birds (Vereshchagin, 1936, 1947d, 1950a).

Semicontrolled nutria breeding, keeping part of the population in cages during the cold period, resulted in considerable economic success in these regions in the 1950's.

FIGURE 198. Raccoon dog

The introduction of muskrat (Ondatra zibethica L. — Figure 199) into the reedy sections of the Kuban, Yeya, Terek and Sulak met with more success.

According to the All-Union Scientific Research Institute of Game Hunting, muskrats were first released on the Kuban plavni in 1944 and in the reedlands of the lower Terek in 1947. The natural dispersion of the animals was greatly accelerated in the years that followed by the artificial dispersion which formed a part of the planned operation (Map 95).

The development of the muskrat populations of Ciscaucasia will be set back by the continuation of plavni drainage and the construction of dams and reservoirs for the regulation of the Kuban, Terek and Sulak rivers.

526 The relatively slow rate of population increase in muskrats in Ciscaucasia to date can be accounted for by specific features of the river regimes (e.g., the heavy June floods which kill the young), and by the tularemic epizootics of the water rats.

Twenty-three specimens of common raccoon (Procyon lotor L.) captured in Azerbaidzhan were released in 1950 in the tugai area of the lower Sulak.

This omnivorous predator found favorable conditions for rapid expansion of population and range in the relict forests of the lower Sulak and Terek, where aged trees provide hollows, and frogs and fruit of wild Rosales provide abundant food. The species also migrates along the Sunzha valley to the approximate latitude of Achaluki.

It is possible to establish raccoon populations in the tugai forests on the Kuma in the area of Budennovsk-Georgievsk and in the forest tracts of Pyatigor'e and along the left tributaries of the Kuban. But the expediency of expanding this predator's range is questionable, since it would be a threat to poultry farming and to game hunting in the fall and spring (Vereshchagin, 1953b).

The prospects for enriching the ecological assemblages of mammals on the Ciscaucasian plains with commercial species depend entirely upon the expansion or restriction of game hunting. The forest belts can be populated by roe deer and deer, thereby increasing the population of European hare, if wolves are exterminated and measures against unlicensed hunting are improved.

FIGURE 199. Muskrat on feeding ground

SEMIDESERT OF EASTERN TRANSCAUCASIA

The central parts of the Kura-Araks lowlands are mainly covered by characteristic wormwood and wormwood—saltwort, or, more rarely, by caper and gramineous groupings. On the northern, southern and western
527 margins the semidesert grades into the beardgrass steppe (Grossgeim, 1932). Semidesert and steppe formations are developed in places in the Gori depression between Mtskheti and Surami.

In the inner part of this zone, gallery forests have survived along the Kura, Araks, Iora and Alazan rivers; also pools grown with reed and bulrush, and sparse juniper—pistachio forests on the Tertiary hills.

The original Holocene assemblages of mammals in the areas described were fairly rich in species. The semidesert and steppe were inhabited by herds of kulan and goitered gazelle. Probably the insectivores and rodents of the open plains were generally similar to those of the Recent. The following species occurred in the area: long-eared hedgehog, long-tailed white-toothed shrew, red-tailed Libyan gerbil, steppe vole, William's and small five-toed jerboa. The tugai thickets and reed—bulrush formations of estuaries and residual lakes in the Shirvan, Mugan and Mil'skaya steppes were inhabited by wolf, jackal, striped hyena, lion, tiger, panther, cheetah, boar, deer and goitered gazelle.

Fluvial lakes of the Araks and Kura and the Caspian bays abounded in aquatic birds, both migrating and wintering. These habitats were also occupied by water rat, otter and jungle cat.

The documented record of human influence on the animal assemblage of this zone dates to the Bronze Age, when settled and nomadic hunters and cattle herders began to draw heavily on the stock of large animals of the steppes (Vereshchagin and Burchak-Abramovich, 1948; Vereshchagin, 1949c). The rapid growth of cattle-herding tribes and large settlements and the development of agriculture and irrigation brought about the next phase of anthropogenic influence on the faunal complex of the Transcaucasian steppes.

The agricultural history of the Shirvan, Mil'skaya-Karabakh and Mugan steppes, which goes back many centuries, has not yet been thoroughly studied by archaeologists and historians.

The relics of ancient canals, fortresses and giant mounds in the Mil'skaya and Mugan steppes indicate that vast areas were put to agriculture and that irrigation techniques had advanced to a high level (Maevskii, 1902a, 1902b). The burial fields and cultural layers under current study at Mingechaur and Uren-Kala are evidence of large settlements in the center of the Kura-Araks lowlands in the early first millennium B.C. (Sysoev, 1925; Pakhomov, 1923; Dzhafar-Zade, 1946, and others).

The small irrigation systems constructed on the tributaries of the Kura and Araks are probably even older. Small communities could readily draw upon the water of these tributaries, whereas the construction of large canals could only be carried out by a local population at a higher state of industrial development. In this respect Latynin's (1935) statements on the history of irrigation in central Asia are equally applicable to Azerbaidzhan. The oldest oases in the Kura-Araks lowlands are marked by the following towns and villages: Barda, Ardash, Geok-Chai, Shil'yan, etc., located on the Tertera, Aldzhigan-Chai, Geok-Chai, Gerdyman-Chai and Akh-Su.

Cereals and, later, cotton were raised in the semidesert, which also provided winter forage for the cattle of nomadic herders. But it was the plowing and irrigation of the semidesert that had the greatest effect on the
528 landscape and animals of the Kura-Araks lowlands. Destruction of the tugai forests, winter cattle-grazing of the vegetation cover and drainage of river lakes and flooded areas were of secondary importance to the wild-mammal fauna.

Preliminary observations on reptiles and amphibians in the area of newly-established cotton sovkhozes in the Mil'skaya steppe show that irrigation produces differentiated effects on species populations: it causes extermination or decrease in some, and growth in others (A. Bogachev, 1938). Sudden changes in the composition and abundance of nesting and wintering bird assemblages occur when irrigation is installed in semideserts (Satunin, 1912a; Vereshchagin, 1950b). In the case of the mammalian fauna, the evolution of its specific composition on irrigated and unirrigated lands depends upon the season of the year and the agricultural techniques employed, i.e., the type of the main crop, rotation and treatment of crops, irrigation and development of shrub and tree plantings between the fields.

The contemporary Apsheron Peninsula with its orchards, vegetable gardens, trade centers and settlements is a good example of qualitative and quantitative changes in mammalian assemblages caused by the development of agricultural and industrial settlements in the semidesert. At present there are 18 species of mammals on the Apsheron, as contrasted with 15 in the neighboring areas of the Kabristan semidesert. There are 5 species of small mammals in the cultivated areas of the Apsheron which do not occur in the adjacent virgin semidesert: Norway rat, black rat, house mouse, Kühl's vespertilio, common hedgehog. Goitered gazelle and wolf have been exterminated from this area. The populations of hare, migratory hamster and steppe mouse increased as the result of new protective vegetation and fodder plantings (Vereshchagin, 1938b, 1949c).

The concentration and distribution of bats furnishes interesting examples of the effects of human activity. Bats appear in the semidesert and settle at structures as isolated as water towers, tombs, sheep pens and, in the oases, in the hollows of old plane and walnut trees.

Between the years 1935 and 1945 we observed and captured specimens of the following bats in the agricultural settlements of the semidesert zone:

Rhinolophus ferrum-equinum
Rh. hipposideros
Myotis mystacinus
Vespertilio kühlii
V. nathusii
V. pipistrellus
V. serotinus
Nyctalus noctula

All these species use residential and service structures for their day resting places; they feed on the outskirts of settlements and along the borders of gardens and parks (Vereshchagin, 1942b; Kuzyakin, 1950). They mainly inhabit crevices under roof beams and openings in the corners of window frames of railroad stations, schools and other buildings constructed of cut limestone blocks or bricks, and the stone domes of mausoleums and mosques. The vespertilio, particularly the Mediterranean species (Vespertilio kühlii), has become adapted to catching insects near electric light. In the urban center of Baku, large as it is, V. kühlii is now the dominant bat species, although in the 1930's it was exceedingly rare there. We believe that its appearance and increase in numbers over these decades can be attributed to expanded cultivation, the growth of the flying insect population and the construction of freshwater pools as watering places. Following a certain route through the central sections of the city
529 in 1935, I noted 1–3 specimens of vespertilio, in 1940 — 3–5 specimens, and in the summer of 1949 — 3–7 specimens.

The examples of animals belonging to other orders were selected from areas irrigated by local canals and consisting of small fields alternating with virgin land.

Observations made in the Shirvan and Mugan steppes on changes in composition and relative abundance of the surviving mammals caused by irrigation and planting are given in Table 107.

TABLE 107. Changes in specific composition and relative abundance of mammals occurring with the irrigation of the eastern Transcaucasian semidesert

Species	Virgin semidesert	Crops			Two-year-old wasteland	Road shoulders, ditches with weeds	Untended gardens in villages
		Cotton	Barley	Alfalfa			
Insectivora							
Hemiechinus auritus	x	–	–	–	x	xx	x
Crocidura russula güldenstaedti	x	–	x	x	xx	xx	xx
C. leucodon	x	–	–	–	x	xx	x
* Erinaceus europaeus	–	–	–	–	–	–	x
Carnivora							
Vulpes vulpes	x	x	x	x	xx	xx	xx
Canis lupus	x	–	–	–	x	x	x
Meles meles	x	–	–	–	x	xx	x
Vormela peregusna	x	–	–	–	x	x	x
Mustela nivalis	x	–	–	x	x	xx	xx
Canis aureus	–	–	–	–	x	x	xxx
* Felis chaus	–	–	–	–	–	–	xx
Lagomorpha							
Lepus europaeus	x	x	x	x	x	xxx	xxxx
Rodentia							
Mus musculus tataricus	x	–	x	x	x	xx	xx
Cricetulus migratorius	x	–	–	–	x	xx	xx
Microtus socialis	xxxx	–	xxxxxx	xxxxxxx	xxx	xxxxx	xxxxx
Meriones erythrourus	xxx	–	–	–	x	xx	x
Allactaga williamsi	x	–	–	–	x	xx	x
A. elater	x	–	–	–	–	–	–
* Mus musculus musculus	–	–	–	–	–	–	x
* Apodemus sylvaticus	–	–	–	–	–	–	xxxx
* Rattus rattus	–	–	–	–	–	–	x
* R. norvegicus	–	–	–	–	–	–	x
* Dyromys nitedula	–	–	–	–	–	–	x

TABLE 107 (continued)

Species	Virgin semidesert	Crops			Two-year-old wasteland	Road shoulders, ditches with weeds	Untended gardens in villages
		Cotton	Barley	Alfalfa			
Artiodactyla							
Gazella subgutturosa	×	–	–	–	×	×	×
* Sus scrofa	–	–	–	–	–	–	–
Total	16	2	5	6	16	16	23

Notes. 1. Symbol × designates presence and relative abundance of species.

2. Data from summer and winter counts are combined for virgin land, waste land, road shoulders and gardens. The data on the presence and number of animals shown in the fields is drawn from large areas planted to winter crops. During irrigation almost all the species are driven from the fields.

3. Species migrating from other zones and biotopes are indicated by an asterisk.

4. Table does not include water rat, which occurs only in the Agdam oasis and is absent from other lowland oases.

5. For widely distributed species – jackal and fox – only the habitats where they feed and rest are given in the table.

The data show the greatest changes in the original assemblage of semidesert mammals when the semidesert is planted to cotton. The game animal population, however, is promoted by inadequate agricultural techniques, local methods of irrigating with an insufficient water supply; alternating sections of virgin land and waste land, and abandoned ditches and plantings of tree and shrub thickets.

The species composition of the animal assemblages is most variable in old oases with long untended gardens, particularly those adjacent to tugai and lowland forests. All the new immigrant species which invade the human environment originate in gallery and lowland forests and reed swamps: common hedgehog, jackal, jungle cat, black rat, common field mouse, forest dormouse and boar.

The mammals which inhabit the vast semidesert areas irrigated by a system of water canals live under a variety of environmental conditions. The complete displacement of steppe vole and gerbil from the well-irrigated lands of the first, second and third Mil'skaya sovkhozes was recorded in 1936–37. White-toothed shrew, hedgehog and steppe mouse, however, survived on the embankments of the canals, because ground holes are not so essential to their existence.

The populations of these species were stabilized and steppe vole, hare and fox appeared in these habitats in later years as weed development and planted tree stands took hold on the banks of the ditches.

Some specific examples of the reactions of various species to environmental changes in the semidesert are given below.

Insectivores and rodents. The regular heavy irrigation of the cotton fields drives the long-tailed white-toothed shrew, steppe mouse, gerbil and steppe vole off the land. The environmental conditions created by weeding the cotton fields are unsuitable for rodents, at least until the start of winter. The two-stage irrigation method used in grain and alfalfa fields affect the animals less adversely, as they can find refuge in the "dry gaps," the margins of the fields and the banks of the canals during irrigating. When the animals reinvade the dry fields, their reproduction rises rapidly, particularly in the case of the steppe vole (Rodionov, 1924) which inhabits alfalfa fields in masses. The increase in the rodent population and in its harmful affects is directly related to haphazard alternation of planted fields with waste land of different ages and with virgin land, and to inefficient agricultural techniques (Vereshchagin, 1942c, 1946b).

The irrigation network is very important to the development of viable assemblages of small mammals in the semidesert. Canals under constant use are sometimes inhabited by water rat and also serve as dispersion routes for this species.

531 On a nutria farm at Karayazy water voles and Norway rats dug holes in the ditches which collect and distribute water to the concrete cages of the nutria. At this farm the water rat has become a synanthropic species which feeds on the residue of grain and roots washed out of the cage basins.

Steppe vole, red-tailed Libyan gerbil and steppe mouse usually inhabit the outer slopes and tops of banks of irrigation canals, attracted there by the good aeration of the soil, the ease of hole-digging, the rapid runoff of rainwater and the growth of weeds suitable for forage.

The remains of ancient irrigation ditches in the steppes, often recognizable only as small depressions and low ridges, are invariably inhabited by steppe vole and red-tailed Libyan gerbil. These old ditches, overgrown with green ephemerals and shrubs of saltwort and caper, serve as important dispersion routes for the animals during the fall when population and activity increase.

Railroads are similarly significant to the life and distribution of rodents in the semidesert. The elevated sections are regularly inhabited by steppe vole, red-tailed Libyan gerbil, steppe mouse and long-tailed white-toothed shrew. The soft sandy soil, suitable for hole-digging, the weed vegetation rich in grains (Xanthium strumarium, Cirsium, Artemisia, Salsola, Sueda), and the seeds of melons and bits of bread thrown out of the railroad cars — all these attract the gerbils.

The gerbils occasionally dig their holes under the crossties in much the same way as they dig under stones: they penetrate the soil at the face of the crosstie and burrow deep into the embankment. These holes are constantly disturbed by passing trains which leave an accumulation of debris at their entrances, and by the repacking of the excavated sand by railroad maintenance crews. Nevertheless, the gerbils persist in renovating them over and over.

In the summer steppe voles inhabit the lower sections of the shaded northern slopes of the railroad enbankments, where the soil is cooler and moister and there are more succulent plants. In the winter they settle on the southern slopes where the growth of ephemeral grasses begins two to three weeks earlier and proceeds faster than on the northern slopes.

The shoulders and ditches beside both unsurfaced and hard-surface roads are important to the dispersion and maintenance of the micropopulations of steppe vole. Even in years of decline in population and reproduction, viable colonies survive in such areas.

The great adaptability of William's jerboa is displayed in its hole-digging on soft-surface roads in spite of the noise, shocks and clogging of the holes with debris from passing carts and automobiles.

The populations of the European hare of the Kura area fall into two different categories, one of which may be called the "domestic" population, the other the "wild." The first inhabits the outskirts of settlements, where they usually remain by day among weeds and heavy growth of Imperata cylindrica, often as close as 30-50 m from the yards of houses. A thorough search near small settlements (e. g., ten to fifteen clay brick houses) may reveal three to five hares. They are not disturbed by the usual daytime noises of the village — the movement of people and cattle, and the barking of dogs. A zone 2-3 km wide, which is completely devoid of hares, begins 80-100 m from the settlement. Beyond this zone the hares of the "wild" population begin to appear. It would appear that the "domestic"
532 hare habituated itself to life near human settlements because it was relatively undisturbed and the dogs afforded protection for its day resting places from foxes and jackals.

For a long time the distribution of rodents in the semidesert and the viability of their populations has been noticeably affected by the driving of cattle, the winter-pasturing of large herds of cows, sheep, camels and horses and the establishment of cattle-herders' stations. In past centuries these stations consisted of a few felt tents for living and a number of pits, surrounded by reed screens, for the protection of the young cattle. They were usually located on ancient alluvial ridges, which are highly attractive to the red-tailed Libyan gerbil. When the sites were abandoned they remained for decades as depressions and manured, overgrazed fields overgrown by milk thistle, white wormwood and orach. These sites are a characteristic element of the landscape of the Kura-Araks steppes.

It is on these "wounds of the virgin land" that the viable populations of the steppe vole and red-tailed Libyan gerbil usually survive the years of low reproduction. High weeds protect the voles from dangerous heat exposure in summer; fast-growing ephemerals provide forage in winter. The abandoned pits are used by long-eared hedgehogs, white-toothed shrews, foxes, badgers, tiger polecats and ruddy sheldrakes for digging burrows and building nests and shelters.

Over the millennia the overgrazing of the wormwood—grass cover of the semidesert greatly limited the size of the local populations of vole, gerbil and jerboa, and affected their redistribution.

In newly-built villages — temporary or permanent — the synanthropic assemblage of mammals develops at first from local forms: long-tailed white-toothed shrew, steppe vole, migratory hamster, steppe mouse and black rat.

In the mud huts of fishermen and hunters built around reed lakes on the lowland, steppe mice and long-tailed white-toothed shrews are very common and are a great nuisance.

Norway rats are always found in profusion near the fisheries on the lowland lakes. Steppe voles rapidly invade the new huts and tents of nomadic cattle breeders in the Shirvan and Mil'skaya steppes. They steal bread and other food, unperturbed by the presence of people. The migratory hamster always inhabits residential structures, primarily in the southern part of the lowland from the village of Pushkino and further south, and in the foothills of the Lesser Caucasus and the Talysh uplands.

As the settlement continues to develop, cosmopolitan synanthropic species appear, sometimes after several decades — house mouse, black rat and Norway rat. The Norway rat, however, also emerges from "wild" natural environments (i.e., from populations inhabiting the reed marshes of Transcaucasia) to invade human dwellings. This is also true of the black rat originating in local relict colonies.

The author's expedition of March 1940 to the foothills of Karabakh yielded the following sampling, totaling 1,536 animals trapped in the houses of the larger villages:

Mus musculus musculus	– 78.2%
M. musculus abbotti	– 12.1%
M. musculus tataricus	– 2.7%
Microtus socialis	– 1.4%
Cricetulus migratorius	– 1.2%
Crocidura russula güldenstaedti	– 0.3%

533 Tables 108-110 set forth the small-mammal yield from traps and the large-mammal count in various types of human settlement in the semidesert zone as examples of the continuous development of synanthropic (house) and oasis assemblages.

TABLE 108. Species of small mammals from sheep-breeders' winter station in caper formation in the center of the Shirvan steppe (5 April 1939)

Species	Number of specimens per 100 traps over all the sites	Trapping site
Insectivora		
Hemiechinus auritus	1	Pit overgrown with weeds
Crocidura leucodon	2	Pit for keeping lambs covered with reed roof
Rodentia		
Meriones erythrourus........	2	On enbankments near abandoned pits
Mus musculus tataricus	6	2 specimens from a tent; 4 specimens from sheep pen
Microtus socialis	16	6 specimens from area between tents; 10 specimens from tents

TABLE 109. Species of small mammals from the village station of Kerar in the Shirvan steppe (10–15 April 1939)

Species	Number of specimens per 100 traps over all the sites	Trapping site
Insectivora		
Crocidura russula güldenstaedti	3	In firewood storage sheds
Chiroptera		
Vespertilio kühlii	3	In garret of station building
V. serotinus	1	
Rodentia		
Mus musculus musculus	8	In residential barracks
M. musculus tataricus	7	In firewood storage sheds and poultry houses
Rattus norvegicus...........	5	In residential barracks

Note: The village consists of ten wooden residential barracks and a stone station building. There are a few young acacia trees.

Traps set at the same time in the surrounding semidesert yielded 15 steppe voles and 2 red-tailed Libyan gerbils for 100 trap-nights. In addition, 2 foxes, 1 hare and 5 goitered gazelles were counted near the field station.

534 At the time of the sampling, steppe voles and red-tailed Libyan gerbils inhabited the surrounding open wormwood—saltwort and cereal—ephemeretum semidesert, as well as the unirrigated experimental barley fields. Long-eared hedgehogs, foxes, weasels, hares and goitered gazelles were also either caught or observed in the vicinity of the settlement.

Observations taken while crossing an untended garden (area 15 ha) on the outskirts of the settlement showed 3 hares, 2 foxes, 5 jackals and 1 jungle cat.

In the large cities of the lowland the synanthropic assemblage is impoverished because of the disappearance of the local rodent and insectivore species.

Baku is an example of this phenomenon: Kühl's vespertilio, house mouse, Norway rat and black rat are the only four species of small mammals to occur within the city limits.

Carnivores. Wherever fox, jackal, weasel, badger, tiger polecat and jungle cat appear and prosper in the oases and among the agricultural
535 settlements in the Transcaucasian desert, a relationship can be established to the available food resources (insects, rodents and poultry), a favorable relief and protective vegetation cover, which is particularly important

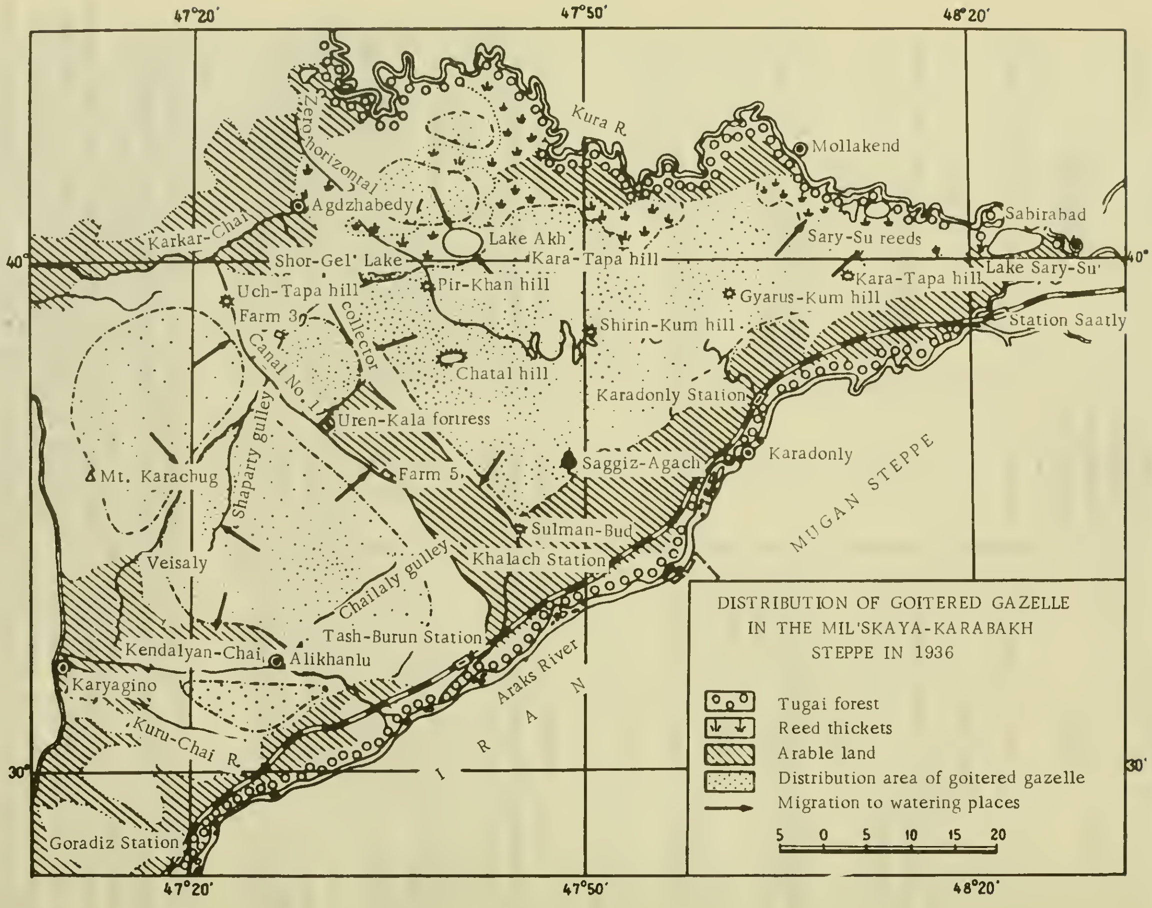
in raising the young. These environmental factors are still dominant even where game hunting is widespread.

(534)TABLE 110. Species of small mammals from the town of Agdam (24-30 April 1940)

Species	Number of specimens per 100 traps over all the sites	Trapping site
Insectivora		
Crocidura russula güldenstaedti	5	In gardens and alfalfa
C. leucodon	3	In alfalfa
Chiroptera		
Vespertilio pipistrellus.......	1	Killed in garden
Myotis mystacinus...........	1	In garret of residence
Carnivora		
Mustela nivalis	1	Killed in garden
Lagomorpha		
Lepus europaeus cyrensis	2	Killed in garden
Rodentia		
Mus musculus musculus.......	29	In warehouses and residences
M. musculus tataricus	36	In gardens and stacks
Cricetulus migratorius	2	In gardens and edges of fields
Meriones blackleri...........	1	On sunny empty lots in settlement
Apodemus sylvaticus arianus	5	In garden ditches
Microtus socialis	186	In alfalfa and winter barley crop
Arvicola terrestris...........	3	In banks of irrigation ditches in gardens

Note. Town in the Karabakh steppe with apple orchards, vineyards and gardens surrounded by barley and alfalfa fields and old wasteland. Sampling in the alfalfa and barley fields and in the buildings was done in 400 trap-nights; sampling in gardens, ditches and waste land in 200 trap-nights.

Ungulates. The goitered gazelle and boar provide some interesting examples of existence and behavior in the cultural landscape of eastern Transcaucasia. Although the goitered gazelle has been an officially protected animal during the last 30 years, it is gradually being exterminated by unlicensed shooting from cars and by shepherds. It is also being driven from its habitats by destruction of its feeding grounds and formation of a soft-ground footing by plowing and irrigating the steppes. The species lives well, however, among the unirrigated cereal crops on the Adzhinọur plateau. The animals remain in the area even when the barley and wheat are high in May and June, because the soil of the dry fields is sufficiently firm to allow their escape from wolves. The goitered gazelle is persistent



DISTRIBUTION OF GOITERED GAZELLE
IN THE MIL'SKAYA-KARABAKH
STEPPE IN 1936
Tugai forest
Reed thickets
Arable land
Distribution area of goitered gazelle
Migration to watering places
5 0 5 10 15 20
47°20'
47°50'
48°20'
40°
30'
Kura R.
Mollakend
Sabirabad
Sary-Su reeds
Lake Sary-Su'
Kara-Tapa hill
Kara-Tapa hill
Gyarus-Kum hill
Station Saatly
Shirin-Kum hill
Karadonly Station
Karadonly
MUGAN STEPPE
Zero horizontal
Agdzhabedy
Lake Akh
Karkar-Chai
Shor-Gel' Lake
Pir-Khan hill
Uch-Tapa hill
Farm 3
collector
Canal No. 1
Chatal hill
Uren-Kala fortress
Saggiz-Agach
Mt. Karachug
Shaparty gulley
Farm 5
Sulman-Bud
Khalach Station
Veisaly
Chailaly gulley
Tash-Burun Station
Kendalyan-Chai
Alikhanlu
Karyagino
Araks River
I R A N
Kuru-Chai R.
Goradiz Station

FIGURE 200

in its habitation of the saltwort—rape thickets covering wasteland 2-3 years old in the Mil'skaya and Shirvan steppes. This could be particularly well observed on the lands of the Mil'skaya sovkhozes in 1936 (Vereshchagin, 1938b) (Figure 200).

The first flocks of sheep and herds of cows and camels which commence to fill the steppe after October cause a redistribution of the goitered gazelle population. They at first occupy the poorer pastures and salines. Because
536 of the increase in the number of herds and herding stations, and the flooding of the salinas in mid-winter, the gazelles are forced to graze near the the sheep, and sometimes among them. This type of distribution, however, is always temporary and unstable.

When goitered gazelles are persistently pursued by mounted hunters, they are likely to change habitats abruptly, hiding for two to three days in tugai brush and reeds. They flee into the salinas and to hillocks and gulleys from hunters in automobiles.

As oases were developed, boars took up habitats near the settlements. Their day resting places are now commonly found among dewberry bushes in gardens in Agdash, Karabudzhakh and other towns and villages of the Shirvan and Mugan steppes. Their lairs often occur on the banks of reservoirs and in ditches overgrown with reeds and plumegrass in the proximity of residences and traveled roads.

A secondary anthropogenic effect on the mammals of the semidesert was produced by the destruction of tugai forests on the Kura and Araks and their tributaries.

In eastern Georgia the tugai forests began to disappear rapidly in the 19th century, until by the mid-century they were presumably placed under protection and developed for economic purposes through reforestation (Ketskhoveli, 1942). The tugai forests of Azerbaidzhan were being rapidly destroyed as early as the first half of the 20th century.

As the tugai vegetation disappeared, bear, panther, tiger, lion and deer were displaced from the semidesert and the range of boar shrank.

This brief review of the direct and indirect effects of human activity on the Holocene faunal complex of the Kura-Araks lowlands shows that it resulted in an impoverishment in large mammals. Some enrichment in the specific composition of the complex was caused by the appearance of bats and the enlargement of the ranges of small mammals inhabiting protected biotopes (white-toothed shrew, common hedgehog, jackal, hare, common field mouse, black rat, etc.).

The destruction of tugai forests and the expansion of cultivated and irrigated areas resulted in the gradual enlargement of the ranges of small semidesert mammals on the margins of the semidesert, and in the migration of forest species to the central parts of the semidesert.

The most recent changes in the ecological assemblages and faunal complex of the semidesert mammals in eastern Transcaucasia were caused by purposeful human activity: the continuing efforts to exterminate the steppe vole, red-tailed Libyan and Asia Minor gerbil, jackal, wolf and jungle cat, and the drawing upon wild-life resources (as game) such as hare, fox and boar. The goitered gazelle remains officially under protection, but, lacking a steppe preserve and adequate supervision, is gradually becoming extinct.

Large-scale extermination of the steppe vole, the chief pest in grain fields, began early in the 20th century through extensive irrigation and the spreading of poisoned bait (Satunin, 1912a; Rodionov, 1924; Vereshchagin, 1942c, 1946b).

Not until the 1940's were attempts made to exterminate the red-tailed Libyan gerbil by introducing chloropicrin into its holes and by trapping. This was done on the Apsheron Peninsula and, to a lesser extent, on the Mugan and in the Karabakh foothills. In no instance were these operations successful
537 in reducing the total distribution area of this gerbil, although in years of high reproduction rates they were carried out in areas of many hundreds of thousands of hectares. The complete extermination of steppe vole and gerbil on the Kura-Araks lowlands does not appear to be economically feasible at the present technological level. With this in mind, it is suggested that the populations of these pests can be restricted by plowing stubble fields and using poisoned bait, giving due consideration to the viability of the populations and weather forecasts (Polyakov, 1950).

The greatest damage to livestock and game is caused by wolves, jackals and jungle cats, which are far from being completely exterminated by the usual hunting methods. The statistics of pelt yields of these species for the years 1925-1955 show that fluctuations in the yields were controlled by the activity of the fur trade and the amount of the premium paid for each pest that was killed. For example, a 500% increase in the price paid for a jackal in 1949 increased the yield by 500%.

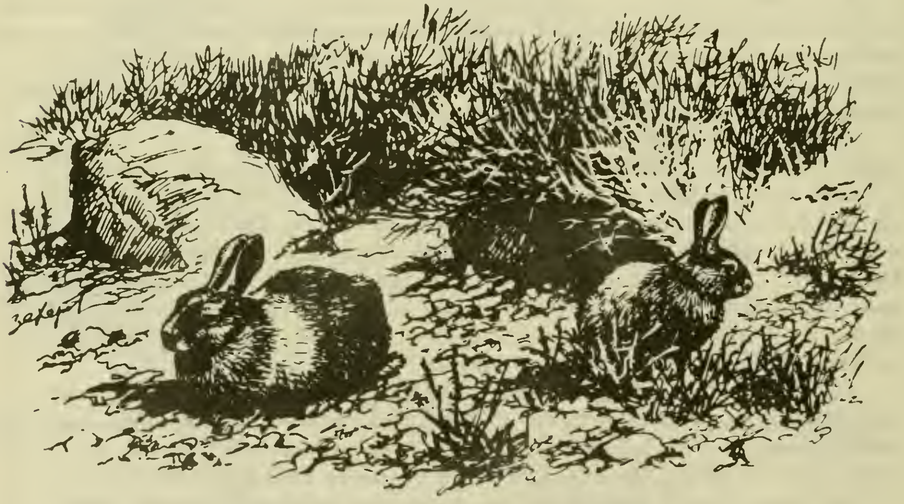


FIGURE 201. Rabbits grown wild on Bulla Island

Planned introduction of alien species into the ecological assemblages of the semidesert was carried out in order to increase the yield of the valuable furs.

In the second half of the last century, rabbits of the species Lepus cuniculus L. were introduced by sailboat captains and lighthouse keepers onto the Caspian islands of Zhiloi, Nargen, Bulla, Oblivnoi and Svinoi. They became acclimatized and grew wild. In 1931-1952 [sic] small groups of the Viennese blue rabbit were released on the islands of Urunos, Zhiloi, Bulla, Los' and Oblivnoi in order to establish a rabbit trade.

These varicolored wild animals, whose average weight is 1.5 kg, live and reproduce on these islands almost entirely without peril from terrestrial enemies, and unhindered by lack of fresh water (Figure 201). In 1940 approximately 500 rabbits inhabited Bulla Island (Vereshchagin, 1942b). The only check on their population increase is unlimited shooting
538 by lighthouse keepers and visiting hunters and inadequate food and shelter. The compacted volcanic mud of the islands is easily eroded by winter rains and becomes unsuitable for digging holes. The rare Salsola dendroides, Frankenia, Ephedra, glasswort and shoots of hare barley and meadow grass, which die out by June, do not provide sufficient forage. Constructing artificial shelters and supplying additional food would be the important steps in organizing rabbit farming in this area.

Since 1931 nutrias have been introduced into a number of plain water bodies overgrown with reedmace—cattail (Figures 202, 203; Map 95).

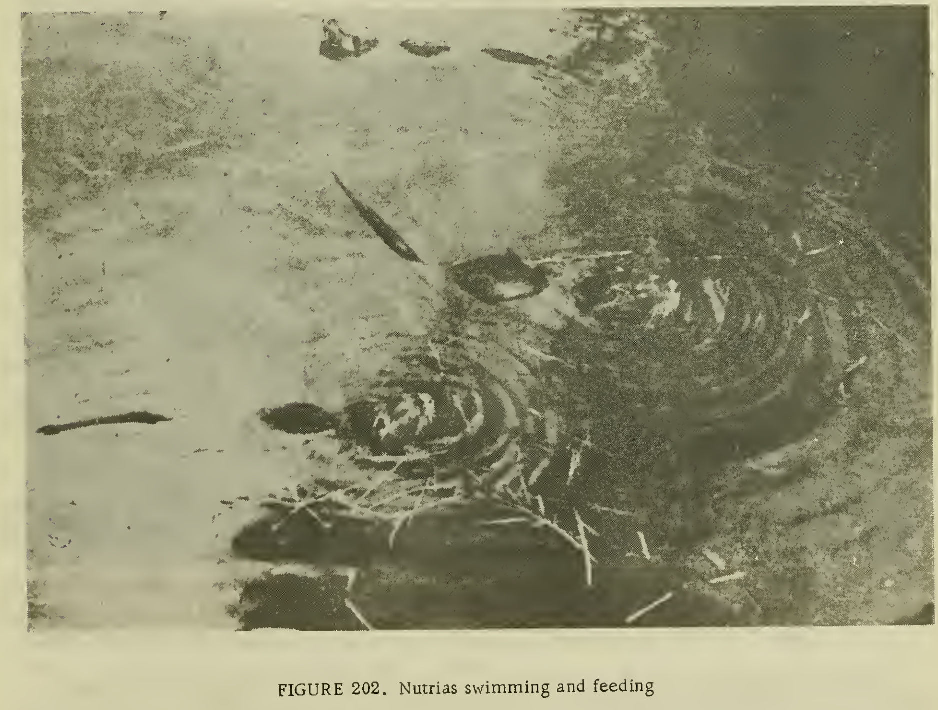


FIGURE 202. Nutrias swimming and feeding

Photograph by author, 1948

The factors limiting the increase and dispersion of nutria populations were frost, winter-freezing and summer-drying of water bodies. Under these circumstances large numbers of nutria are easy prey for jackals and dogs (Vereshchagin, 1936, 1939c, 1942b, 1950a). The natural dispersion and range development of nutria followed the basins of the interconnected lakes, Shil'yan and Kara-Su, at the rate of 15-20 km a year. The populations and the yields, however, were unstable (Graph 20).

At present stable natural populations of nutria occur only on sections of spring-fed rivers which never freeze, e.g., Lake Khuluflu in the Shamkhor District and the Kara-Su rivulets at Karayazy. Notwithstanding these difficulties, there are good prospects for the free breeding of nutria in Azerbaidzhan if certain conditions are met: a regular water supply to the basins, the availability of winter corrals and a stock of animals in the corrals for emergency situations, such as heavy frost or drought.

It can be anticipated that large-scale irrigation operations and afforestation will produce much more pronounced changes in the semidesert
539 ecological assemblages in the near future. The construction of the Mingechaur reservoir has already created the possibility of irrigating another million hectares of steppe land.

FIGURE 203. Cattail thicket, thinned by nutrias, on Lake Shil'yan

Photograph by author, 1948

The construction of the irrigation network will allow heavy repeated irrigation, further expansion of cotton planting and grassland crop rotation. Improved methods of extermination used on the dry gaps, canal banks and other places will depress the populations of jerboas, gerbils and steppe voles in the vast lowland areas. The planting of shelterbelts and shrub thickets will expand the distribution ranges of white-toothed shrew, common hedgehog, jackal, weasel, jungle cat, hare and steppe mouse and, to a certain extent, black rat.

Hunting, therefore, must be controlled and measures taken to prevent the development of dangerous epidemiological conditions.

Any further enrichment of the mammalian complexes of the Transcaucasian steppes and semideserts by new species of game animals has limited prospects in the environment of the cultural landscape.

Commercially useful rodents, as well as those that are pests, are not tolerated in fields of grain and industrial crops. And, lacking the rodents which are their chief food supply, small species of furred carnivores either die out or begin to prey on poultry and wild birds. Therefore, the project of introducing Siberian polecat into eastern Ciscaucasia, where the rodent populations are subject to considerable fluctuation, is economically and biologically unsound. Wild ungulates such as goitered gazelle, saiga and some other African antelopes (gnu, bubaline and other species) will be
540 able to live on those sections of land which are unsuitable for irrigation and agricultural development, e.g., in Kabristan and the Dzheiran-Cheli steppe.

The Pleistocene occurrence of saiga in Transcaucasia and the experimental release of 20 specimens on Bulla Island in 1950 indicate that the introduction of this species is quite possible. Clearly, however, without adequate protection, these new immigrants to the steppes would be as disadvantaged as the goitered gazelle.

FOREST-STEPPE AND FOREST ZONES

In the development of the most recent ecological assemblages and mammalian complexes of the forest-steppes and forests of the Caucasus, the anthropogenic factors are interwoven in a complicated pattern with the natural factors.

The postglacial mountain landscapes of the Caucasus formed under conditions of general warming and lower humidity. As the glaciers melted, vast areas in the glacial valleys and on the slopes of the Main Range in the western Caucasus became covered by meadow and mountain-forest vegetation which migrated from the lower zones and over the spurs of the longitudinal ranges.

Biocenotic relationships of the Recent type formed in the mountain-forest zone as developing forest groupings expanded over the subalpine meadows (Tumadzhanov, 1947). The continued warming and increasing drought created an encroachment of steppe formations on the forests.

The uplift of some sections of the foothills forest-steppe zone during the xerothermal phase of the Holocene was considerable and, because of it, chernozems developed at altitudes as high as 1,000 m on the western spurs of the Greater Caucasus and near El'brus (Yakovlev, 1914; Zakharov, 1935; Berg, 1947; Klopotovskii, 1948).

During the next phase of the Holocene (the beginning of our epoch), the process probably operated in reverse with the forest formations encroaching on the steppes, a development which was particularly pronounced on the piedmont plains.

The cenotic evolution of Caucasian forest assemblages in the Quaternary has been discussed by Sinskaya (1933) and Kolakovskii (1947a) on the basis of geobotanical analysis. In the present epoch, however, the natural development of successive formations of trees was not significant in the formation of landscape and ecological assemblages of mammals; indeed, haphazard cutting and burning of forests and cattle grazing greatly outweighed the natural processes. Because of human activity the oak, pistachio and hornbeam forests of the foothills degenerate to thickets of xerophytic deciduous thorny shrubs, which are later replaced by beard-grass steppe, or even by phrygana. Cutting of the mountain beech forests promotes the growth of hornbeams, and grazing further results in the development of birch groves and rhododendron thickets, which finally grade into subalpine meadows (Bush, 1935; Yaroshenko, 1940, 1945).

According to botanists and soil scientists, the foothill and plateau forests of the Caucasus covered a larger area in the earlier historical epoch than they do at present. Their conclusion is based principally on the occurrence of relics of ancient forests in areas which are now steppes, particularly in Ciscaucasia and Armenia (Bush, 1900, 1935; Kuznetsov, 1900; Troitskii, 1927, 1939; Takhtadzhyan, 1941; Grossgeim, 1948).

541 The formation of other plant assemblages in areas of destroyed forest and new forest growth in various regions of the Caucasus was undoubtedly controlled by specific local conditions created by the ecological situation and the natural process of vegetation replacement.

However, the most recent natural trend caused by climatic changes toward replacement of steppe formations by forests (Zakharov, 1935) and conversely of forests by steppe formations (Yaroshenko, 1940, 1956) is completely overbalanced by human activity which always leads to the development of xerophytic vegetation (Map 97).

Man's early influence on the mountain forests was mainly reflected in the contraction of the upper and lower boundaries. But commercial deforestation during the last centuries has exposed the slopes on a large scale and caused the formation of forest glades and woodless belts over the entire altitudinal range (see Zaklinskii, 1931; Solntsev, 1940).

Deforestation in the Caucasus produced these general consequences: the soil became desiccated; vegetation of a definitely xerophytic type replaced the forests; the climate changed, becoming less humid and having less atmospheric precipitation, because fog no longer condensed on the leaves and branches of trees; erosion increased sharply and as the soil layer was removed, gulleys and mudflows formed (Kirillov, 1915; Roshchin, 1928, 1930, 1931).

Almost everywhere the destruction of the forests brought about a displacement of typical forest ungulates — deer, roe deer, elk, bison; of forest carnivores — bear, pine marten; and of arboreal rodents — fat dormouse, Persian squirrel and, partially, Caucasian yellow-spotted mouse. The effects of deforestation on those rodent species which do not depend heavily on forest habitats (e.g., vole and common field mouse) were more complex. Another result was the invasion of the mountain slopes, exposed and desiccated by deforestation, by relatively xerophilous rodents and carnivores from adjacent zones of open landscape. Specific local changes also occurred in each geographic district; these were associated with the particular composition of the mammalian fauna and the particular structure of the environment. They are discussed below according to natural zones.

Ciscaucasian forest-steppe

The broad belt of the Ciscaucasian sloping plains extends from the Taman Peninsula in the west to the Caspian coast and Mount Beshbarmak in the east. Its southern boundary is formed by the steep slopes of the Greater Caucasus, its northern by the latitudinal sections of the Kuban and Terek and the northern slopes of the Stavropol Plateau.

In the xerothermal postglacial epoch this zone was probably covered by steppes and in the sub-Atlantic epoch by oak forest alternating with meadow and meadow steppe on the divides. The contemporary forest-steppe landscape of this zone is clearly secondary and anthropogenic (Bush, 1900; Tumadzhanov, 1947, and others).

The ancient sections of the dry steppe, Lower Quaternary in origin, have survived only between the Tertiary hills of the Terek and Sunzha ranges and on the southern cliffs of the limestone ridges of the foothills, and in the northern foothills of Dagestan.

The archaeological studies of Gerts (1870), Farmakovskii (1914), Uvarova (1900), Gorodtsov (1935, 1936), Anfimov (1935), Iessen (1940), Krupnov (1946, 1947, 1948, 1949) and Kruglov (1946a) show Early and Late Bronze Age settlements built on these piedmont plains. The settlements
542 are representative of Maikop, north Caucasian, Koban, Scytho-Sarmatian and Hellenic cultures. In the present era the region was settled by Alanis who were gradually driven out by migratory Moslem tribes. Mischenko (1923, 1928) and Zakharov (1935) report that the relict oak—hornbeam forests of the Trans-Kuban Plain have in this era overgrown the Scythian mounds which were originally built on the steppe.

There were still many isolated forest islands and ritual groves of the Adygeians ("kodoshi" or "kudoshi") remaining on the plain in the middle of the last century, indicating that in the past the area was covered by extensive tracts of forest (Veidenbaum, 1878).

The destruction of these forests by the local population was nearly complete by the time of the first large-scale settlements of the Cossacks in the mid-19th century (Felitsin, 1884; Shcherbina, 1913).

Their large settlements of warriors and hunters were built at that time in the valleys of the left tributaries of the Kuban and the right tributaries of the Terek and Sunzha. These valleys grown with tugai thickets were main routes for the seasonal migrations of large animals (boar, roe deer, deer, bison) from the mountains to the plain, and were particularly important for the survival of these species during catastrophic snowfalls in the mountains. The deforestation of the divides and the establishment of villages ("check-posts") in the valleys therefore disrupted the established pattern of migration and led to death from starvation which, along with hunting, brought about the extermination of the ungulates. The boar, forced to remain in the mountain forests during winters of heavy snow, was particularly affected. The clearing of tugai thickets in the lower floodplain valleys of the left tributaries of the Kuban and the concomitant changes in the hydrological regime of the streams resulted in the disappearance of river beaver from this area.

The continuing replacement of forest-steppe by the contemporary cultural landscape on the Trans-Kuban Plain with great areas of arable land, pastures and settlements caused the displacement of pine vole to the foothills, reduction in the population size and distribution area of the common field mouse, and an increase in the population size of the common vole, Asia Minor and common hamsters, migratory hamster, steppe mouse, mole rat, hare and fox.

Overgrazing by cattle formed bare dry areas on the bottoms of the valleys and near the canyon mouths; this promoted the rapid migration of the species mentioned to the zone of the mountain forests, as, for example, in the vicinity of Krymskaya, Il'skaya and Goryachii Klyuch.

On the sloping Kabarda Plain small forest islands were preserved only in some gulleys and river valleys, and in the Pyatigor'e area.

The width of the deforested zone between Pyatigorsk and Georgievsk and between Nal'chik and Prokhladnaya is at present 30–40 km.

Only 200 years ago this plain was still inhabited by roe deer, deer, elk and bison; at present it is characterized by a relatively impoverished assemblage of synanthropic species and small agricultural pests. The continued extermination of the forests on the low ridges of the piedmont in the Nal'chik District results in the drying of the rivers. The mountain slopes, desiccated by deforestation and overgrazing, remain for some time covered with nut trees and hornbeams, which gradually retreat up the slope. Hare, common and black hamsters, steppe mouse, mole rat and northern mole vole follow this retreat.

543 Forest belts have recently been planted on the Kuban-Kuma divide to lessen gulley erosion and summer drought.

Similar changes have taken place in the ancient landscapes of the more humid Terek-Sunzha valley. Near Alagir there is a grove of 300-year-old lindens, beeches and filberts called Khetag, sacred to the Ossetians, which was visited by Pallas. The existence of this grove indicates that the area was covered in the past with well-developed piedmont forests, which were inhabited by bison, elk, deer and roe deer.

The consequences of deforestation can be seen in the changes in specific composition and distribution ranges of the mouse-like rodent fauna.

Pine vole and common field mouse have been displaced to the wooded foothills from the plains, which were then occupied by wheat-crop pests, common vole, hamster and migratory hamster. In this region the extensive fields of vegetables and corn and the rivers which never freeze provide a suitable habitat for Norway rat which does damage to the fields and vegetable gardens (Bogdanov, 1929). The xerophilous tiger polecat migrated here from the direction of the arid Sunzha Range; its distribution area extends to the wooded slopes of the Chernye Gory Mountains (Turov, 1926b).

As the result of cutting and overgrazing, the oak and beech forests of the Chechen foothills and northwestern Dagestan between the lower Sunzha and Sulak canyons were replaced by a peculiar bushy thicket consisting of filbert (Coryllus avellana), pear (Pyrus caucasica), plum (Prunus divaricata), common buckthorn (Rhamnus cathartica), Cornelian cherry (Cornus mas) and other species (Grossgeim, 1948).

Of the earlier assemblage of forest mammals in this area only mole, European wildcat, lynx, forest dormouse, boar and roe deer still occur in some places; bear, fat dormouse and deer have disappeared.

Between Makhachkala and Derbent some parts of the low foothill ridges have been planted for centuries to grapes and corn. Of the old forests of these foothills there now remains a xerophytic formation in which Christ's-thorn (Paliurus spina christi) and hornbeam forests predominate. All of these changes were favorable for the widespread infiltration of little suslik, steppe vole and migratory hamster into the foothills. Geptner and Formozov (1941) noted that the species which has invaded Dagestan the most extensively is the vole. However, it can be deduced from the situation in eastern Transcaucasia that the more mobile and widely distributed migratory hamster, although less numerous, was more rapidly dispersed through the deciduous shrub formation in the gulleys.

Farther south along the lower Samur and other rivers on the Khachmas lowlands, the forests are partially preserved. The continuous wooded tracts of the past are now reduced to a forest "network" — narrow belts, covered by liana, surrounding large clearings now converted to the cultivation of corn and vegetables. Even in its present state, however, the region is still inhabited by some boars, roe deer and numerous fat and forest dormice and steppe mice.

The steppe vole has migrated from the dry hills of the Kusary Plain to the deforested sections and forest glades. On the rice fields peculiar hydrophilous populations of steppe mouse, Mus musculus tataricus, similar to M. musculus hortulanus, have developed. Their hydrophilous habits were, of course, formed long ago, since they
544 also inhabit the margins of cattail marshes and are not solely dependent on the rice fields. These do, however, provide them with abundant food, shelter and storage places in the demarcation embankments (Vereshchagin and Mamedov, 1946).

Corn and sunflower crops in melon cultures attract equally large numbers of steppe mice to clearings as to the old rice soil (chaltyk). This is due to rapid development of wheat strains: green bristlegrass — Setaria viridis, reed canarygrass — Phalaris arundinacea, barnyardgrass — Echinochloa crus-galli. European hare and common field mice feed in the clearings at night.

TABLE 111. Composition and relative abundance of small mammals (number of animals per 100 traps) in various biotopes in the Samur forests in October 1945

	Old forest on dry lands		Edges of forest with liana bordering streams and fields		Corn and sunflower fields		Land under melon cultivation with weeds		Rice fields		Total number of specimens
	number of specimens	%	number of specimens	%	number of specimens	%	number of specimens	%	number of specimens	%	
Crocidura russula güldenstaedti	2	22.2	4	44.4	1	11.1	1	11.1	1	11.1	9
Mus musculus formosovi	2	25.0	5	62.5	—	—	—	—	1	12.5	9
M. musculus tataricus	—	—	—	—	13	36.2	5	13.9	18	50.0	36
Apodemus sylvaticus	10	55.5	5	27.8	2	11.1	1	5.5	—	—	18
A. agrarius	—	—	7	100	—	—	—	—	—	—	7
Microtus socialis	—	—	—	—	7	100	—	—	—	—	7
Dyromys nitedula	1	20.0	4	80.0	—	—	—	—	—	—	5
Glis glis	1	25.0	3	75.0	—	—	—	—	—	—	4

Table 111 sets forth the count of insectivores and rodents from trappings in this district in October 1945.

As a result of the conversion of the Khachmas lowland forests to crop areas, the ranges of hare, fox and jackal expanded, steppe vole appeared in the area and the striped field mouse, which concentrates in the margins of forests, increased in population.

The broad Kusary (or Kuba) sloping plain, covered with Quaternary gravels and loams, lies between the Khachmas lowland and the ranges of southeastern Dagestan. The forests of this plain were cut down during the last centuries and the deforested areas grown over mainly with Christ's-thorn, hawthorn, blackberry, hornbeam and filbert, or planted to wheat and barley. Large apple and quince orchards were planted near the villages.

During the present era far-reaching and complicated changes took place in the distribution and populations of the carnivores, hares, mouse-like rodents and ungulates of this plain. Bear disappeared; fox, jackal, badger and hare populations have probably increased somewhat, and steppe vole and steppe mouse became widely distributed.

545 The distribution of the common field mouse assumed a mosaic pattern, corresponding to relict forests and shrub thickets. Abandoned plowed lands and pastures were extensively occupied by steppe vole and mouse and the lower boundary of the common vole range moved upward somewhat.

The recent construction of the Samur-Divichi canal and cultivation of rice favored the formation of hydrophilous populations of steppe mouse.

Fat dormouse occurs in only a few parts of the relict aged forest, although forest dormouse is still widely distributed.

The prospects for introducing new species into the mammalian fauna of the Ciscaucasian foothill forest-steppe plains is rather poor.

Desmans have been released at a number of lake and reservoir locations. Raccoon dog and common raccoon occur in some parts of the Trans-Kuban and Terek-Sunzha plains (Map 94).

The immediate future for this zone is further development of gardening, acceleration of agriculture, rapid population growth and expansion of settlements. Forest belts should be established in the driest areas. Game control measures should take into account the moderate increase in the population of European hare, the increased abundance of fox and the localized increases of mink and Siberian polecat. Agricultural planning should be directed toward the extermination of hamsters and voles in the western half of the zone, and of steppe voles and mice in the eastern half.

No nature preserves have been established in the area, and by now such measures are long overdue.

Changes in the landscape and the mammalian assemblages, similar to those described above, also occurred on the piedmont plains of eastern Transcaucasia.

Transcaucasian forest lowlands

In the Holocene the warm, humid lowlands of western and eastern Transcaucasia (Colchis, Alazan-Avtaran and Lenkoran) were covered by marshland forests with broadleaf species and thorny liana predominating.

The nature of these primitive virgin forests has not been adequately studied (Al'bov, 1892; Sinskaya, 1933; Maleev, 1938; Grossgeim, 1948). Typical species are Quercus longipes, hornbeam, elm, Pterocaria caucasica, black alder and, in the Lenkoran lowland, Parrotia persica.

Man's selective destruction of the lowland forests produced many marginal sections overgrown with lianas: Smilax excelsa, Hedera helix, Clematis vitalba, Periploca graeca, and glades overgrown with bracken, blackberry or Christ's-thorn and spiny Juncus.

The mammalian assemblages developed in different ways in various sections in response to human activity because, while the landscapes are homogeneous, the topography is diversified,

The relics of human culture have been more completely studied in western Transcaucasia where monuments of the Bronze Age (Colchidian, Hellenic and later) are common in Middle and Upper Paleolithic sites throughout peripheral areas of Colchis (Rion lowlands).

In the present era large settlements with corn plantations and fruit orchards were established in Colchis. The populations and specific
546 composition of the mammalian fauna were heavily damaged through direct extermination efforts and shrinkage of the forest-covered areas. In this region river beaver became extinct at the end of the 19th century, red deer disappeared later, and boar and roe deer survived only in some isolated marshes.

In 1930 operations to drain the Rion marshland (Figure 204) by means of silting and canals were commenced (Zunturidi, 1931; Shaposhnikov and Vereshchagin, 1932). At the same time the alder forests were cut and the land was planted to tea, corn, tangerines and eucalyptus.

FIGURE 204. Alder—water lily marshes near Poti — typical habitat of nutria and Norway rat

Photograph by author, 1931

All these processes created abrupt changes in populations and composition of the mammalian fauna.

The populations of jackal and wolf were supported by poultry- and cattle-breeding activities. Gardens and many marginal sections of relict forests overgrown with liana promoted an increase in the fat and forest dormouse populations, while the deforested, arid meadows became inhabited by pine vole.

The evolution of mammalian assemblages promoted by the drainage of the alder marshes and other kinds of production-oriented human activity is shown in Table 112. Our observations, trappings and tabulations were made in the fall and winter of 1938-39 and 1940 near the eastern shore of Lake Paleostom and near Lake Bebesyri.

Most of the mammalian species disappeared from areas planted to tea, tangerine, lemon and tung-tree because the plantations did not furnish the animals with shelter and food.

The synanthropic assemblage in the agricultural settlements of Colchis developed partly from introduced species (Norway rat and house mouse) and partly from native species (black rat and common field mouse). Shidlovskii (1947) tabulated the following numbers of rodents caught per 1,000 traps in residential buildings on the Black Sea coast: house mouse —
547 158; Norway rat — 125; black rat — 17; common field mouse — 13. The latter species does not occur in the larger settlements of the lowland. Stepanov's data on rodents caught and studied by the anti-plague laboratory at Batumi show for an 18-year period: 44,771 mice, 40,000 Norway rats, 3,505 black rats and 1,588 Alexandrine rats. According to Stepanov, the mice and rats are approximately equal in numbers at Batumi.* The mice mainly inhabit residential (apartment) buildings, while rats live and feed outside the apartments.

548 Clearly the general trend of evolution of the mammalian assemblages during the development of the contemporary cultural landscape of the Colchis lowlands is toward extreme impoverishment of the assemblages. The large ungulates and medium-sized carnivores disappear, and the populations and species composition of most local rodents decline.

Human activity in the Alazan-Avtaran lowland in northwestern Azerbaidzhan, which has a different topography, affected the mammals in a very different way than in the Colchis lowland. The Alazan-Avtaran lowland is a valley 20-25 km wide and almost 300 km long, extending from the village of Akhmeti in Georgia to the village of Ismailly in Azerbaidzhan. Relict forests of Quercus longipes and hornbeam remain mainly in the eastern part of the valley. Human activity here reaches back as far as it does in Colchis. Remains of settlements of the first millennium B. C. are known from the vicinity of Belokany, Kutkashen and Nidzh. The lowland is now quite densely populated, the chief centers being in the middle and at the canyon mouths. The mountain rivers have been diverted by means of additional channels and ditches for irrigation of the rice (Figure 205), wheat and tobacco fields and the fruit and nut orchards. Man worked the greatest changes in the landscape and in the mammals of the area by cutting the forests and subsequently planting walnut, hazel nut, chestnut, apple, pear, wild cherry, plum, medlar, quince and grape and by plowing the forest glades for cultivation of barley, wheat, corn, rice, tobacco and sesame.

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* This is highly questionable; as a rule, mice are more abundant.

549 The margins of fields, banks of irrigation ditches and sections of pasture became overgrown with hawthorn, blackberry, blackthorn, Christ's-thorn, plume grass and reeds. The edges of forests and settlements are characterized by strongly developed annual weeds, shrubs and trees, particularly European elder and ailanthus.

(547) TABLE 112. Changes in the specific composition and relative abundance of mammals caused by drainage and cutting of lowland forests in western Transcaucasia

Species	Forests of Colchidian type	Forest glades with bracken and marshy meadows and pastures	Corn fields	Tea and citrus plantations
Insectivora				
Sorex araneus	x	x	x	x
Crocidura russula monacha	x	x	x	x
Talpa coeca	x	x	—	x
Erinaceus europaeus	x	x	x	x
Carnivora				
Cannis aureus	xxx	xx	xx	x
C. lupus	x	x	x	—
Vulpes vulpes	—	x	x	—
Mustela nivalis	x	x	x	x
Meles meles	x	x	x	—
Lutra lutra	x	—	—	—
Felis silvestris	x	—	—	—
Lagomorpha				
Lepus europaeus	—	x	x	x
Rodentia				
Mus musculus	x	xx	xx	x
Apodemus sylvaticus	x	x	x	x
Rattus rattus	xx	xx	xx	—
* R. norvegicus	xxxxxx	xx	xx	—
Microtus majori	x	xx	xxx	x
Arvicola terrestris	x	—	—	—
Dyromys nitedula	x	—	—	—
Glis glis	x	—	—	—
* Myocastor coypus	x	—	—	—
Artiodactyla				
Sus scrofa	x	—	—	—
Capreolus capreolus	x	—	—	—
Total	21	15	14	10

Note. Symbol x designates the presence and relative abundance of each species; asterisk (*) denotes species introduced either accidentally or purposefully.

The original thickets were often restored on the sites of abandoned settlements. However, the original species of trees were replaced by different groupings with an admixture of introduced species. For example, the site of the town of Chukhur-Kabala was overgrown with alder, Pterocarya caucasica, poplar, maple and species which made a secondary return in a wild state, such as hazel nut, walnut and plane.

The cutting and burning of the jungle drove out the large animals such as boar, deer, roe deer, bear, lynx, European wildcat and panther, as well as pine marten, fat and forest dormice and squirrel, while increasing at the same time the populations of fox, jungle cat, badger, hare, vole (steppe, water and common) and black rat.

(548)

FIGURE 205. Flooded rice field in the Agri-Chai valley — an example of complete seasonal displacement of mammals

Photograph by author, 1950

As the nut and fruit orchards age, the assemblage of forest mammals is almost completely restored. Some species increase because of the abundant food supply and available shelters in rock walls. These are fat and forest dormice, Persian squirrel, common field mouse (to some extent), Transcaucasian subspecies of the Caucasian yellow-spotted mouse, mountain house mouse and long-tailed white-toothed shrew. The common field mouse became a synanthropic house rodent in this region. The changes in the specific composition and relative abundance of mammals in diverse habitats of this lowland are shown in Table 113.

In summary, then, the deforestation and planting of the lowlands to cereal and industrial crops in recent times resulted in the disappearance of 6 species of game animals (deer, roe deer, bear, lynx, European wildcat and squirrel) and the increase of 2 species (fox and hare). These processes also brought about the migration of William's jerboa, steppe

(550) TABLE 113. Changes in specific composition and relative abundance of mammals caused by cultivation of field and garden crops in the Alazan-Avtaran lowland

Species	Lowland virgin forest	Forest glades with cereal crops and shrubs	Old nut and fruit orchards
Insectivora			
Crocidura russula güldenstaedti	×××	××	××××
C. leucodon	—	×	—
Sorex araneus	×	×	×
Erinaceus europaeus	×	×	××
Carnivora			
Canis aureus	×	××	××
C. lupus	×	×	×
Vulpes vulpes	×	××	×
Ursus arctos	×	—	×
Mustela nivalis	×	××	×
Martes foina	×	—	×
Meles meles	×	×	××
Lutra lutra	×	× (on rivers)	×
Felis chaus	×	××	×
F. silvestris	×	×	×
F. lynx	×	—	×
* Procyon lotor	×	—	××
Lagomorpha			
Lepus europaeus	—	××	×
Rodentia			
Mus musculus abbotti	××	××	×××
* M. musculus tataricus	—	××	—
Apodemus sylvaticus	×××	×	××××
A. fulvipectus	××	×	×××
Rattus rattus	—	×	× (near settlements)
* Microtus arvalis	—	×× (near mountain slopes)	—
* M. socialis	—	××××	—
Arvicola terrestris	—	× (on rivers)	—
* Allactaga williamsi	—	×	—
Dyromys nitedula	×	×	×××
Glis glis	××	—	××××
Sciurus anomalus	×	—	××
Artiodactyla			
Sus scrofa	××	×	×
Cervus elaphus	×	—	—
Capreolus capreolus	×	—	×
Total	24	23	24

Note. Symbol × designates the presence and relative abundance of each species; asterisk (*) denotes acclimatized species and immigrant species from other zones.

mouse and steppe vole from the southern steppes and of common vole from the mountain-forest zone.

In large nut and fruit orchards the assemblage of game species is almost completely restored, and the number of arboreal rodents is on the increase. This is, however, mainly a seasonal phenomenon controlled by the fall migratory pattern which brings these animals, inhabitants of mountain forests and wooded gulleys, to the orchards which are rich in food.

The synanthropic assemblage of the large market-gardening villages in the lowland consists almost entirely of local species: common field mouse, house mouse (variety with dark abdomen), black rat, and, to a lesser extent, forest dormouse and long-tailed white-toothed shrew.

The garrets and crevices in houses are inhabited by sharp-eared mouse-eared bat and small vespertilio. The introduced synanthropic forms, house mouse and Norway rat, are now found in all large settlements interconnected by highways.

Much more pronounced changes in landscape and fauna occurred in the lowland-forest zone on the northeastern border of the Karabakh, on the lower Tertera and in southeastern Mugan along the northern margin of Talysh, where the cultural has completely obliterated the original landscape. The nature of the original features can only be deduced now by inference. Because the nut and fruit orchards are limited, there is no possibility of even a partial restoration of the earlier assemblage of forest animals.

551 Only the occurrences of porcupine in the recent past and of black and Norway rat in isolated gardens in the present indicate that the region was previously inhabited by assemblages of forest mammals.

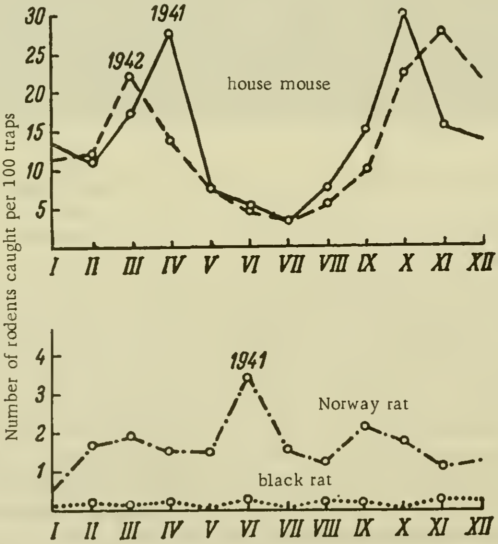

FIGURE 206. Variations in abundance of house rodents (house mouse, Norway and black rats) in Lenkoran and adjacent settlements in 1941-42

Most of the Lenkoran lowland has been subjected until now to changes similar to those described for the Alazan-Avtaran valley. Originally it was completely wooded with thick Hyrcanian forests of oak, alder and Persian ironwood, covered by thorny liana. Large forest glades were first converted to rice fields; later, extensive areas were cleared for tea and tangerine plantations. Combined with the growth of settlements and the development of hunting these landscape modifications have reduced the populations of boar and porcupine and completely driven out bear, tiger, deer and roe deer. Hares migrated to this region from the Mugan following routes along deforested sections and tea plantations. The steppe vole, however, could not migrate either from the upland steppes or from Mugan because of the wet ground in winter. The common field mouse is completely absent and hydrophilous populations of steppe mouse, so characteristic of the rice fields of the Khachmas lowland and southeastern Karabakh, are nowhere to be found in this region.

The populations of jackal, jungle cat, fat dormouse, black and Norway rats and house mouse thrived as landscapes developed: large settlements, orchards and fruit gardens, rice fields, clearings, many strips of dense marginal forest, thorny thickets and hedges surrounding fields, and water reservoirs overgrown with reeds. Boar, which feeds on cereal crops, also remained in the area. There is no large-scale hunting to decelerate the increase in jackal and jungle cat populations which partly subsist by preying on poultry.

Since there are fewer aged trees, the fat dormouse often uses the garrets of residential and industrial buildings as day resting and hibernation places. Garrets and crevices in wooden and stone buildings are also inhabited by Myotis mystacinus. The synanthropic assemblage of house pests consists of only 3 species of rodents: house mouse, Norway rat and black rat. Their relative occurrences, as given by the results of large-scale trappings, are: house mouse — 90.0%; Norway rat — 9.49%; black rat — 0.5% (Vereshchagin, 1949) (Figure 206).

Continuing development of tea, tung and citrus plantations will undoubtedly lead to the cutting of the remaining original forests and a decrease in the area planted to rice. This will produce the most drastic impoverishment in all the ecological assemblages of mammals, creating a situation similar to that described for Colchis.

552 Sparse juniper—pistachio forests of eastern Transcaucasia

It is known from paleontological and archaeological studies (Petrov, 1939; Vereshchagin, 1949c; Gummel and Yatsenko-Khmelevskii, 1941) that the dry foothills of the southeasternmost Greater Caucasus in Kabristan and the Gil'gin-Chai basin, on the Nukha, Kartalinia and Iora plateaus, on the Kirovabad Plain and southeastern slopes of Karabakh and in the Gori depression were covered in the Holocene by the so-called "light forests" consisting of groves of Turkish terebinth (Pistacia mutica) and junipers (Juniperus polycarpos) alternating with sections of beardgrass steppe. By now there remain only small relict sections of these forests, heavily damaged by cutting, on the barely accessible southern cliffs and northern slopes of the Tertiary hills in the Tsivi-Tskaroi, Samukh, Agdash and Geok-Chai districts. Some preserved and ritual groves and trees protected by the Moslems, as, for example, in Kabristan, are also relicts of these juniper—pistachio forests (Vereshchagin, 1949c). Observations in these residual forests show that the light forest was inhabited by bear, striped hyena, wolf, fox, badger, stone marten and red deer.

FIGURE 207. Remains of the riverain and juniper forests in the Tur'yan-Chai ravine

Photograph by author, 1949

The first result of uncontrolled cutting of the forests for firewood and building materials and of accelerated cattle-grazing was the replacement of the juniper—pistachio by Christ's-thorn thickets; at a later stage upland-xerophytic formations of thorny astragali predominated. The pre-18th-century destruction of vast tracts of sparse forest has considerably
553 restricted the distribution of bear, boar and deer. Increased erosion and desiccation of the slopes (Figure 207) have driven the populations of steppe vole and Asia Minor hamster to the northern slopes of the hills and to the plain areas.

Mountain forests of the Greater Caucasus

In the main, the most recent evolutionary stages of the species' ranges and of ecological assemblages in the mountain-forest belt of the Greater

Caucasus are related to the development of the hunting, timber and cattle-breeding industries.

During the last fifty years, bison was exterminated in this zone; the distribution of deer and panther has drastically declined; in many places the populations of bear, boar, roe deer, chamois and Caucasian goat have also considerably decreased.

Extermination of the forests of the lower belt and, later, of the fir forests of the middle and upper belts has been described by Dinnik (1911) for the northwestern Caucasus. Commercial cutting of fir and beech forests in the valleys of the Zelenchuk, Teberda and other rivers began in the 1890's.

The greatest deforestation caused by cutting and cattle grazing occurred on the crests of the ridges descending in a fan-like pattern to the Taman Peninsula. The formation of forest glades with mesophytic meadows increased the population of pine vole and improved the food supply of boar, roe deer and deer.

Deeper in the canyons the process of deforestation was accompanied by orchard planting. Long ago the Circassians planted pear, quince and medlar along the tributaries of the Afips, Psekups and other rivulets; and after they were driven out in the second half of the last century, the pear plantings grew wild and expanded over the canyon bottoms penetrating to and sometimes into the broadleaf forests. These peculiar pear forests, described by Maleev (1939a), were rich in food, particularly in the fall, and highly attractive to marten, badger, bear, fat dormouse, forest dormouse, boar, deer and roe deer.

Distribution of the mouse-like rodents was most strongly affected by man's intrusion into the canyon bottoms from which the striped field mouse, harvest mouse and steppe mouse, like the forest-steppe rodents, migrate to the highest points as the canyon bottoms are settled.

The synanthropic mountain assemblage of house species initially develops from the native species, particularly the common field mouse and long-tailed snow vole. The latter species commonly occurs in cellars and house basements and inhabits seed beds and vegetable garden environs (Zharkov, 1949).

To the east, the effects of anthropogenic deforestation of the slopes on the evolution of biocenoses rapidly increase in magnitude due to the progressively drier climate. Extensive clearing of beech and pine forests on the slopes of the Cherek, Urukh, Ardon, Fiagdon and Terek ravines (see Bush, 1931, 1935) resulted in the development on the southern slopes of a dry forest-steppe with formations of tragacanth Astragalus inhabited by hare and migratory hamster, and on the northern slopes of mesophytic meadows inhabited by mole and common and pine voles.

In Transcaucasia, the beech—hornbeam and chestnut forests of the lower belt on the Black Sea coastal terraces from Batumi to Novorossiisk were
554 subjected to particularly extensive destruction.

The once extensive areas of thicket were reduced to small sections of shrubs alternating with bracken. Factors in the deforestation of the mountain slopes in Abkhazia are extensive cutting, goat grazing and forest fires, which prevent new forest growth (Zaklinskii, 1931).

Extermination of forests and development of numerous settlements proceeded concomitantly with the planting of orchards, mainly apple and pear, and decorative plants, and the establishment of parks with planes, eucalyptus, firs, bamboo and other exotic plants.

Under these conditions a patently synanthropic assemblage of mammals developed which is poor in species. These aspects are due to the occurrence of Norway rat in wild habitats, black rat and fat dormouse in fruit plantings, and European wildcat and jackal near the poultry houses in villages and in fishermen's and porpoise-hunters' stations.

One can see additional evidence of the biological reactions of rodents to the newest agricultural methods in the common field and yellow-heeled mice, which have adapted to feeding on cork oak plantings (Sviridenko, 1940, 1944), and in the house mouse which feeds on and inhabits seed beds (Shidlovskii, 1947).

The population of mouse-like rodents in the mountains near Sochi has greatly increased in habitats formed by broken, fallen trees and branches left in forested areas cleared during the war. This waste material provides many additional shelters for the common field mouse, harvest mouse and pine vole. In addition, hares and foxes migrate to the mountains along the cleared sections. At the same time there is a decrease in the Caucasian yellow-spotted mouse population. However, with planned cutting and complete disposal of the fallen branches and twigs, the number of mouse-like rodents drops abruptly in the first year following the cutting, but is restored in the second year when the cleared sections become overgrown with meadow grasses and shrubs. Under these conditions, the black rat is added to the assemblage mentioned (Sviridenko, 1945). Extensive unplanned cutting of forests reduces the abundance of arboreal rodents — forest and fat dormice — which only completely disappear during planned cutting. These observations confirm to some extent Shidlovskii's (1948) conclusion that the distribution ranges of the striped field mouse and harvest mouse expanded in a southerly direction only in the last few centuries under the influence of man on the coastal landscapes.

Deforestation of the mountain slopes of Abkhazia and Adzharia produced a localized population increase in long-clawed mole vole, which occurs in relict forest glades of the forest zone.

On the spurs of the Rachin ridge and on the Surami, Kartalinian and Kakhetian ridges, particularly in the vicinity of Staliniri, Tbilisi and Mtskheti, extensive cutting of beech forests brought about the most recent extension of the distribution area of the Asia Minor hamster and shifts in the ranges of many forest species. The Mukhran valley, which, in the last century, was inhabited by bear, lynx, European wildcat, common field mouse, fat dormouse, boar, roe deer, and deer, was cleared of forests only in the last 50-60 years. By now the sacred "witness" trees are the only remains of the beech—hornbeam forests which covered the area in the past (Figure 208). In recent time the valley has been planted to barley and corn except for the marshlands which are used for haymaking and pastures. The plowed sections were invaded from the west by the Gori
555 steppe vole, European hare, steppe mouse and fox. Only the long-tailed white-toothed shrew remains of the former assemblage of forest mammals.

Deforestation of the mountain slopes and subsequent cattle grazing in the vicinity of Tiflis and Mtskheti has promoted desiccation of the slopes and the eventual replacement of meadow formations by steppe.

There has been no reforestation of this region. Overgrazing is exterminating even the secondary shrub groupings which develop on the northern slopes following cutting of the beech forests. These shrub groupings consist of representatives of the genera Crataegus, Mespilus, Rosa, Prunus, Jasminum, Cerasus, Cotoneaster, Spiraea and Coryllus. On the southern slopes even such shrubs as Juniperus and Paliurus disappear. Christ's-thorn is more viable, but eventually this species also retreats up the slope, not only because of physical destruction, but also because of changes in the physico-chemical properties of the soil which take place during consolidation, desiccation and heating by the sun (Sosnovskii, 1915). This anthropogenic process of progressive aridity promoted the expansion of the Asia Minor hamster, migratory hamster, steppe vole, steppe mouse, hare and fox. The same process has reduced the distribution areas of the forest carnivores, rodents and ungulates. The anthropogenic replacement of the forest by meadow-forest and meadow landscapes took place under more mesophytic conditions on the plateaus of South Ossetia (N. A. and E. A. Bush, 1936).
556 In this region the forest assemblage of large species (bear, deer, roe deer, boar) became impoverished, whereas the populations of common and pine voles increased.

FIGURE 208. Sacred "witness" trees in deforested and plowed Mukhran valley, inhabited by steppe vole

Photograph by author, 1945

Farther east, on the southern slope, the results of the deforestation created by cutting are observable in the districts of Kvareli, Zakataly, Nukha, Kutkashen and Shemakha. Cattle grazing on the upper margins of the forest prevents new forest growth, as the soil is compacted and desiccated (Yaroshenko, 1956). As the forests were gradually cleared, cattle-drive routes, several tens of meters in width, developed to connect the lowland with the highland pastures. These bald belts, which, as a rule, follow the crests of the longitudinal ridges, serve as migration routes for foxes and hares which inhabit the lowlands and the highlands.

FIGURE 209. Desiccated mountain slopes resulting from forest cutting on the middle Gerdyman-Chai River, inhabited by stone marten and common field mouse

Photograph by author, 1949

Migrations of these animals are easily observable in the fall and during snowfalls. In the districts of Kvareli, Lagodekhi and near Vartashen the extensive deforestation of the slopes over a long period of time has probably enabled the common vole to migrate from the highlands and to inhabit the Alazan-Agrichai valley.

The recent extermination of forests has had a particular and radical effect upon the composition of the mammalian fauna near the eastern end of the Greater Caucasus, between Shemakha, Lagich and Konakhkent. In this area the beech—hornbeam and oak forests of the upper belt were mostly replaced by mesophytic meadows on the northern slopes of the gorges or by thickets of low shrubs.

In the middle zone, at altitudes from 700 to 1,300 m, the desiccation of the slopes and development of the steppe assemblages result from the 557 cutting of forests and cattle grazing. The effects of these processes were compounded by the karst topography (Figure 209).

Of the large animals, east Caucasian goat survived in the upper reaches of isolated canyons, and boar and some bears in relict islands of oak forests. The pine marten, deer and roe deer have been completely driven out.

Xerophilous mammals migrate to this region from Shemakha on the piedmont steppe.

Migratory hamster, steppe mouse and hare occur at altitudes near 1,200 m in the vicinity of the village of Demerchi. The boundary of the distribution range of the steppe vole is at a lower altitude — 800-900 m.

As a whole, the area is characterized by steppe landscapes on the plateaus and by mammalian assemblages which are peculiarly impoverished by an undersaturation of species.

In summary it may be noted that the direct influence of man and the development of anthropo-cultural landscapes in the forest zone of the Greater Caucasus result everywhere in a general decline in the populations of the large game species (bear, boar, deer, roe deer, goat, chamois), in the disappearance of characteristic forest species (pine marten, fat dormouse, squirrel), and in a highly differential redistribution of the mouse-like rodents.

LONGITUDINAL VALLEYS OF THE GREATER CAUCASUS AND INNER DAGESTAN

The so-called longitudinal valleys are located between El'brus and inner Dagestan in the east, between the Peredovye range. The valleys form a line of giant funnels, separated by low ridges. This peculiar xerophytic warm zone, protected in the north by the ranges as by a screen, is a refuge for a number of xerophilous and thermophilous animals and plants. Botanists Krasnov (1893-1894) and Kuznetsov (1909) regarded this zone as equal in importance to inner Dagestan in the development of special xerophilous flora. Grossgeim (1948) related the upland xerophytic formation of this zone to the type of tragacanths, which is characteristic of the dry uplands of southwest Asia. However, the xerophytic upland formations with feather grass, wormwood and barberry occur in places west of the El'brus in longitudinal glacial valleys on the Kuban, the Teberda, and the Malyi and Bolshoi Zelenchuk rivers, and in the upper Ingur valley in western Transcaucasia. The longitudinal valleys have been inhabited by man since the Bronze Age; they were the source area of the so-called Kobanian culture (Uvarova, 1900), dated as the first half of the first millennium B. C. The population of these valleys was engaged in cattle breeding and hunting, and later in agriculture. Toward the end of the Middle Ages the populations of the large hoofed mammals (boar, elk, deer, roe deer, Caucasian goat, chamois and bison) became much smaller on the Peredovye ranges, and they were completely driven out of the longitudinal valleys.

The summer migrations of deer from the southern slope of the range were under heavy attack in inner Dagestan, in the canyons of Andi- and Avaz-Koisu, and on Kara-Koisu. The east Caucasian and Bezoar goats were driven off the major part of the ranges, particularly off the plateaus, and sheep became extinct in these areas. Undoubtedly, the latter two species 558 had already disappeared from the Gunib by the Caucasian war years of the middle of the last century.

Human activity enhanced the natural xeromorphic character of the longitudinal valleys and Dagestan, and is responsible in general for the Recent wide distribution of upland-xeromorphic vegetation on the northern slope of the range (Tumadzhanov, 1947). In inner Dagestan, where the forests were never strongly developed, many centuries of continuous destruction of the pines in the upper reaches of the tributaries of the Sulak resulted in their replacement by birch groves (Betula pendula, B. pubescens). This process has to some extent improved the habitats and feeding conditions of deer, Bezoar and east Caucasian goats. The ancient inhabitants of the ravines of Kara-Chai, Kabarda, North Ossetia, inner Dagestan and Svanetia cleared large areas of the ravine floors of rocks, and planted gardens and fields, arranging the boulders in circular piles and in rows. Giant stone walls and small fortresses with towers were often built of granite blocks and slate (Figure 210).

FIGURE 210. Cereal and potato fields near the village of Ushkul' on the upper Ingur. Pine vole and long-clawed mole vole inhabit the marginal areas

Photograph by author, 1948

The boulder rows mentioned above, when overgrown with shrubs and grass, resemble the remains of terminal and lateral moraines. As a rule, these ridges, like stone fences in villages and residential buildings, are sites of concentration of steppe mouse, Ciscaucasian mouse and Caucasian snow vole. The snow voles use the heaped stones and crevices in fences and walls for drying and storing their winter food stocks and for building nests.

559 In the Ardon ravine near Zaramag, Turov (1926c) observed a stable population of migratory hamster inhabiting these stone piles. On the Baksan, Chegem and Cherek, stone fences and abandoned fields are the favorite habitats of mountain suslik, a pest of cereal and potato crops. The mountain water vole concentrates on irrigated fields and in gardens in Kabarda, Ossetia and Dagestan. In these areas the species develops a strong fossorial tendency much like the mole rats of Central Asia. This species is a pest which feeds on the roots of young apple, pear and apricot trees. Furthermore, irrigation water rapidly fills the holes they make and creates additional damage by eroding large sections of the slopes.

In inner Dagestan the Asia Minor hamster and pine vole became pests of cereal crops. Some populations of snow vole on the Gunib plateau have lost the habit of stocking hay for the winter. Instead, they use the hay stocked by the villagers in niches and caves in limestone rocks.

The synanthropic assemblage of rodents in the isolated mountain villages of Dagestan develops from the local species: common field mouse and snow vole.

The potato, barley and wheat fields in a number of ravines of the Grozny Region attracted the boar to the woodless mountains, and also contributed to some increase in the abundance of European hare.

In western Transcaucasia, on the middle and upper Ingur, the clearing of the fir—maple forests on the slopes resulted in the development of meadow formations with Pontic azalea (Rhododendron flavum). Cattle grazing and cutting of shrubs for firewood led to the development of low, weedy motley grass. Xerophilous species of wormwood grew on the southern slopes. As the deforestation progressed, bear, lynx, European wildcat, pine marten, chamois and goat disappeared from large areas.

Continued desiccation of the slopes by the cultivation of cereal crops has driven out the snow and pine voles, long-clawed mole vole, Caucasian birch mouse and common field mouse. Open areas of new pastures and fields were often free of rodents, since the typical field pests (common hamster, common vole) did not occur in the vicinity.

Such isolated mountain valleys are good examples of presently unoccupied ecological niches formed in the process of development of the cultural landscape.

ALPINE MEADOWS AND ROCK AREAS OF GREATER CAUCASUS

Prior to the appearance and development of nomadic cattle raising, the landscapes and mammalian assemblages of this zone were practically unaffected by man. In historical time cattle grazing contributed to the widening of the meadow zone from below due to the lowering of the upper forest margins. However, the growth of the upper parts of the meadow zone was limited by the development of turf meadows which invaded the talus in the mountain passes. Grazing also promoted the expansion of the Caucasian rhododendron (Rhododendron caucasicum), not grazed by cattle.

This, however, prevented the renewal of birch growth. The upper forest belt was lowered during the last century by 150-200 m at some places in the Caucasus as the result of cattle grazing, and also by shepherds cutting timber for firewood. Widening of the alpine and subalpine meadow zone 560 brought about an expansion in the range of the common and pine voles and of mountain populations of hare and fox. Stone-fenced cattle stations, trampled-down and well-manured, rapidly became overgrown with dock (Rumex), thistle (Cirsium), and other species. These localities are refuge sites of common voles which concentrate on the margins of the trampled-down areas under the protection of multi-layered vegetation. Prior to the arrival of shepherds in early summer, bears feed on the green grass in these places, and boars dig in the ground in search of beetle larvae and worms.

Overgrazing (i. e., overloading the pastures) inhibits the development of meadow vegetation. Numerous paths forming a network of steps are made by the cattle on the slopes. The vertical faces of the steps are broken by many holes dug by common and pine voles and long-clawed mole voles. Rainwater and melting snow easily enter the holes, eroding the soil. Fields are laid out in the uppermost parts of the Caucasian meadows, overgrown, as a rule, by Sibbaldia procumbens and cinquefoil (Potentilla) and often inhabited by pine voles. Eventually this destroys the meadow growth over great areas. Large sections of grassy slopes are displaced by cattle grazing and rodent burrowing. The typically rock-strewn areas thus formed are used by Caucasian goats, mainly as shelters and resting places. Intensified erosion from heavy rains brings mudflows charged with stones. In most regions of the Caucasus mudflows are a new phenomenon in historical time, developing during the last two centuries of extensive cattle breeding. Thus, at Nukha the first mudflows occurred in 1889, and at Vartashen in 1895 (Pyl'tsov, 1904). Pyl'tsov wrote in 1904 (p. 268) of the Demir-Aparan-Chai basin in the Kutkashen district of Azerbaidzhan, where particularly powerful mudflow torrents occur: ". . . approximately 25 years ago (i. e., in the 1880's — N. V.) there were not more than 5,000 sheep on the pastures, whereas now there are more than 10,000." Overloading the mountain meadows with cattle exposed large areas of the slopes in the natural amphitheater of this ravine, which in the past was covered by alpine meadows. As a result, the east Caucasian goat, chamois and common vole have been almost completely driven out of the amphitheater.

Nomadic cattle breeding has also affected the wild hoofed mammals: deer, goat and chamois. The cattle introduced various diseases into the mountain zone: glanders, foot and mouth disease, anthrax, brucellosis, mange, demodecosis, favus and helminthiasis. Mortality among wild ungulates, particularly goats and chamois, from diseases introduced by cattle has been recorded from the Caucasian (Dinnik, 1914a; Nasimovich, 1949a, 1949b) and Zakataly reservations (Markov and Mlokosevich, 1935; Vereshchagin, 1938a).

The intrusions of hunters, shepherds with sheep dogs, and flocks of sheep and goats on the highland meadows during the three summer months has considerably affected the natural habits and diurnal cycles of deer, chamois and goat. The deer and chamois developed the summertime habit of remaining during the day in the forest zone and upper forest belt, leaving for the pastures only at night. This is also true of the Caucasian goat in the west (Nasimovich, 1949a). In the eastern part, on the southern slope, the east Caucasian goats form two clearly distinguishable populations in the summer: one inhabits the passes and rock-covered areas of the range and does not descend to the forests; the other remains in the forest, leaving for the upper forest belt and mountain pastures only at night (Vereshchagin, 1938a).

561 FORESTS ON THE NORTHERN SLOPES OF THE LESSER CAUCASUS

In historical time landscape changes were probably minimal on the northern slopes of the Adzhar-Guri ranges, where large tracts of broadleaf and fir forests were preserved. These forests still supply appreciable quantities of bear and pine marten pelts. Nevertheless, a rapid lowering of the upper boundary of the forest is traceable recently throughout the area. In the Akhaltsykh District the faunal complex of the dry uplands of southwest Asia has infiltrated the forest zone.

The rapid displacement of bear, deer, roe deer and marten from the Aten ravine of the Trialet ridge, caused by the merciless extermination of the pine and beech forests since World War I, has been described by Belov (1924).

In northern Armenia, on the Somkhet, Bezobdal and Pambak ridges, small forest islands were preserved in some gulleys (Troitskii, 1934). The ancient age of human settlements in these regions is substantiated by archaeological and paleontological materials. Desiccation of the slopes caused by human activity in the upper parts of the forest zone is particularly noticeable on southern exposures along the upper reaches of the rivers which originate on the plateau, as, for example, on the Debeda-Chai. The section of canyon between the Amamly and Kirovakan stations is an example of a characteristic interpenetration in a mosaic arrangement of the distribution ranges of xerophilous species of mammals of the upland steppes and mesophilous species of the forest zone. Human activity always promotes encroachment of the xerophilous assemblage of small mammals on the mesophilous assemblage, following expansion of xerophytic formations. The distribution ranges of the Asia Minor hamster, steppe vole and Transcaucasian mole vole show a definite tendency toward extension to the north down the river valley.

In the lower forest belt and partly in the middle belt, the extermination of the forest resulted in the development of characteristic formations of drought-resistant shrubs and meadow-steppe. This enabled the xerophilous species of the east Transcaucasian semidesert (Asia Minor gerbil, steppe vole and steppe mouse) to migrate up the ravines.

Anthropo-cultural biotopes of the canyon bottoms (settlements, gardens, orchards, grain fields) are the main junctions of the ranges of small mammals of the east Transcaucasian steppes and the upland steppes of the Armenian upland.

A number of groups can be recognized in the fairly large collection of species which is increasing in abundance in the cultural landscape of the canyons. The first group, associated with buildings and gardens, includes long-tailed white-toothed shrew, house mouse, common field mouse (in part) and migratory hamster. The second group, associated with plowed fields and cereal crops, consists of fox, hare, steppe mouse, pine and common voles, and, at the boundary of the middle and lower belts, steppe vole. The middle belt is characterized by an assemblage of rodent pests — pine and common voles — which occur on second-growth meadows used for haymaking and pasture. In the upper belt, the bushy thickets of oaks and tall herbage are inhabited by moles and common and pine voles; roe deer also commonly occur in these areas. Where marshes have developed at
562 stream sources and hydrophilous vegetation now predominates in upland valleys which have been deforested, an increase in the water vole population occurs.

Although the settlements in the area (e. g., the town of Kirovakan) are very old, the synanthropic assemblage of rodents still consists mostly of native species. In 1943 these were identified from a total rodent catch as follows: house mouse — 86%, common field mouse — 10.3%, migratory hamster — 3.7% (Sosnikhina, 1946). It is of interest to note that in recently built-up areas the common field mouse occurs only in the winter-spring season. Hamsters occur in towns in the winter and summer, but not in the spring.

Only small tracts of beech—hornbeam forest were preserved farther east in the broad amphitheater of the Dzegam and Shamkhor river gorges. The crests of the longitudinal ridges were completely cleared of forests. The replacement of the forest assemblages of mammals by meadow animals is particularly pronounced in the zone between 1,000 and 2,500 m.

In this area chamois and boar have disappeared, and the abundance of wild goat, roe deer and bear has decreased.

The ranges and populations of the common and pine voles have increased considerably. Those pine voles which inhabit the meadows which have developed on deforested lands have evolved into a slightly modified subspecies, Pitymys daghestanicus nasarovi (Shidlovskii, 1938; Ognev, 1950).

Because of early human activity in the mountains, the primary beech forests on the eastern slopes of the Karabakh were preserved only in the Tertera gorge and on the northern and eastern slopes of Mount Kirs. Extermination of the forests restricted distribution ranges of the mole, bear, Persian squirrel, fat dormouse, common field mouse, pine vole and roe deer.

The slopes which were subjected to timbering, plowing and desiccation became inhabited by steppe vole, migratory hamster and steppe mouse which migrated from the foothills. In the Tertera gorge the steppe vole begins to occur at altitudes of 650-700 m; the pine vole at this altitude still clings to the northern shaded rocky areas and oak—hornbeam groves.

The development of the woodless dry mountain landscapes is even more clearly pronounced in the south of the Karabakh and on the Armenian plateau proper.

Sections of beech—hornbeam forests, subalpine tall herbage and upland steppes occur on the high plateaus of the Lesser Caucasus. On the southern slopes of the plateaus, towards the Araks valley, the mesophytic landscapes are contiguous to arid thin forests and dry sheep's fescue steppe, which grades into the zone of thorny Astragalus and Acantholimon. The upland wormwood—saltwort semidesert is developed in the middle Araks valley.

Man has inhabited the plateau since the Early Paleolithic (Zamyatnin, 1947; Panichkina, 1948). However, during the second half of the Quarternary the pronounced changes in the landscapes were due mainly to tectonic and climatic phenomena.

Even in the postglacial and historical epochs the vegetation of the plateau has changed considerably.

Sections of upland steppe which developed in the postglacial xerothermal 563 epoch grew smaller because of somewhat higher humidity and the advance of the forest phase. The landscapes began to be noticeably affected by man in the Bronze Age when human activity was immediately reflected in the distribution of forests and abundance of large mammals. Pedological studies (Klopotovskii, 1948), geobotanical studies (Kuznetsov, 1900; Troitskii, 1927, 1939) and archaeological studies (Grossgeim, 1948) all indicate that the pine and oak—beech forests in Dzhavakhetia covered much larger areas in the earlier stages of the historical epoch than in the present.

However, deforestation of large areas in Dzhavakhetia and Armenia by lava flows occurred in the Pleistocene (Yaroshenko, 1941).

In the Lower Holocene the plateau was still heavily inhabited by horse, bear, deer, roe deer, bison, primitive bull and sheep. The woodless highland areas were summer pastures for forest ungulates which sought refuge from the bloodsucking dipterans of the forest zone.

The very end of the second millennium B. C. is the beginning of the Bronze Age of human culture in Transcaucasia. Bronze Age culture was characterized by the development of agriculture and, at a later stage, of cattle breeding (see Piotrovskii, 1947, 1949).

Remains of the ancient irrigation systems have recently been discovered on the slopes of Alagez and in the Gekham Mountains. It is known from Urartu cuneiform writings that the tribes of the Armenian plateau possessed large herds of cattle in the first millennium B. C. Sardur, son of Agrishti, twice drove herds (totalling 23,194 head of large cattle and 63,420 of small cattle) from Yeriarkh (a country to the north of Alagez) (Piotrovskii, 1949). The development of agriculture and cattle husbandry in the Lake Sevan area were directly responsible for the beginning of the forest extermination in that area three thousand years ago.

However, the leafy forests on the Armenian plateau were mostly exterminated in the 19th century (N. B., 1861; Dal', 1947a).

On the southern slopes of the Armenian upland, in the Armenian and Nakhichevan A.S.S.R., large areas of drought-resistant thin forests were exterminated in historical time. The thin forests consisted of silver hawthorn (Crataegus orientalis), willowleaf pear (Pyrus salicifolia), juniper (Juniperus polycarpos) and almond (Amygdalus fenzliana). In the present epoch the only remains of these forests are sacred "witness" trees which we and Burchak-Abramovich have described elsewhere (1950).

During recent centuries the development of xerophytic vegetation on the southern slopes of the Zangezur and Daralagez ranges and of Alagez was promoted by an expanded nomadic cattle husbandry and by overloading the pastures. As a result, the grass cover was trampled down and weeds appeared in the natural grass assemblages.

As the mountain slopes of the Zangezur became desiccated, the lower boundaries of some rodent ranges (common and snow voles) were raised by 350-400 m. The occurrence of these animals at lower altitudes in the immediate past is evidenced by isolated colonies which inhabit mesophytic sections of the Akulis-Chai gorge, rock-covered areas overgrown by buckthorn (Rhamnus pallasi, R. spathulaefolia) and dog rose (Rosa canina) at altitudes near 1,200-1,300 m. In this area the colonies exist next to populations of Persian gerbil. The distribution of the gerbils gradually extends over dry, rocky slopes which have been overgrazed by sheep and follows the spread of phrygana higher into the mountains. The
564 present vertical distribution of assemblages of mouse-like forms is shown in Figure 211.

Similar cases of mutual interpenetration of the distribution ranges of the highland (upland-steppe and meadow) and semidesert mammals are known in the upper reaches of the Arpa-Chai and on the Aiodzor ridge. In these areas, three species of gerbils (Meriones persicus, M. blackleri and M. vinogradovi) invade the phrygana zone, whereas the Asia Minor hamsters concentrate on the boundaries and margins of barley fields and on wastelands in the mountain-steppe zone. In spite of human activity, the relatively xerophilous upland-steppe complex displays a tendency toward expansion (Dal', 1949b).

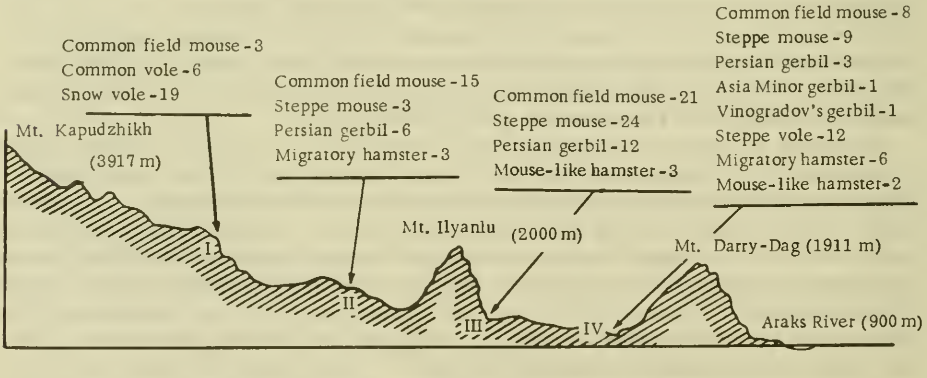

FIGURE 211. Zonal distribution of rodents in the middle Araks region (on combined longitudinal profile) based on 100 trap-nights in October 1947

I — rock-covered areas and meadows with weeds (2,200-2,300 m); II — thorny astragali and rock-covered areas with dog rose and hawthorn (1,600-1,700 m); III — rock-covered areas with buckthorn and almond shrubs (1,200-1,300 m); IV — vineyards in river valleys and on hill slopes (1,000-1,100 m)

The process of xerophytization of the middle Araks valley and the southern slopes of the Armenian upland developed concomitantly with a reverse process — plantings of tracts of walnut, plane, almond, apricot and apple trees. Examples of such plantings are the nut orchards in the vicinity of Yerevan and the large groves of centuries-old plane trees in the valleys of the Nakhichevan-Chai and Bazar-Chai. There is even some disagreement among botanists as to whether these groves are of anthropogenic or natural (autochthonous) origin. Fruit-tree oases in the valleys of the Alindzha-Chai and Akulis-Chai also cover large areas. The canal on the right bank of the Zanga River, penetrating granitic rock through a tunnel several hundred meters long, was built in the 8th century B. C. in the slave-holding state of Urartu. The canal is still in use for irrigation of large areas of the upland semidesert. Cuneiform writings of the Urartus tell us that, at the time it was constructed, a number of groves, gardens and orchards were planted (Piotrovskii, 1949).

(565)

FIGURE 212. Apricot gardens inhabited by Transcaucasian mole vole and common field mouse in the Alindzha-Chai valley

In general the planting of trees and development of deserts in the valleys of the Middle East and central Asia during historical time depended less on climatic fluctuations than on the development of human culture and, above all, on irrigational techniques (see also Berg, 1938). The rapid disappearance of one of the large piedmont oases occurred in recent times in the Akulis-Chai ravine, near the town of Ordubad, where several tens of
565 hectares of dense fruit-tree plantings were exterminated by drought within 10-15 years of the destruction of the Armenian village of Akulis by the Turks in 1917.

In historical time, horse, boar, Asiatic wild ass, deer and Persian gazelle have been exterminated in the middle Araks valley. There was a sharp decline in the abundance of sheep. The populations and ranges of steppe vole, migratory hamster and mole vole have increased on the irrigated lands of the Araks valley and its tributaries. The population of gerbils and jerboas were displaced to the upper terraces. The garden-oases (Figure 212) in the valleys and orchards, with their stone walls, became the habitats of the long-tailed white-toothed shrew, hare, forest dormouse, common and steppe mice, migratory hamster and Transcaucasian mole vole. The activity of the Transcaucasian mole vole, which inhabited the artificially irrigated sections of the Vedi-Chai and Arpa-Chai valleys, has also increased (Dal', 1948a, 1949b). We observed similar trends in the Alindzha-Chai valley.

Hydrophilous populations of steppe mice developed on the rice fields of the Araks valley (Pogosyan, 1945). The increase in mouse-like rodents was followed by an increase in carnivores (fox, tiger polecat, weasel), although hunting was well developed.

As a whole, anthropogenic landscape changes in this dry valley promoted an increase in the number of individuals in small-mammal assemblages which were in the process of adaptation to the peculiar environmental conditions of the oases.

Buildings built of raw bricks were inhabited by migratory hamsters, which became house pests. The numerous churches and monasteries attracted bats, particularly horseshoe bats, pipistrels and noctules.

566 The original synanthropic assemblage of rodents in small settlements developed from local species: steppe mouse and migratory hamster. The results of rodent night-trapping in October 1947 in residential buildings of some villages in the Alindzha-Chai valley are given in Table 114.

TABLE 114. Species and abundance of rodents (number of individuals per 100 traps) in small settlements in the middle Araks valley

Species	Khanagya		Abrakunis	
	number of individuals	%	number of individuals	%
Mus musculus subsp.	—	—	4	11.7
M. musculus tataricus.	24	66.6	22	64.7
Cricetulus migratorius.	10	27.7	8	23.5
Apodemus sylvaticus.	2	5.5	—	—
Total.	36		34	

At Leninakan and Yerevan, located on the plateau and connected by railroad with Baku and Tbilisi, the local residents were displaced by recently introduced cosmopolitan species. The results of rodent trapping carried out in these cities in the early 1940's are shown in Table 115, based on the data of Sosnikhina (1944), and Shidlovskii and Sosnikhina (1944).

Such changes in the original synanthropic assemblage on the plateau and in small settlements are at present related to highway construction and development of motor transport.

TABLE 115. Species and abundance (in %) of rodents in cities of the Armenian Highland

Species	Leninakan	Yerevan
Mus musculus subsp.	80	50.5
Cricetulus migratorius	15	32.0
Rattus norvegicus	5	17.5

Of the measures taken to enrich the mammalian fauna of the plateau, the following are noteworthy: the highly successful breeding of nutria on the Kara-Su rivulet (Sev-Dzhur) near Echmiadzin, which began in 1940 (Sarkisov, 1946b), and the release of 100 raccoon dogs in 1934 near Voskresenovka and of 15 female and 4 male axis deer in 1954 in the Khosrova forest near Garnya; the latter two experiments met with little success. The breeding of desman was planned for the lakes of the Akhalkalaki upland.

567 FOREST AND UPLAND STEPPE ZONES OF TALYSH

The landscape and biocenotic changes which occurred in Talysh in historical time are very similar to those described for the Lesser Caucasus.

Hunting with firearms caused the disappearance of tiger and deer from the area in the 1920's and a considerable decrease in the abundance of panther and bear. Bison and wild goat, which probably inhabited the highlands, disappeared much earlier, possibly at the beginning of the last century. The agriculatural activity of man resulted in large changes in the composition of the assemblages and the distribution of many species of mammals.

The cutting of broadleaf forests and cattle grazing were particularly extensive on the northern spurs of this range. These processes led to the formation of large, dry forest glades, overgrown on the margins by ferns, bracken and blackberry. In the upper reaches of the Vilyazh-Chai, plowed fields of barley and wheat occupy the southern slopes of the ravines.

On the eastern slopes, the upper forest boundary was artificially lowered by 250-300 m, even more in some places. Deforestation and desiccation of the mountain slopes resulted in the displacement of forest animals from this area and in a large-scale increase in the distribution areas of the European hare, steppe vole and migratory hamster, which disperse from the upland xerophytic steppe. The voles migrate over the deforested crests and slopes of the ranges to the bottom of the gorges at altitudes of 1,200-1,500 m, whereas the old, natural boundary of their distribution was 1,700-1,800 m. The rapid drying of the slopes enables the voles to withstand the high humidity in the deep canyons with an annual precipitation of up to 1,500 mm. However, in the zone of the ecological optimum of this species, precipitation does not exceed 500-550 mm, and the upper limit on the plains is 800 mm. This example of variability in the ecological stability of this small rodent is unique on the Caucasian Isthmus. The infiltration of xerophilous mammals into the humid mountain-forest zone, traced by us over vast piedmont and mountain areas of the Caucasus, reached its maximum development in this area. However, this infiltration is not from below, as in many other regions, but from above. In the Lerik and Yardymly districts of Talysh the high reproductive rate of the steppe vole endangers the cereal crops almost every year. In June large numbers of boar are attracted to the upper forest margins by the cereal crops.

The range expansion of the xerophilous species in this area was accompanied by a decrease in the distribution areas of mole, porcupine, common field mouse, boar and roe deer (in part).

The assemblage of house mammals in the small settlements located in the mountain forests is extremely poor, consisting only of the dark long-tailed shrew, house mouse and Norway rat.

The development of cattle husbandry and agriculture in the upland steppe of Talysh resulted in the complete extermination of the arid sparse forests. A similar process occurred in the Nakhichevan District. At present the 2,000-2,500 m upland steppe zone of Talysh is an arid region of unstable agricultural crops; barley, wheat and rye are grown at higher altitudes. Wild ungulates (Asiatic wild ass, sheep, Bezoar goat) probably still inhabited the area 150-200 years ago. The development of agriculture on the plateau during the last centuries promoted a population
568 increase in mouse-like rodents (steppe and common vole, Transcaucasian mole vole, Asia Minor hamster) and in the European hare. The extensive digging in the alfalfa crops by Transcaucasian mole vole is particularly noticeable in the Zuvanda valley, at altitudes of 1,800-2,000 m. In gardens and alfalfa fields the mole vole forms piles of earth up to 1 m in diameter and 30 cm in height, whereas on virgin lands such piles are never over 25-30 cm in diameter.

The assemblage of house mammals in the settlements of this upland is very similar to that described for the middle Araks valley. Trapping in the mountain villages of Kel'vyaz and Dyman yields mostly local species. In a June 1945 trapping, the migratory hamster amounted to 80% and house mouse to 20% of the catch. Migratory hamster even inhabits garrets and second floors of residential houses in the summer, withstanding very high temperatures (Vereshchagin, 1949d). The introduced house mouse and Norway rat are so far common only in the district centers of Yardymly and Lerik, which are connected with Lenkoran by highways.

PROTECTION AND ENRICHMENT OF FOREST AND HIGHLAND MAMMALIAN FAUNA

The known record of game animal protection on the Caucasus goes back to the Early Middle Ages. However, there is no doubt that protective measures were in use also in the slave-holding states.

Originally, protection consisted of restricting hunting on particularly valuable hunting grounds, as, for example, the lands of the feudal barons in Iran, Armenia and Georgia. Such local rules against hunting on the lands of beks, khans, shahs, princes and tsars also included the protection of the natural landscape: groves, reed swamps, water springs, etc.

In ancient Armenia, in the reign of Khosrou (4th-5th centuries A. D.), oak forests were planted and fenced and later populated by game animals in the districts of Garni and Dvin and in the Metsamor valley. "Then the tsar ordered all kinds of wild animals to be collected and released within the enclosure, in order to make this the place of the tsar's hunt, feasts and recreation" (Buzand, 1953, p. 17). In the 19th century, large sections of mountain forests were selected and leased for the Grand Duke's hunt. These were the Kuban hunting grounds, nearly 500,000 hectares in area, in the canyons of the left tributaries of the Kuban; the Caucasian hunting grounds in the Karayaz tugai forest (Figure 213) on the Kura, east of Tbilisi, and the Borzhomi animal reserve near Borzhomi (Shil'der, 1892; Bashkirov, 1940).

On the grounds of the Borzhomi animal reserve, 500 hectares of mountain slopes were surrounded by a high fence with entrance traps and no exits for the animals. The Myzym-Chai and Belokany ravines on the southern slope of the Greater Caucasus near Lagodekhi were leased by Count Demidov San-Donato in 1903-1917 for hunting mountain ungulates (Markov and Mlokosevich, 1935; Markov, 1935, 1938). As these areas were efficiently guarded and rarely hunted, they became, in effect, game reservations, where a large stock of large mammals was preserved.

In the early 20th century, the idea of maintaining such hunting reserves evolved into the idea of organizing state game reservations.

569 After the Soviet revolution the following mountain and mountain-forest reserves were established in the twenties and thirties: Caucasian, Borzhomi, Teberda, Zakataly, Lagodekhi, Gumista, Rits, Telavo-Kvareli and Saraibulakh. Their total area is approximately 550,000 hectares (Markov, 1935; Makarov, 1940; Gambarashvili, 1937; Knyazev, 1946; Vereshchagin, 1947d).

FIGURE 213. Results of one day's boar hunt at Karayazy in 1909 — 43 boars killed

Photograph by E. L. Markov

In addition a number of temporary game reservations were established in the thirties in the foothills and in the mountains. In the 1930-40's the total number of reserves was 17, comprising a total area of 200,000 hectares. The value of these reserves was negligible, since the protection of animals, which consisted of prohibiting shooting and trapping, did not extend to the forests, which were subject to logging and cattle grazing (Map 97).

The establishment of the Caucasian game reservations stopped the decline in the large mammal population, particularly goats and chamois, and later contributed to a gradual population increase in these species.

In view of the prospects for great changes in the landscape of the Caucasus in the next decades from mineral exploitation and agricultural expansion, conservation measures must be developed by every available means. Reducing the size of the Caucasian reservations and permitting logging on their lands is extremely shortsighted and a false economy.

570 At the end of the 19th century some attempts were made to enrich the mountain-forest mammalian fauna of the Caucasus with foreign species.

Following Shil'der's recommendations in 1888, 54 European fallow deer (Dama dama L.) were released in the Borzhomi game reservation. The animals became well acclimatized, and by 1918 there were several hundreds of them. Herds of 50-80 head wandered through the area, but in 1919-1920 they were all killed by the local population. Also, in 1888, 7 European red deer (Cervus elaphus L.) from Vilna and 58 from Austria were released in the reservation in order to "improve the antlers" of local deer. According to the hunting specialist E. L. Markov, the number of deer in the reservation was nearly 1,000 by 1918; their numbers later decreased to less than a hundred head as the result of unlicensed hunting.

Ten east and west Caucasian goats were also introduced into the reservation. The crosses between the two species, and between each of the two with the local wild goats, produced a number of interesting malformed hybrids. By 1918 the total goat population of the reservation was presumably 500, which were wiped out during the Civil War. Such large numbers of animals as these constantly required increasing food supplies to maintain them in the reservation even in an environment of mountain relief. At any rate, the experience of the Borzhomi game reservation is a spectacular example of the great potential in breeding both local and introduced species of ungulates in the Caucasus.

More or less planned attempts to enrich the mountain-forest fauna of the Caucasus were made only in Soviet times. Unfortunately, these operations were concerned only with fur animals.

It should be noted that the methods by which new species were introduced into the mountain-forest zone of the Caucasus were strictly empirical. The theory of acclimatization was not at all well developed and only occasionally were more or less rational propositions advanced and put into practice.

Formozov (1930) has recommended that the fir forests of the Caucasus be populated with common squirrel; Markov (1931b, 1935) has suggested the introduction of axis deer into the Talysh forests, and of rabbit, skunk, raccoon dog and chinchilla into the mountains and forests of the Caucasus. Manteifel' (1943) considered it desirable to introduce the following forms into the Caucasus: goral, markhor, Pamir argali, chinchilla, Himalayan panda and Australian phalanger. Other proposals concerned the introduction of mink, raccoon and Siberian polecat into Transcaucasia, and the extension of the ranges of Caucasian goat and chamois to the Lesser Caucasus (Vereshchagin, 1939b).

Attempts to introduce fur animals into the Caucasian forests have been discussed by zoologists (Shaposhnikov, 1938; M. Stepanov, 1939; Kurapova and Stepanov, 1941; Dal', 1941; Vereshchagin, 1941b, 1947c; Rukovskii. 1950).

Some of the more successful cases of acclimatization of fur and hoofed species in the forest and highland zones of the Caucasus are given below.

Experimental acclimatization of squirrel, raccoon dog, axis deer and bison has been carried out in the western Caucasus.

(571)

FIGURE 214. Altai squirrel in the pine forests on the upper Kuban

In 1937, 134 specimens of Altai squirrel (*Sciurus vulgaris altaicus* Serebr.) (Figure 214) were released in the Teberda ravine in the Teberda game reservation. In 1940 the number of squirrels increased to 2,400, and in 1941 to more than 3,500 (Kurapova and Stepanov, 1941). In 1944 squirrels inhabited the forests in the basins of the Aksaut, Kuban, Teberda, Bolshoi Zelenchuk and Malyi Zelenchuk, feeding on the seeds of firs, spruces, pines and beech nuts. By 1948 the squirrels appeared in the Caucasian game reservation and on the southern slope of the range near Sukhumi, probably bypassing the glacier fields in the upper reaches
571 of the Laba. Squirrel pelts were being procured as early as the fall of 1948 from the forests of the Bzyb and Kodor basins. The advance of the squirrels to the east in the zone of the fir—maple forests of Svanetia

proceeded very rapidly. They appeared in the Rion basin in 1951. In 1954 gardens in the Gagry area were damaged by squirrels (Rukovskii, 1956)*. Undoubtedly, squirrels will inhabit the entire forest zone of Transcaucasia in the future, and will probably migrate through the Surami ridge forests to the broadleaf and coniferous forests of the Trialet and Adzhar-Imeretian ranges.

At present the expediency of introducing squirrels into the Caucasian forests is in doubt because the animal is a garden pest, particularly destructive of nut-tree plantations. The organization of commercial squirrel hunting is urgently required.

The present (1956) and future distribution ranges of the red squirrel are shown in Map 95.

Experimental acclimatization of raccoon dogs, raccoons, minks and Canadian skunks was carried out on the Zakataly-Ismailly lowland in eastern Transcaucasia. Of these only the acclimatization of raccoons was successful.

From an initial release of 22 specimens in 1941 west of the village of Ismailly, the raccoons increased in numbers and distribution, in spite of unlicensed hunting and extermination efforts in the village gardens. The entire valley of the Agri-Chai was a suitable habitat for this omnivorous predator (Figures 215, 216). By 1945 there were 180-200 raccoons

(572)

FIGURE 215. Common raccoon from the forests of the Agri-Chai valley

Photograph by author, 1949

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* Rukovskii's geographical data are lacking in accuracy: the occurrences of squirrels which he shows in the woodless areas near Novorossiisk, Gelendzhik and other cities are incorrect.

distributed over an area of nearly 250 km^2 (Vereshchagin, 1947c, 1953b). By 1949 the distribution area was approximately 850-900 km^2, 572 and the number of animals was 800-850. Under favorable conditions, the rate of distribution and formation of the range on the humid wooded lowland was very high — as much as 15-20 km per year. Raccoons often tend to concentrate in the vicinity of settlements where they can always find food: fruit, frogs and poultry.

In order to increase the rate of natural distribution of raccoons throughout the region, 23 raccoons were caught in August-September 1949 in the Ismaily area. Of these, 18 were released in the forests on the lower Samur and on the Khachmas lowland (Rukovskii, 1947, 1950). Additional animals, caught in the Kutkashen and Ismailly areas in 1950 and 1951, were released in the gallery forests on the Terek and left tributaries of the Kuban, in spite of our warning that they might cause damage to poultry and game (Vereshchagin, 1953b).

Introduction of other carnivores was not successful. The Canadian skunks and minks died within one year of unknown causes. A small number of raccoon dogs still inhabit the lowland forests of the Avtaran valley.

Equally unsuccessful were the attempts to acclimatize raccoon dogs in the mountain forests of the Teberda game reservation in Transcaucasia and the Gumista reservation in Abkhazia, South Ossetia and Kartalinia (Map 94). The animals, as a rule, died of unknown causes during the few years 573 following their release; they often migrated over great distances (Stepanov, 1939; Dal', 1941; Vereshchagin, 1947d).

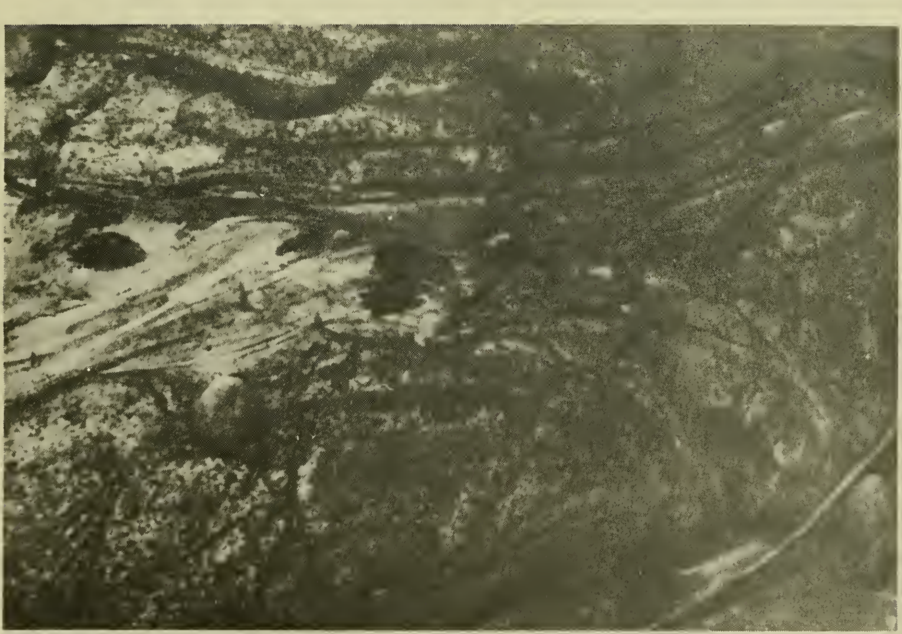

FIGURE 216. Footprints of raccoon, black stork and black partridge on river shoal near the village of Nidzhi

Photograph by author, 1949

During the last few decades nutrias were introduced into the alder-covered swamps and thickets of the Colchis lowland. The first 48 nutrias were released in 1932 east of Lake Paleostom. In 1936 the species was observed in the region of Kobuleti, Supsa, Lanchkhuta and the mouth of the Khupa, 20-25 km from the point of release. In the fifth year of breeding the distribution area covered at least 500 km^2. However, the areas actually inhabited by the animals probably comprised no more than 3,000-4,000 hectares (Vereshchagin, 1941b).

The rapid distribution of the species through suitable marshland sections of the Black Sea coast, particularly in Abkhazia, was aided by the artificial distribution of acclimatized animals in the region.

In some areas nutria disappeared as the result of poorly organized hunting and inadequate protection from enemies in the thicket during frost and drought periods.

The prospects for free breeding of nutrias in the water bodies of Colchis will become steadily poorer as the alder-covered marshes are drained and deforested. However, semi-free breeding may continue to develop successfully in lakes of the Bebesyri and Inkit type (Vereshchagin, 1950a).

The subalpine meadows of central Dagestan were used for an experiment in breeding Altai marmot (Marmota baibacina Brandt). In 1934, 113 marmots from the Kosh-Agach District of the Oirotian autonomous
574 region were released on the high plateau west of the village of Gunib. The animals occupied areas of rocky calcareous sandstone; some dug holes under the blocks of limestone on the grassy slopes (Figure 217). An August 1935 census revealed 47 marmots, none of which were new generation. At that time the total area of distribution was nearly 25 km^2. In 1936 only 15 mature and 2 young marmots were counted (Shaposhnikov and Krushinskaya, 1939; Lavrov, 1946). In 1937 18 holes with 27 animals were counted. Our observations in August 1952 showed that the marmots were distributed over the entire Gunib plateau, an area of approximately 45 km^2. The densest colonies occurred along the faults on the northern of the plateau at an altitude of 1,800 m (Figure 218). Occasional groups of young marmots occurred even near the village of Gunib at altitudes of 1,300-1,400 m. The natural distribution of the animals proceeded westward, in spite of unlicensed hunting. The distribution of the colonies on the Gunib shows that the major part of the low slopes and ravine bottoms in Dagestan, covered by ephemeral upland-steppe vegetation, are unsuitable habitats for marmots. The prospects for artificial distribution of animals are better on high plateaus similar to the Gunib and Khunzakh with extensive rock-covered areas in the marginal zone.

The distribution and breeding of marmots is evidently feasible over the entire upland-steppe zone of the inner valleys of the northern slope of the Greater Caucasus to El'brus. The better areas for new releases are the limestone talus at the base of the cuestas on the southern cliffs of the
575 Skalistyi ridge and in the canyons of the Argun, Ardon, Cherek and Baksan, as well as in the Ingur and Rion river valleys. Marmots can also be distributed on the ridges of the Armenian Upland, for example, in the Lake Sevan area. The present and future distribution ranges of marmots are shown in Map 95.

(574)

FIGURE 217. Habitats of Altai marmot on the northern drop of the Gunib plateau

Photograph by author, 1952

In 1939, 59 specimens of axis deer (Cervus nippon Temm.) were released in the Teberda ravine for the purpose of developing a stock of animals to be used for their antlers. By 1942 the number of deer increased to approximately 150, but during the German occupation of the area it was halved. In 1954 a small herd of axis deer was released in the Kusary area of Azerbaidzhan.

In order to restore the population of European bison in the Caucasus, 5 relatively pure crosses of European and American bison from Askaniya-Nova (Bison bison L. × B. bonasus L.; European bison strain: 1/16) were released in the Caucasian game reservation in 1940. In 1944, a herd of 11 relatively pure crosses lived in the reservation; the number increased to 21 (6 males and 15 females) in 1951 and in 1956 to 106. The animals are kept in open-air enclosures and in open areas under the protection of mounted shepherds. They are driven in summer to pastures in the subalpine and alpine zones. At present there is sufficient evidence to believe that the crosses of the two bison species will be viable for distribution over the entire forest zone of the northwestern Caucasus.

These attempts to introduce new species into the Caucasian fauna show that distribution ranges develop instantaneously (in the geological time-sense), provided free ecological niches are available. The development of new biocenotic relationships when biotopes are saturated with the introduced species must be a special field of study of applied zoology.

Future work on the redistribution and enrichment of the highland mammalian complexes of the Caucasus must be organized to take into account the natural conditions and main trends of human activity in different sections of the region.

FIGURE 218. Altai marmots in Dagestan

576 Planning for future enrichment of the mammalian complex of the mountain-forest zones of the Caucasus should be based on the following general theoretical considerations:

1. The mammalian complex of the forest zone of the Caucasus was recently impoverished as regards large species because of human activity. The species affected were: European bison, elk, and at some places deer and chamois.
2. The highland assemblage of hoofed animals and rodents of the Greater Caucasus is poor in species because it was so long isolated, and because the relief of the alpine zone is highly diversified and snowfalls are heavy, particularly in the western part of the range.
3. For the rodents and carnivores of the forest zone, the food regime is more stable in the western part of the Greater Caucasus than in the eastern part.
4. A number of valuable species of hoofed mammals and carnivores, characteristic of the Greater Caucasus, do not occur in the lesser Caucasus area of the Caucasian District.

Taking these specific features into consideration, more attention should be devoted to the possibility of restoring the populations of European bison (or the European-American hybrid), elk and red deer in the Caucasus, and to the introduction of fallow and axis deer. The food resources of the forest zone are evidently sufficient for one more fur carnivore of the sable type. Caucasian goats and chamois should be introduced into the Lesser

Caucasus. Pine marten and chamois should be bred in the Karabakh, Talysh and other areas.

In general, artificial transgressions over ecological barriers have great potentialities for increasing the distribution areas of local and introduced species.

It would be particularly interesting for studies of speciation and directed variability to attempt an introduction of the east Caucasian goat in the west, i. e., into the Adzhar-Imeretian Range, and of the west Caucasian goat into Karabakh or Talysh and El'brus.

Inner Dagestan must play a special role in the breeding and preservation of highland ungulates. The mountainous rocky relief and thin vegetation cover in inner Dagestan prevent an extensive development of agriculture, gardening or cattle breeding. These factors, as well as the geographic isolation of the area, could well make inner Dagestan a large reservation for breeding hoofed mammals which do not depend on the forests.

The following species could be introduced for breeding into this area: Pamir argali (Ovis ammon L.), bharal or blue sheep (O. nahura Hodgson), tahr (Hemitragus jemlaicus Smith), markhor (Capra falconeri Wagner), Barbary sheep (Ammotragus lervia Pallas).

The abundance of Bezoar goat (Capra aegagrus), which once inhabited the entire plateau, must be restored. Beyond question all these operations must include the planned extermination of wolves.

The dry uplands of the Lesser Caucasus and Talysh are not as potentially valuable as Dagestan for the breeding of mountain ungulates, since it is expedient to use the tragacanth—astragali zone for pastureland and for plantings of almond, pistachio and olive. Nevertheless, the populations of Persian gazelle must be restored in the middle Araks valley. The species could occupy the area between Vagarshapat and Ordubad which is unsuitable for farming.

The semifree breeding of nutria must be further developed in the zone of the valley forests in Colchis, Zakataly-Ismailly and the Lenkoran lowlands, as well as on the Kara-Su rivulets in Armenia.

577 SUMMATION

The study of the direct and indirect effects of man on the mammalian fauna of the Caucasian Isthmus during the Holocene shows that this epoch is a distinct qualitative, anthropogenic stage in the evolution of the fauna.

At this stage the distribution ranges of species, ecological assemblages and faunal complexes evolved under the direct and indirect influence of chaotic human activity, which often completely overshadowed the natural processes of evolution of the landscapes and biocenoses.

Some general and specific regularities in the development of the mammalian fauna of the Caucasus during the Anthropogenic stage may be summarized as follows:

1. In the historical epoch the mammalian fauna of the Caucasus was directly affected by man through unplanned hunting, limited only by the contemporaneous level of technological development. The principal cause of the rapid impoverishment of the Caucasus in large mammals lay in the

large-scale game hunts practiced by the feudal barons in the mountains and foothills and by the nomadic tribes on the plains.

The extinction of lion, tiger, river beaver, horse, Asiatic wild ass, elk, primitive bull and European bison which inhabited the Isthmus was in some cases greatly accelerated and in others directly caused by man. Man was also responsible for the decrease in population and range of bear, striped hyena, panther, boar, roe deer, red deer, saiga and Persian gazelle.

The composition and abundance of commercially valuable fur species was much less affected in historical time. During the last centuries and decades there has been a drastic decline in abundance and distribution of only two species: corsac fox and Siberian polecat. The data of the state fur stations for the last 25 years indicate that various natural causes are responsible for the fluctuations in numbers in the other fox species. These generally take place over several years.

The planned extermination of wolf, jackal, little suslik, common and steppe voles and house mouse, which was begun in Soviet time, has not yet been successful in decreasing the distribution areas of these species.

2. The process of extinction and reduction of distribution areas of game mammals was accelerated everywhere by the indirect activity of man as he altered various types of landscape. The universal extermination of the forests had particularly grave consequences.

3. The most recent evolutionary stages of species ranges and behavior can be largely traced to the anthropogenetic effect on the higher nervous system of some Caucasian game animals. These are reflected in choices of habitats and often in the complete suppression of ancient instincts toward horizontal and vertical migrations, diurnal activity, etc.

The main reaction of the hoofed animals to the approach of man and his domestic animals was escape to protected biotopes such as forests, mountains and deserts. A number of carnivores and ungulates (bear, jackal and boar), drawn by new feeding grounds and little threatened by human pursuit, inhabited areas near human settlements in Azerbaidzhan. Man also promoted the development of local ecological populations of mammals such as the "forest" and "rock" populations of the east Caucasian goat on the southern slope of the eastern Caucasus and the "house" and "garden" populations of boars and European hares in the oases of Azerbaidzhan.

578 The formation of new types of biotopes was reflected in some small mammals, particularly rodents, by changes in ecological features, and even in the development of new features. This point is also discussed below (7).

4. Man-made changes in the landscape have also produced changes in the more or less stable boundaries of the landscape and zoogeographic zones. Deforestation has resulted in the replacement of mesophilous ecological assemblages by advancing xerophilous assemblages.

Thus the Ciscaucasian boundaries of the steppe immigrants shifted southward into the foothills, whereas the boundary of the southwest Asian upland-desert district moved north into Transcaucasia. This shift of xerophilous assemblages and complexes of mammals was particularly advanced in the east, southeast and south of the Caucasus. In these areas the advance of the xerophilous forms was aided by the natural zonation and the drier continental climate. The Caucasian mountain-forest and alpine district became a mesophytic refuge — a refuge for mesophilous mammals. Infiltration of the upland-steppe faunal complex into the zone previously covered by forests resulted in lowering the northern boundary of the Armenian transitional district down the canyons on the northern slope of the Lesser Caucasus, made arid by human activity. A similar picture was even more strongly developed in Talysh.

5. The development of new ecological assemblages and faunal complexes of mammals on the plowed and irrigated steppes and semideserts of the Caucasian Isthmus was made possible by the extinction of large game species of hoofed mammals (tarpan, Asiatic wild ass, saiga, goitered gazelle) and rodents (suslik, mole rat, jerboa, gerbil), which do not tolerate plowing and irrigation. Qualitative enrichment of the faunal complexes proceeded concomitantly with irrigation and development of the cultural landscape. The enrichment was due to the migration of mesophilous insectivores and rodents from the intrazonal habitats: gallery forests, reed thickets and adjacent sections of the lowland and foothill forests. Parallel to these developments, there came an increase in the populations of some widely distributed carnivores: fox, jackal, weasel, tiger polecat.

6. Partial restoration and, in some cases, enrichment of the original assemblages of forest mammals were the results of the replacement of the piedmont and lowland forests in Ciscaucasia and Transcaucasia by extensive plantations of fruit and nut trees wherever they were contiguous to the forests of the lower mountain belt. The seasonal migrations of large game animals and the increased abundance of arboreal forest rodents and carnivores which permanently inhabited the area were the main contributing factors in the restoration and reorganization of the assemblages of forest mammals.

7. Assemblages of agricultural pests and synanthropic (house) assemblages developed initially in each zone from the local species.

The cultural landscapes created many possibilities for the development of new ecological features and mammal assemblages. The best examples of these processes are the development of hydrophilous populations of steppe mouse on rice fields and populations of steppe vole on the unirrigated wheat and barley fields of eastern Transcaucasia.

The accidentally introduced species play only a minor role in the
579 development of assemblages of agricultural pests. The Norway rat is an example of this phenomenon: the species became established in the vegetable gardens of Ciscaucasia and the Black Sea coast.

8. Development of synanthropic assemblages of mammals occurred many times and independently in different zoogeographic districts and sections of the Caucasian Isthmus. The development was based on the adaptation of native species to various local construction techniques, according to the evolution of morphological features, ecological possibilities and needs of individual species. The synanthropic assemblages developed, and still continue to develop, from the representatives of three orders: Rodentia, Chiroptera and Insectivora. Rodents are the group which comes most into contact with man.

Adaptation of the Caucasian rodents (steppe and mountain-steppe races of house mouse, common field mouse, migratory hamster, snow vole) to life in man-made structures is undoubtedly as old as the adaptation of the cosmopolitan races of house mouse and rat.

Improvement in residential quarters and increase in human population under the conditions provided by cultural landscapes universally resulted in the replacement of the native synanthropic assemblage by the cosmopolitan assemblage.

Introduction of species (Norway rat and synanthropic races of house mouse) into the cultural landscape and human dwellings proceeded at first along the Black and Caspian sea coasts, where the animals were introduced from boats. The development of the house rodent assemblages in the coastal settlements has essentially been completed. At present the inner regions of the Caucasus are rapidly being inhabited by introduced synanthropic rodents. This process is due to the development of rail and motor transport. The displacement of native rodents from the house assemblage can best be observed on the high plateaus, for example in Armenia.

9. The planned reconstruction of Soviet agriculture includes planting of forests and construction of irrigational networks, organization of forestry and hunting, and development of settlements. All these measures will promote rapid evolution of ecological assemblages and faunal complexes of the Caucasian mammals.

10. In addition to the planned alteration of the landscape, measures aimed at enrichment of the landscape zones and sections described with Caucasian and alien game animals will also affect the future development of the mammalian fauna of the Caucasus.

Particularly interesting and economically important results may be obtained from the introduction of central Asian highland hoofed species into Dagestan, and of goats of the Greater Caucasus into the Lesser Caucasus section of the Caucasian District.

CONCLUSION

580 This concludes the review of the main stages of the history of the mammalian fauna of the Caucasus as known from faunological materials now available. These stages, developing as marks in the Tertiary, become progressively clearer throughout the Anthropogene towards recent times. A generalized summary is given below.

The history of the mammalian fauna of the Caucasus begins in the Oligocene. The Caucasian mountain-forest complex probably began to develop in the Middle Miocene. The Hipparion faunal complex migrated to the plain and foothills of the Caucasus from the south in the Upper Miocene, when the fauna of the Black Sea, Caucasus and Caspian coasts did not differ essentially from the west Mediterranean fauna. These similarities in the development of the mammalian fauna were also pronounced in the Middle Miocene under increasingly differentiated conditions of climate and landscape in the Caucasus. Mastodons and Hipparion became extinct; horses, bulls and elephants appeared.

The transition to the Pleistocene on the Caucasus was also similar to the transition in Europe. The distribution ranges of large animals, the index species of the Lower Pleistocene (Elephas trogontherii, horses, Rhinoceros mercki, giant deer and European bison), covered the Caucasian Isthmus, i. e., the ranges extended from the Russian Plain to southwest Asia. The specificity of the faunal development somewhat increased following the new stages of landscape differentiation and the increased influence of the Greater Caucasus as an ecological mountain barrier. Ciscaucasia was infiltrated by the steppe species of the Russian Plain and semidesert species of northern central Asia, whereas Transcaucasia was penetrated by the upland-steppe species of southwest Asia.

The process of evolution of the mammalian fauna of the Isthmus in the Quarternary mainly consisted of extinctions and immigrations, rather than endemic speciation.

The known data indicate that evolution of the species in the Quaternary — evolution of mammoths from Elephas trogontherii, evolution of Caucasian bison from the primitive bison, etc. — did not result in the qualitative enrichment of the fauna.

The rates of evolution and speciation and the adaptational trends of Caucasian mammals vary greatly within orders. This indicates that there are no unifying laws or general regularities in these processes.

The glacial epoch did not produce noticeably northern effects in the composition of the mammalian complexes in the Caucasus. Undoubtedly, the glaciations did result, however, in the shifting of distribution ranges and in increased rates of evolution of many species.

A number of xerophilous and thermophilous mammals migrated to the Caucasus from the south in Lower Holocene time because of the development 581 of xerothermal conditions. Direct and indirect human influence on the development of ecological assemblages and complexes of mammals in the plains and foothills increased toward the Upper Holocene, at which time the fauna became strongly impoverished in large carnivores and hoofed mammals. However, consideration of all the facts on the extinction of individual species, changes in their distribution ranges and evolution of their complexes in the Anthropogene of the Caucasus (Chapters II, III, VI), attests to the importance of the role played by natural factors in the above processes. In particular, this applies to those mammals which originated in the steppes of central Asia.

The newest stage of development of the Soviet economy opened great perspectives for the restoration and enrichment of the mammalian fauna of the Caucasus by exterminating harmful species and introducing useful ones. Further development of the economy and natural resources of the Caucasus will require the Government to undertake large-scale protection of sample natural faunal complexes.

Tasks for immediate investigation

The theory and organization of investigations in the near future of the mammalian fauna of the Caucasus and its history present many far-reaching and diverse problems.

The collection of bone material at the known and newly-discovered deposits of Tertiary and Quarternary mammals must, of course, continue.

Systematic observations within the next few years on the eroded Tertiary and Quarternary beds of the shores of the Tsimlyanskaya, Novotroitskii, Tshchikskii and Mingechaur reservoirs may reveal bone materials of great value in future studies.

More thorough investigation must be carried out at such "key" deposits as the Tertiary beds near Belomechetskaya, at El'dar and Udabno, in the Kosyakin quarry near Stavropol and the sand quarries on the northern Azov coast, in the Lower Quarternary deposits on the Taman Peninsula and in the Middle and Upper Quarternary asphalt deposits on the Apsheron. Surveying Pyatigor'e, Karabakh and central Transcaucasia for Paleolithic sites may produce valuable paleontological material and improve our present knowledge of the development of the fauna of these regions in the Anthropogene.

The storage and maintenance of paleontological collections in the republican, regional and district museums must be improved. Systematic work on the collections from the regions mentioned would improve our knowledge of the composition of the ancient mammalian complexes and their correlation with the known Cenozoic faunas of the western Mediterranean, Russian Plain and central Asia. Additional identifications of species in the fossil faunal complexes, supported by paleobotanical studies, will help in the reconstruction of complete paleographic pictures and development of the stratigraphy of the Cenozoic continental sediments.

Further study of the distribution ranges of Caucasian mammals must include ecological analyses of their manifestations of endemism, relict distribution and discontinuities. These analyses are relevant to determinations on climatic and sea level fluctuations, orogenesis and glaciations.

They must be supported by paleontological evidence. Thus, for example, our knowledge of the time of infiltration of the central Asian semidesert and desert species into eastern Ciscaucasia can be improved only through deep drilling in the Terek-Kuma semidesert and by a paleontological survey of the northern foothills of Dagestan.

Our study of the specific composition of the Caucasian fauna in the Cenozoic undertaken to discover general developmental regulations, particularly in the Anthropogene, left many unsolved problems, especially with regard to geographic and intraspecific variation.

In this category belong the genetic and ecological interrelationships of a number of forms described by taxonomists: mole, water shrew and white-toothed shrew among the insectivores; weasel and bear among the carnivores; common field and house mice among the rodents; roe deer among the hoofed mammals, etc.

It appears that these problems cannot be solved by a single morphometric method.

No matter how thorough are such works or how well supported by accepted field observations, many questions remain unanswered: the extent of interbreeding, pattern of inheritance of characteristics, etc.

The complex relief, variability of the climates and sharply differentiated landscapes over short distances produce a very complex picture of geographic variation. In small mammals, rodents being an example, the geographic variation is tied to the variation in weather conditions in different years and seasons.

Studies with material collected in different years and seasons which does not take into account the altitude may only obscure the nature of the geographic variation.

Thus the investigator — morphologist or faunologist — who has spent a great amount of labor on measurements can only make more or less reliable guesses as to the nature and rates of evolution of the forms. We believe that at this stage of science the faunologist must combine morphological analysis not only with the usual ecological observations in the field, but also with experiments under natural or nearly natural conditions.

Organization of such studies is laborious, but nonetheless necessary, since they will contribute to the solution of the basic problems in the study of the evolution of organisms.

Further studies comparing the data on the Recent evolution of ecological and morpho-physiological characteristics of species with paleontological material will establish accurately the rates of evolution of mammals at different stages of the Quarternary, and, employing the fossil mammals for the stratigraphic subdivision of the Quarternary, permit us to foresee faunal changes in the future.

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LIST OF ABBREVIATIONS USED IN THE BIBLIOGRAPHY

Abbreviation	Transliteration	Translation
AN URSR	Akademiya Nauk Ukrayins'koyi Radyans'koyi Sotsialistychnoyi Respubliky	Academy of Sciences of the Ukrainian SSR [in Ukrainian]
Azerb. Neft. Khoz.	Azerbaidzhanskoe Neftyanoe Khozyaistvo	Azerbaidzhan Petroleum Industry
Azneft'	Gosudarstvennoe Ob''edinenie Azerbaidzhanskoi Neftedobyvayushchei Promyshlennosti	State Association of the Azerbaidzhan Petroleum Industry
Byull. Kavkaz. Gos. Zapov.	Byulleten' Kavkazskogo Gosudarstvennogo Zapovednika	Bulletin of the Caucasian State Reservation
Byull. Komiss. po Izuch. Chetvertichn. Perioda	Byulleten' Komissii po Izucheniyu Chetvertichnogo Perioda	Bulletin of the Commission on the Study of the Quaternary
Byull. Mosk. Obshch. Ispyt. Prirody	Byulleten' Moskovskogo Obshchestva Ispytatelei Prirody	Bulletin of the Moscow Society for Natural Research
Dagnarkomzem	Dagestanskii Narodnyi Komissariat Zemledeliya	Dagestan People's Commissariat of Agriculture
DAN SSSR	Doklady Akademii Nauk SSSR	Proceedings of the Academy of Sciences of the U.S.S.R.
DAN ArmSSR	Doklady Akademii Nauk Armyanskoi SSR	Proceedings of the Academy of Sciences of the Armenian S.S.R.
DAN AzerbSSR	Doklady Akademii Nauk Azerbaidzhanskoi SSR	Proceedings of the Academy of Sciences of the Azerbaidzhan S.S.R.
Ezhegodn. po Geol. i Mineral. Rossii	Ezhegodnik po Geologii i Mineralogii Rossii	Russian Geological and Mineralogical Yearbook
Ezhegodn. Zool. Muz. AN SSSR	Ezhegodnik Zoologicheskogo Muzeya Akademii Nauk SSSR	Yearbook of the Zoological Museum of the Academy of Sciences of the U.S.S.R.
Izd. AN SSSR	Izdatel'stvo Akademii Nauk SSSR	Academy of Sciences of the U.S.S.R. Publishing House
Izd. AN UkrSSR	Izdatel'stvo Akademii Nauk Ukrainskoi SSR	Academy of Sciences of the Ukr.S.S.R. Publishing House

Izd. Kavk. Muz.	Izdatel'stvo Kavkazskogo Muzeya	Caucasian Museum Publishing House
Izd. Mosk. Obshch. Ispyt. Prirody	Izdatel'stvo Moskovskogo Obshchestva Ispytatelei Prirody	Naturalists' Society of Moscow Publishing House
Izv. AN SSSR	Izvestiya Akademii Nauk SSSR	Bulletin of the Academy of Sciences of the U.S.S.R.
Izv. AN ArmSSR	Izvestiya Akademii Nauk Armyanskoi SSR	Bulletin of the Academy of Sciences of the Armenian S.S.R.
Izv. AN AzerbSSR	Izvestiya Akademii Nauk Azerbaidzhanskoi SSR	Bulletin of the Academy of Sciences of the Azerbaidzhan S.S.R.
Izv. AN Kazakh SSR	Izvestiya Akademii Nauk Kazakhskoi SSR	Bulletin of the Academy of Sciences of the Kazakh S.S.R.
Izv. Arm. Fil. AN SSSR	Izvestiya Armyanskogo Filiala Akademii Nauk SSSR	Bulletin of the Armenian Branch of the Academy of Sciences of the U.S.S.R.
Izv. Azerb. Gos. Univ.	Izvestiya Azerbaidzhanskogo Gosudarstvennogo Universiteta	Bulletin of the Azerbaidzhan State University
Izv. Azerb. Univ.	Izvestiya Azerbaidzhanskogo Universiteta	Bulletin of the Azerbaidzhan University
Izv. Geogr. Obshch.	Izvestiya Geograficheskogo Obshchestva	Bulletin of the Geographical Society
Izv. Kavk. Muz.	Izvestiya Kavkazskogo Muzeya	Bulletin of the Caucasian Museum
Izv. Kavk. Otdel. Russk. Geogr. Obshchestva	Izvestiya Kavkazskogo Otdeleniya Russkogo Geograficheskogo Obshchestva	Bulletin of the Caucasian Branch of the Russian Geographical Society
Izv. Ross. AN	Izvestiya Rossiiskoi Akademii Nauk	Bulletin of the Russian Academy of Sciences
Izv. Russk. Geogr. Obshch.	Izvestiya Russkogo Geograficheskogo Obshchestva	Bulletin of the Russian Geographical Society
Izv. Turkm. Fil AN SSSR	Izvestiya Turkmenskogo Filiala Akademii Nauk SSSR	Bulletin of the Turkmenian Branch of the Academy of Sciences of the U.S.S.R.
Kabgoizdat	Kabardinskoe Gosudarstennoe Izdatel'stvo	Kabardian State Publishing House
KOIZ	Vsesoyuznoe Kooperativnoe Izdatel'stvo	All-Union Cooperative Publishing House
Kratk. Soobshch. Inst. Ist. Mater. Kul'tury	Kratkie Soobshcheniya Instituta Istorii Material'noi Kul'tury	Brief Communications of the Institute of the History of Material Culture

Mater. k. Pozn. Fauny i Flory Ross. Imp.	Materialy k Poznaniyu Fauny i Flory Rossiiskoi Imperii	Materials for the Study of Fauna and Flora of the Russian Empire
Mater. k Pozn. Fauny i Flory SSSR	Materialy k Poznaniyu Fauny i Flory SSSR	Materials for the Study of Fauna and Flora of the U.S.S.R.
Mater. po. Chetvert. Periodu SSSR	Materialy po Chetvertichnomu Periodu SSSR	Materials on the Quaternary of the U.S.S.R.
MGU	Moskovskii Gosudarstvennyi Universitet	Moscow State University
Nauchno-Metod. Zap. Komit. po Zapov.	Nauchno-Metodicheskie Zapiski Komiteta po Zapovednikam	Scientific-Methodological Notes of the Committee on Nature Reservations
Nauchn. Tr. Erevansk. Gos. Univ.	Nauchnye Trudy Erevanskogo Gosudarstvennogo Universiteta	Scientific Transactions, Yerevan State University
NIIS	Nauchno-Issledovatel'skii Institut Svyazi	Scientific Research Institute of Communications
NKTP SSSR	Narodnyi Komissariat Tyazheloi Promyshlennosti SSSR	People's Commissariat of Heavy Industry of the U.S.S.R.
Sb. Nauchn. Tr., Erevanskii Med. Inst.	Sbornik Nauchnykh Trudov, Erevanskii Meditsinskii Institut	Collection of Scientific Works, Yerevan Medical Institute
SNK	Sovet Narodnykh Komissarov	Council of the People's Commissars
Soobshch. AN Gruz SSR	Soobshcheniya Akademii Nauk Gruzinskoi SSR	Communications of the Academy of Sciences of the Georgian S.S.R.
Soobshch. Gruz. Fil. AN SSSR	Soobshcheniya Gruzinskogo Filiala Akademii Nauk SSSR	Communications of the Georgian Branch of the Academy of Sciences of the U.S.S.R.
Sotsekgiz	Gosudarstvennoe Izdatel'stvo Sotsial'no-Ekonomicheskoi Literatury	State Publishing House of Social Sciences and Economics
SPb	Sankt-Peterburg	St. Petersburg
Tr. Azerb. Fil. AN SSSR	Trudy Azerbaidzhanskogo Filiala Akademii Nauk SSSR	Transactions of the Azerbaidzhan Branch of the Academy of Sciences of the U.S.S.R.
Tr. Biol. Inst. Arm. Fil. AN SSSR	Trudy Biologicheskogo Instituta, Armyanskii Filial, Akademiya Nauk SSSR	Transactions of the Biological Institute, Armenian Branch, Academy of Sciences of the U.S.S.R.

Tr. Erevansk. Zool. Parka	Trudy Erevanskogo Zoologicheskogo Parka	Transactions of the Yerevan Zoological Park
Tr. Geol. Muz. AN SSSR	Trudy Geologicheskogo Muzeya Akademii Nauk SSSR	Transactions of the Geological Museum of the Academy of Sciences of the U.S.S.R.
Tr. Inst. Zool. AN AzerbSSR	Trudy Instituta Zoologii, Akademii Nauk Azerbaidzhanskoi SSR	Transactions of the Zoological Institute, Academy of Sciences of the Azerbaidzhan S.S.R.
Tr. Geol. i Mineral, Muz. AN SSSR	Trudy Geologicheskogo i Mineralogicheskogo Muzeya Akademii Nauk SSSR	Transactions of the Geological and Mineralogical Museum of the Academy of Sciences of the U.S.S.R.
Tr. Kavk. Gos. Zapov.	Trudy Kavkazskogo Gosudarstvennogo Zapovednika	Transactions of the Caucasian State Reserve
Tr. Komiss. po Izuch. Chertvertich. Perioda	Trudy Komissii po Izucheniyu Chertvertichnogo Perioda	Transactions of the Committee on the Study of the Quaternary
Tr. Paleontol. Inst. AN SSSR	Trudy Paleontologicheskogo Instituta Akademii Nauk SSSR	Transactions of the Paleontological Institute of the Academy of Sciences of the U.S.S.R.
Tr. Sov. Sektsii Mezhdun. Assots. po Izuch. Chetvertich. Perioda Evropy	Trudy Sovetskoi Sektsii Mezhdunarodnoi Assotsiatsii po Izucheniyu Chetvertichnogo Perioda Evropy	Transactions of the Soviet Section of the International Association for the Study of the Quaternary of Europe
Tr. Zool. Inst. AN SSSR	Trudy Zoologicheskogo Instituta Akademii Nauk SSSR	Transactions of the Zoological Institute, Academy of Sciences of the U.S.S.R.
Tr. Zool. Inst. AN Gruz. SSR	Trudy Zoologicheskogo Instituta Akademii Nauk Gruzinskoi SSR	Transactions of the Zoological Institute, Academy of Sciences of the Georgian S.S.R.
Tr. Zool. Sektsii Gruz. Fil. AN SSSR	Trudy Zoologicheskoi Sektsii Gruzinskogo Filiala Akademii Nauk SSSR	Transactions of the Zoological Section, Georgian Branch of the Academy of Sciences of the U.S.S.R.
Tr. Zool. Sektsii Gruz. Otd. Zakavk. Fil. AN SSSR	Trudy Zoologicheskoi Sektsii Gruzinskogo Otdeleniya Zakavkazskogo Filiala Akademii Nauk SSSR	Transactions of the Zoological Section, Georgian Division of the Transcaucasian Branch of the Academy of Sciences of the U.S.S.R.

TsIK	Tsentral'nyi Ispolnitel'nyi Komitet	Central Executive Committee
Uch. Zap. Azerb. Gos. Univ. im. S.M. Kirova	Uchenye Zapiski Azerbaidzhanskogo Gosudarstvennogo Universiteta im. S.M. Kirova	Scientific Reports of the Azerbaidzhan State University im. S.M. Kirov
Uch. Zap. Sev.-Osetin. Gos. Ped. Inst.	Uchenye Zapiski, Severo-Osetinskii Gosudarstvennyi Pedagogicheskii Institut im. K. L. Khetagurova	Scientific Reports, North Ossetian State Pedagogical Institute im. K. L. Khetagurov
Uch. Zap. Sev.-Kavk. Inst. Kraev.	Uchenye Zapiski Severo-Kavkazskogo Instituta Kraevedeniya	Scientific Reports of the North Caucasian Institute of Regional Studies
Zap. AN	Zapiski Akademii Nauk	Reports of the Academy of Sciences
Zap. Kavk. Muz.	Zapiski Kavkazskogo Muzeya	Reports of the Caucasian Museum
Zap. Kavk. Otd. Russk. Geogr. Obshch.	Zapiski Kavkazskogo Otdeleniya Russkogo Geograficheskogo Obshchestva	Reports of the Caucasian Branch of the Russian Geographical Society
Zool. Sb.	Zoologicheskii Sbornik	Zoological Collection
Zool. Sb. Arm. Fil. AN SSSR	Zoologicheskii Sbornik Armyanskogo Filiala Akademii Nauk SSSR	Zoological Collection of the Armenian Branch of the Academy of Sciences of the U.S.S.R.
Zool. Zhurn.	Zoologicheskii Zhurnal	Journal of Zoology

629 *Supplement. Part 1*

YIELD AND SUPPLY OF ANIMAL PELTS ON THE CAUCASIAN ISTHMUS FROM 1925 to 1955

(Graphs 1-23, pp. 692-703)

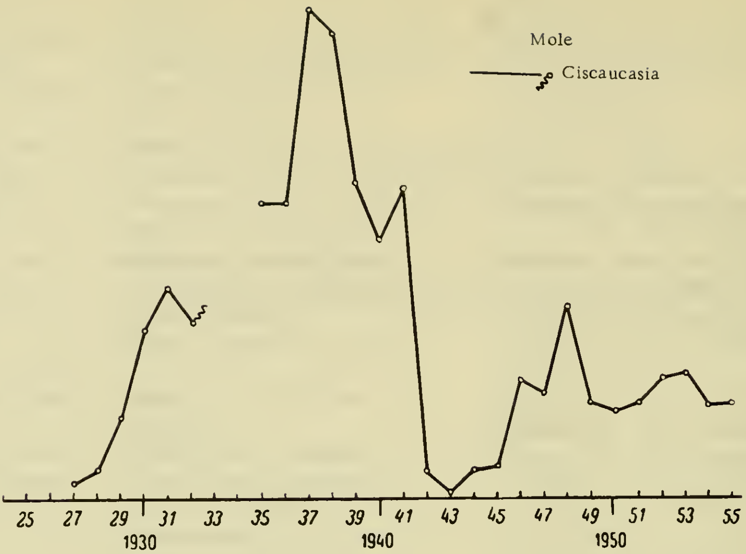
(643) *Part 2*

MAPS OF ANIMAL DISTRIBUTION ON THE CAUCASUS

(Maps 1-97, pp. 705-801)

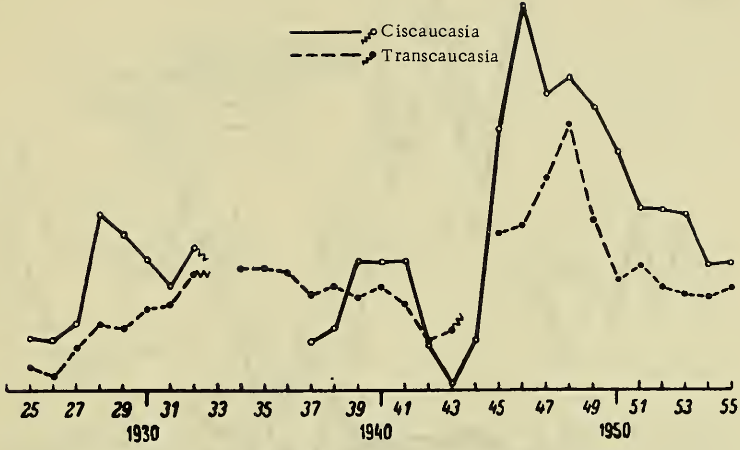
631

Graph 1



Graph 2

Graph 3



Graph 4

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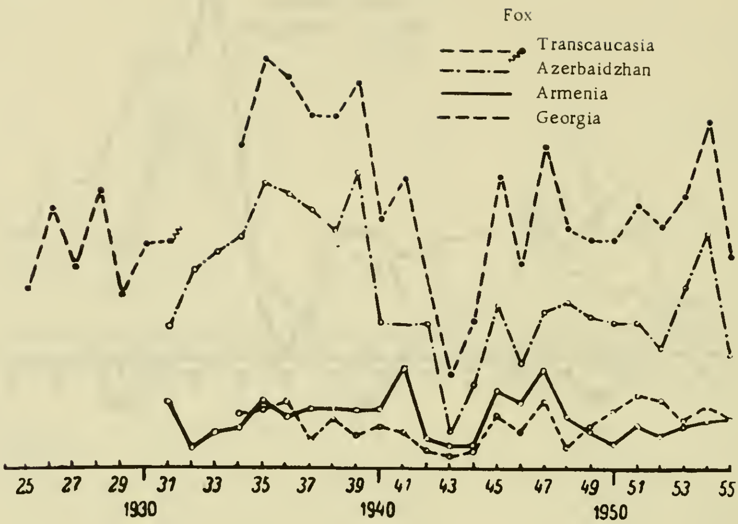
Graph 5



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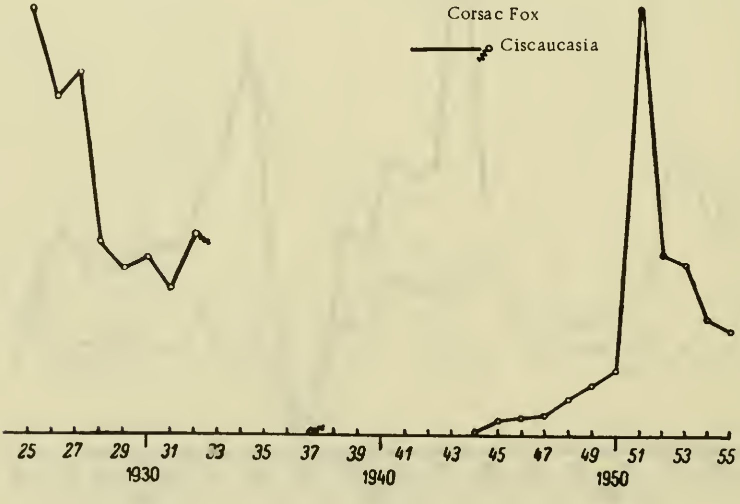

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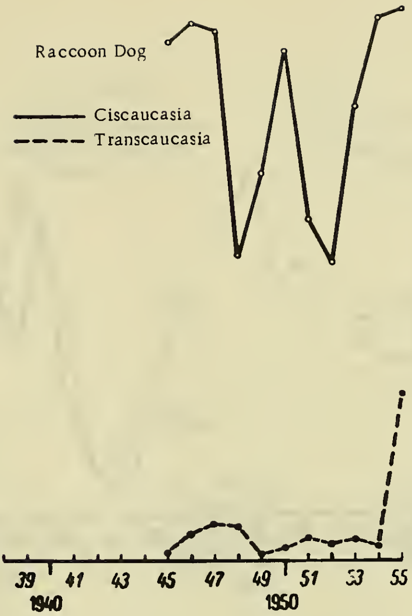

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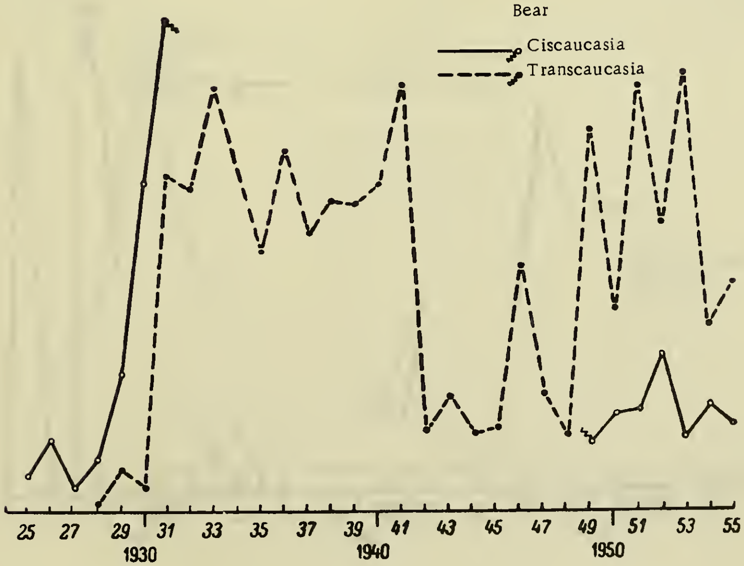

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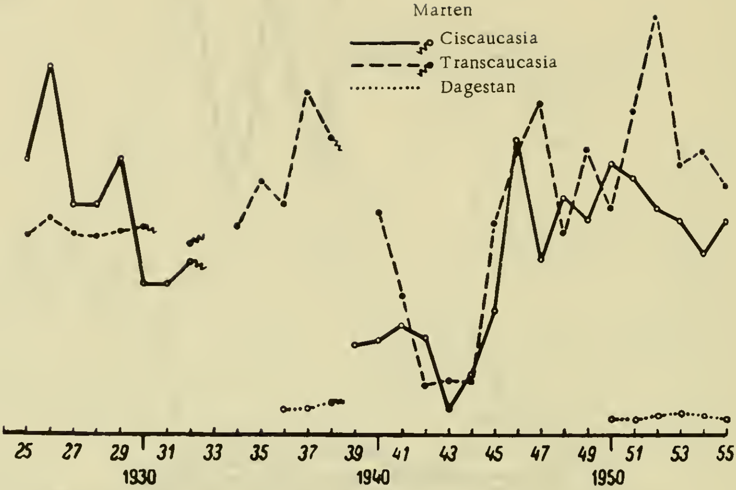

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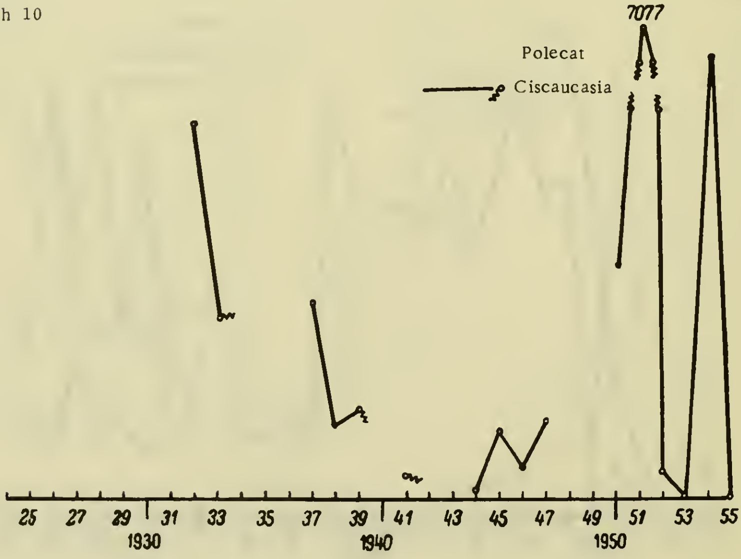

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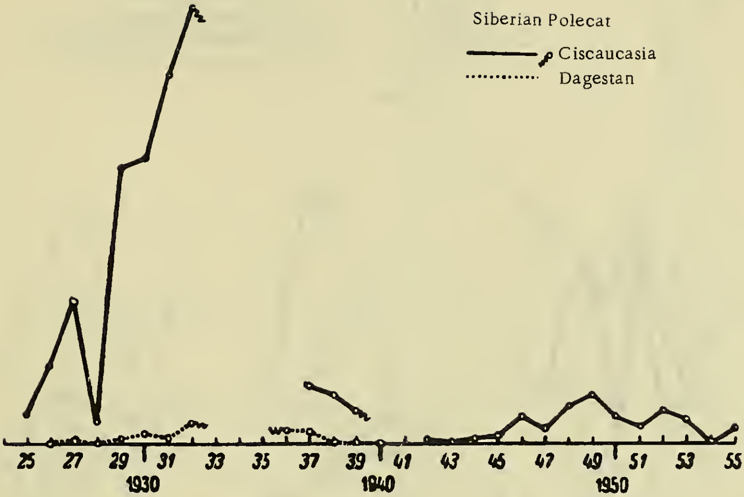

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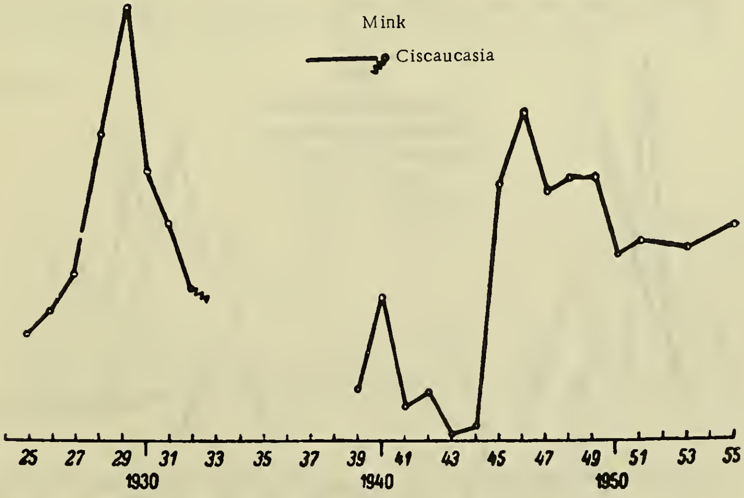

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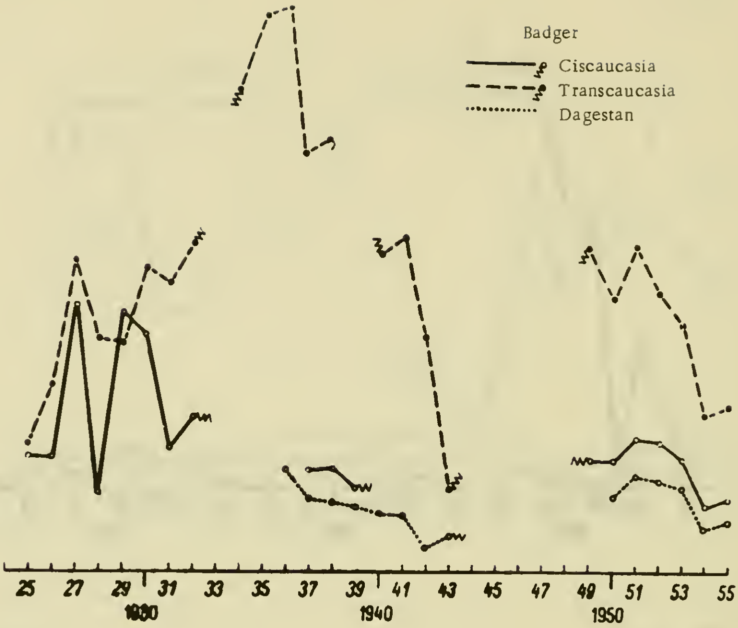

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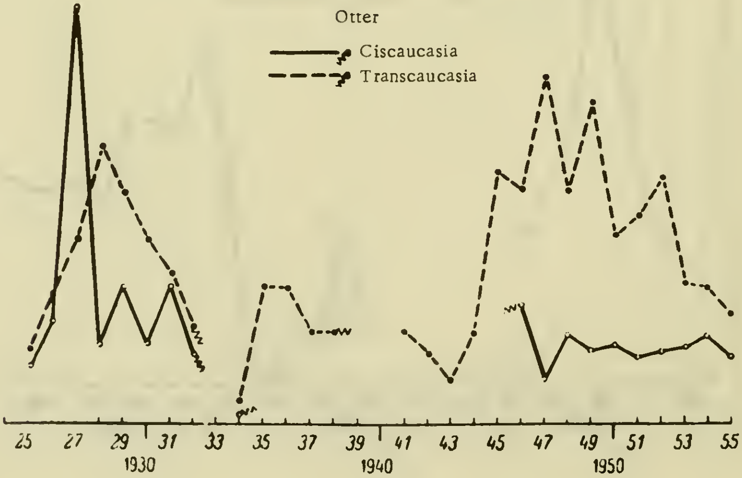

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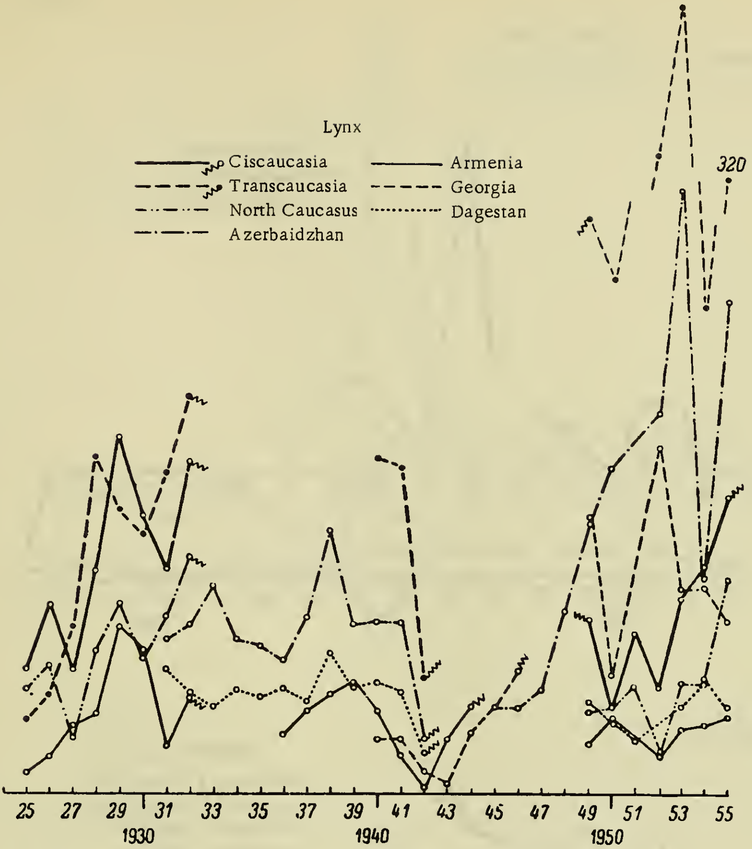

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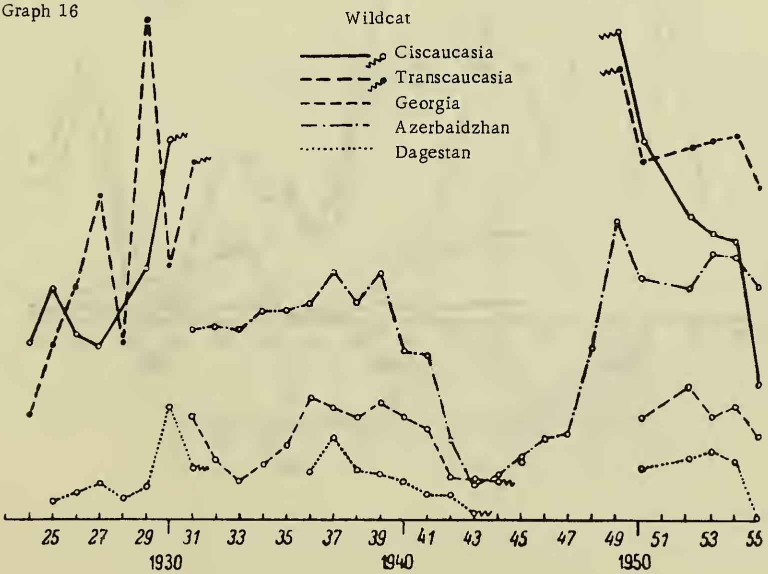

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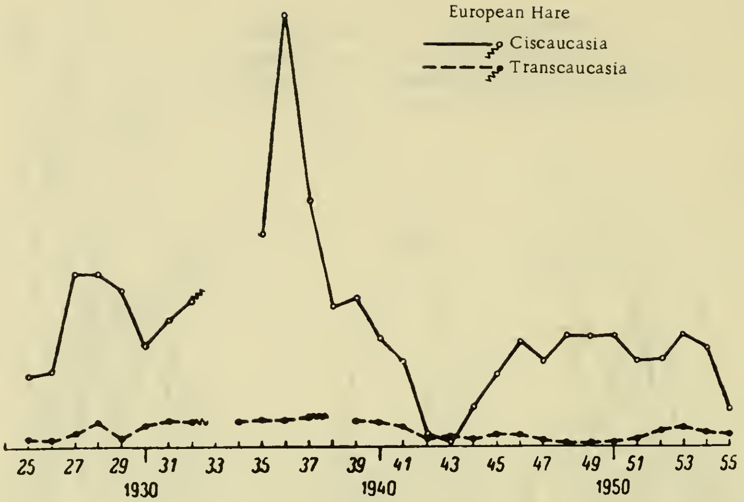

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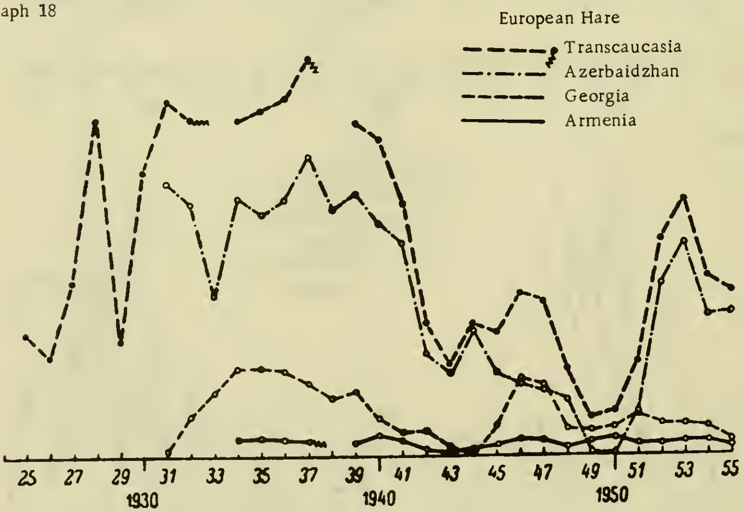

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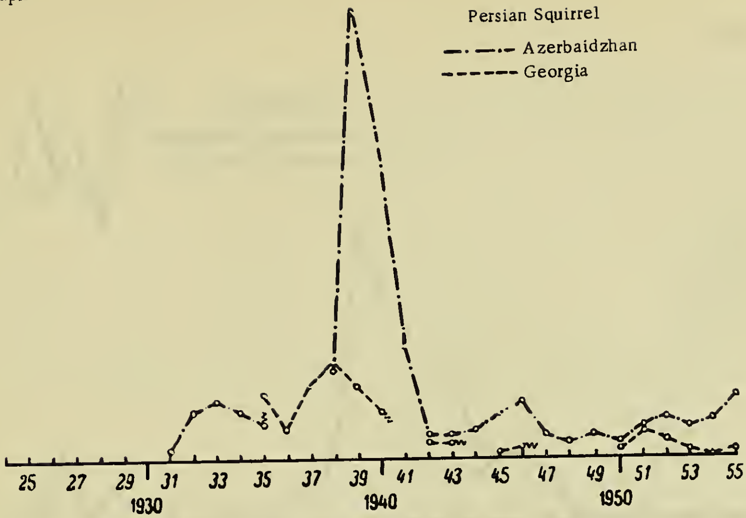

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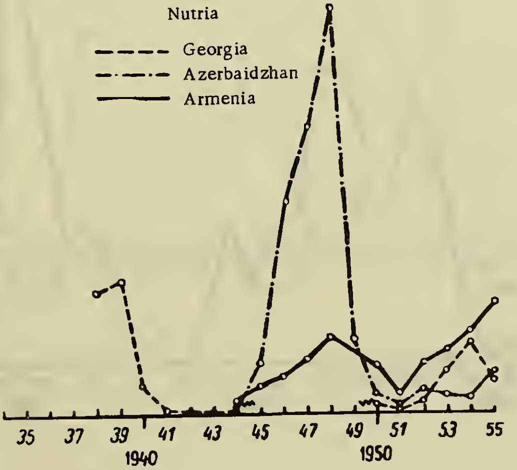

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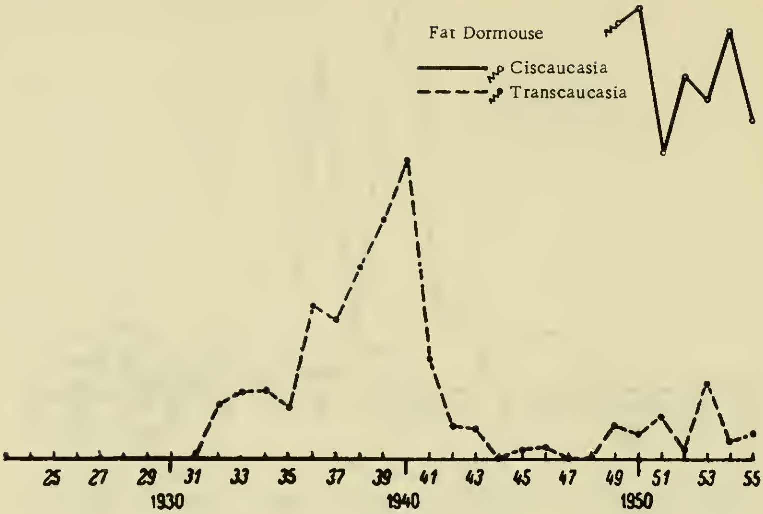

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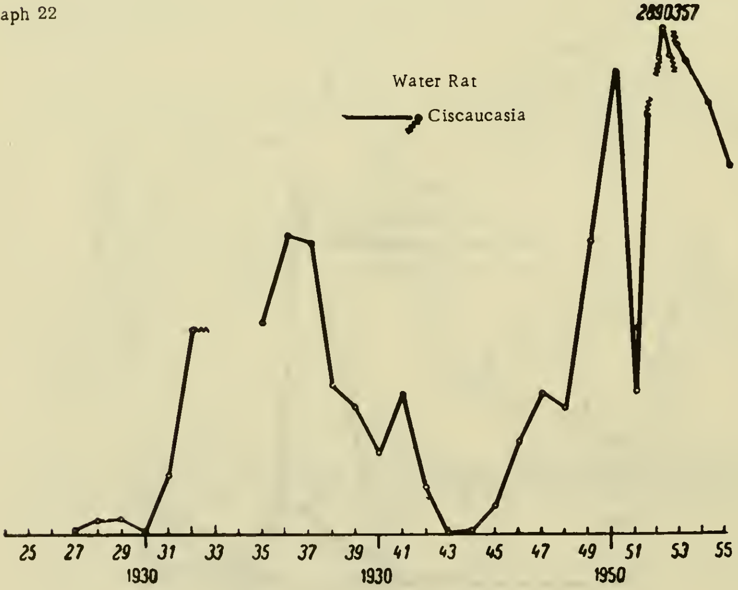

Graph 23


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Ciscaucasia
North Caucasus
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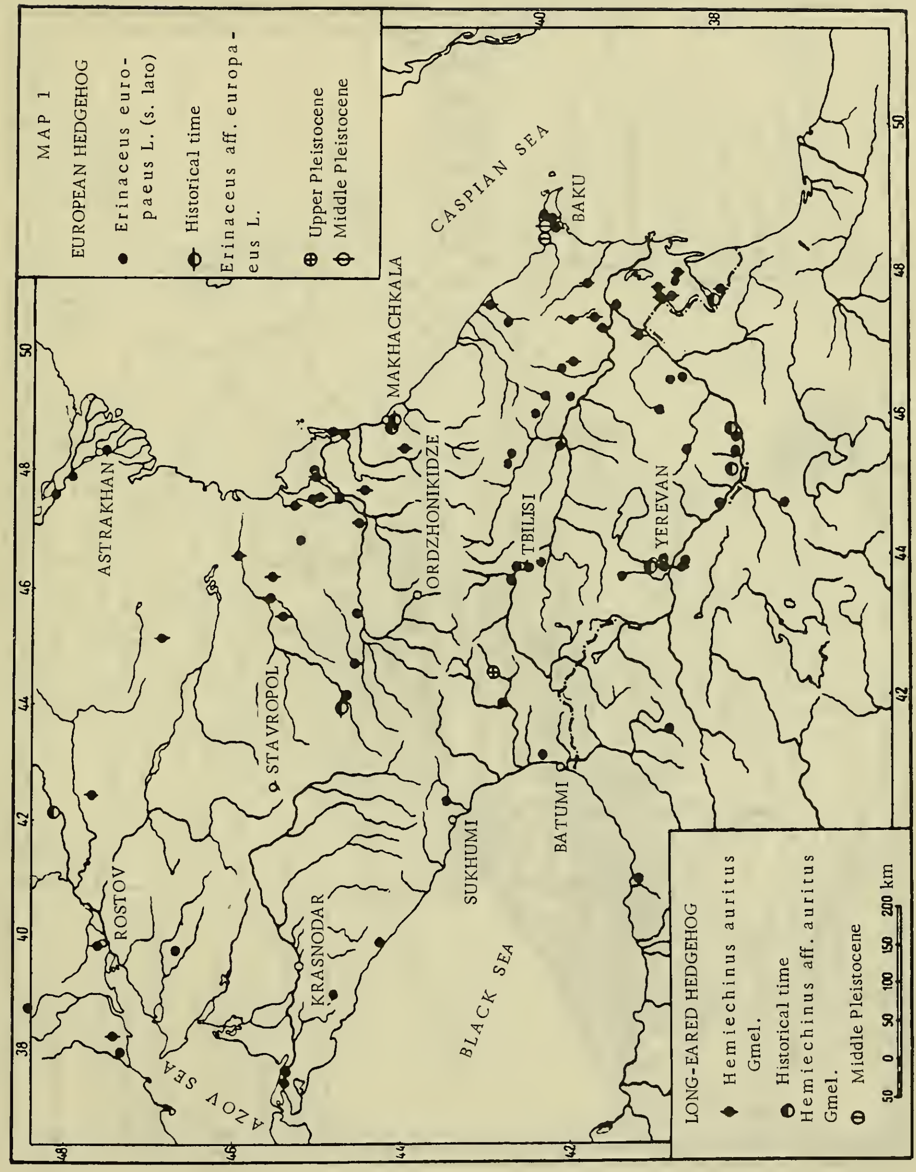
MAP 1
EUROPEAN HEDGEHOG
● Erinaceus europaeus L. (s. lato)
Historical time
Erinaceus aff. europaeus L.
⊕ Upper Pleistocene
Middle Pleistocene
LONG-EARED HEDGEHOG
Hemiechinus auritus Gmel.
Historical time
Hemiechinus aff. auritus Gmel.
Middle Pleistocene
50 0 50 100 150 200 km
CASPIAN SEA
BAKU
MAKHACHKALA
ASTRAKHAN
ORDZHONIKIDZE
TBILISI
YEREVAN
STAVROPOL
ROSTOV
KRASNODAR
SUKHUMI
BATUMI
BLACK SEA
AZOV SEA
38
40
42
44
46
48
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MAP 2
MOLES
● Talpa orientalis Ogn.
♦ Talpa caucasica Sat.
◐ Historical time
Total range
◆ Talpa caucasica ognevi Strog.
▨ Probable range
Talpa cf. caucasica Sat.
⊕ Upper Pleistocene
. 100 pelts
Talpa sp.
▲ Lower Pliocene
50 0 50 100 150 200 km
DESMAN
Desmana moschata L.
● Collected specimens
Desmana aff. moschata L.
⊕ Upper Pleistocene
Desmana sp.
△ Lower Pliocene
ASTRAKHAN
ROSTOV
AZOV SEA
CASPIAN SEA
STAVROPOL
KRASNODAR
MAKHACHKALA
ORDZHONIKIDZE
BLACK SEA
SUKHUMI
TBILISI
BATUMI
BAKU
YEREVAN
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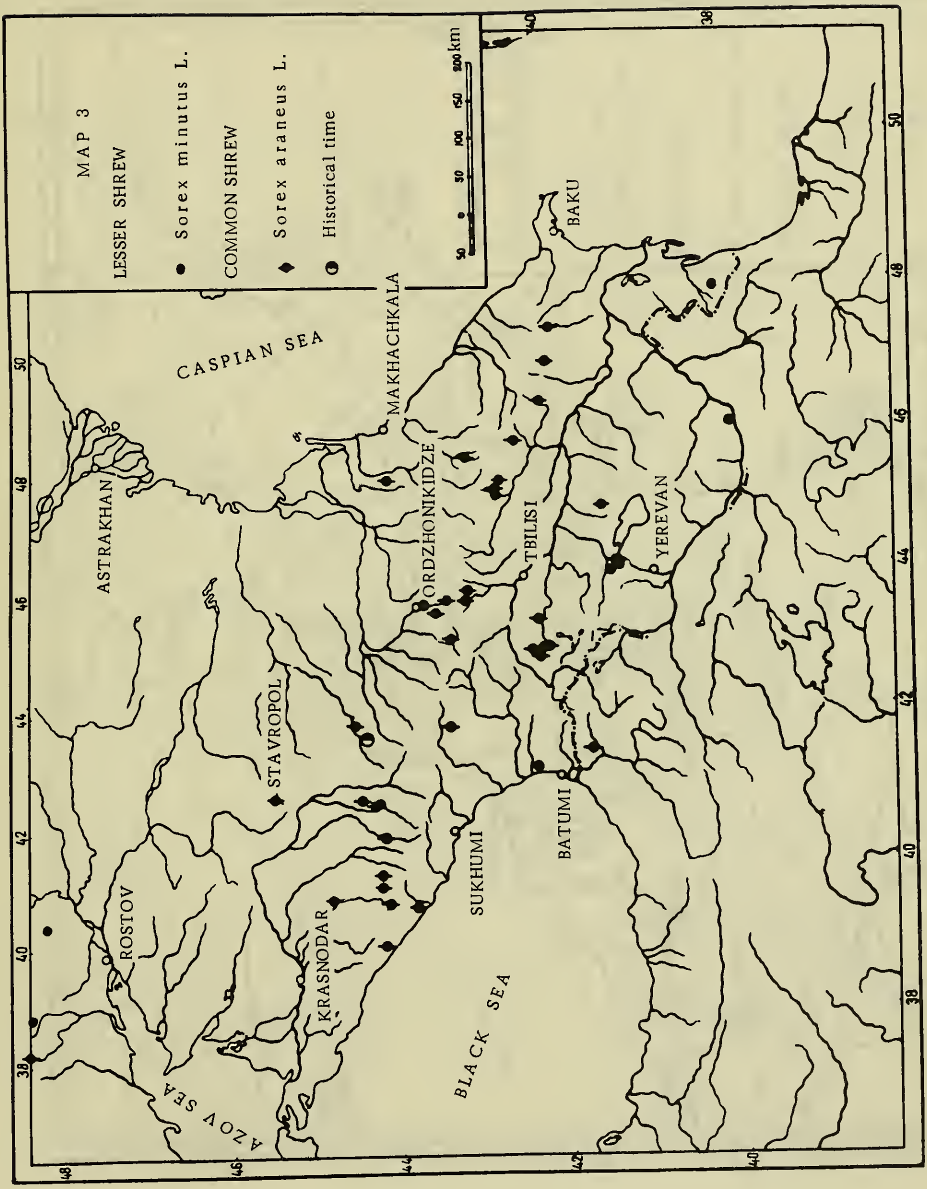
MAP 3
LESSER SHREW
● Sorex minutus L.
COMMON SHREW
◆ Sorex araneus L.
◐ Historical time
50 0 50 100 150 200 km
CASPIAN SEA
BLACK SEA
AZOV SEA
ASTRAKHAN
MAKHACHKALA
BAKU
ORDZHONIKIDZE
TBILISI
YEREVAN
STAVROPOL
ROSTOV
KRASNODAR
SUKHUMI
BATUMI
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42
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48
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MAP 4
CAUCASIAN SHREW
● Sorex raddei Sat.
WATER SHREW
◆ Neomys fodiens Schr. (s. lato)
50 0 50 100 150 200 km
ASTRAKHAN
CASPIAN SEA
ROSTOV
AZOV SEA
STAVROPOL
KRASNODAR
MAKHACHKALA
ORDZHONIKIDZE
BLACK SEA
SUKHUMI
TBILISI
BATUMI
BAKU
YEREVAN
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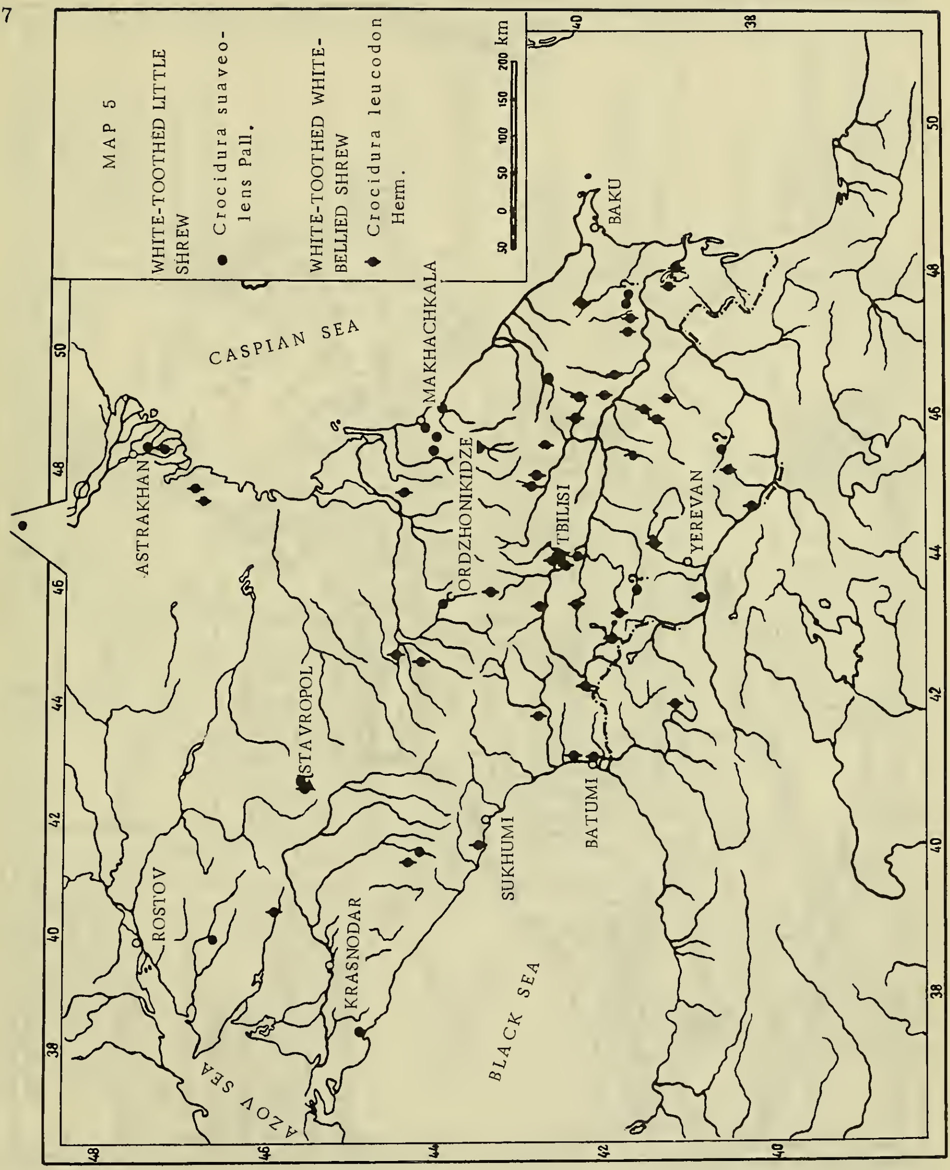

MAP 5

WHITE-TOOTHED LITTLE SHREW
● Crocidura suaveolens Pall.
WHITE-TOOTHED WHITE-BELLIED SHREW
◆ Crocidura leucodon Herm.
50 0 50 100 150 200 km
CASPIAN SEA
BLACK SEA
AZOV SEA
ASTRAKHAN
MAKHACHKALA
BAKU
ORDZHONIKIDZE
TBILISI
YEREVAN
STAVROPOL
ROSTOV
KRASNODAR
SUKHUMI
BATUMI
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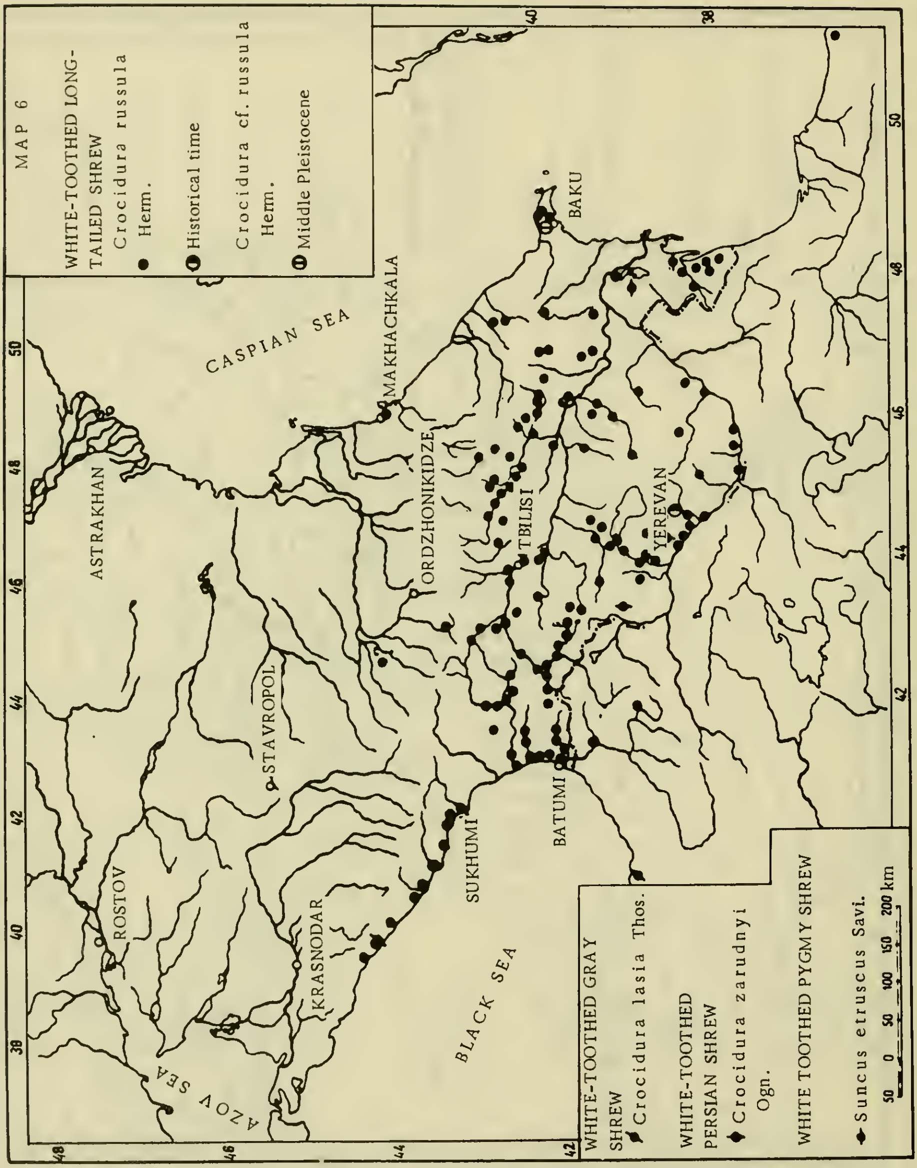
MAP 6
WHITE-TOOTHED LONG-TAILED SHREW
Crocidura russula Herm.
● Historical time
Crocidura cf. russula Herm.
● Middle Pleistocene
WHITE-TOOTHED GRAY SHREW
Crocidura lasia Thos.
WHITE-TOOTHED PERSIAN SHREW
Crocidura zarudnyi Ogn.
WHITE TOOTHED PYGMY SHREW
Suncus etruscus Savi.
50 0 50 100 150 200 km
CASPIAN SEA
BLACK SEA
AZOV SEA
ASTRAKHAN
MAKHACHKALA
BAKU
ORDZHONIKIDZE
TBILISI
YEREVAN
STAVROPOL
KRASNODAR
ROSTOV
SUKHUMI
BATUMI
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MAP 7
GREAT HORSESHOE BAT
● Rhinolophus ferrum equinum Schr.
⊕ Upper Pleistocene
SOUTHERN HORSESHOE BAT
Rhinolophus euryale Blas.
MEHELY'S HORSESHOE BAT
Rhinolophus mehelyi Matschi
50 0 50 100 150 200 km
ROSTOV
ASTRAKHAN
CASPIAN SEA
AZOV SEA
STAVROPOL
KRASNODAR
MAKHACHKALA
ORDZHONIKIDZE
SUKHUMI
BLACK SEA
TBILISI
BATUMI
BAKU
YEREVAN
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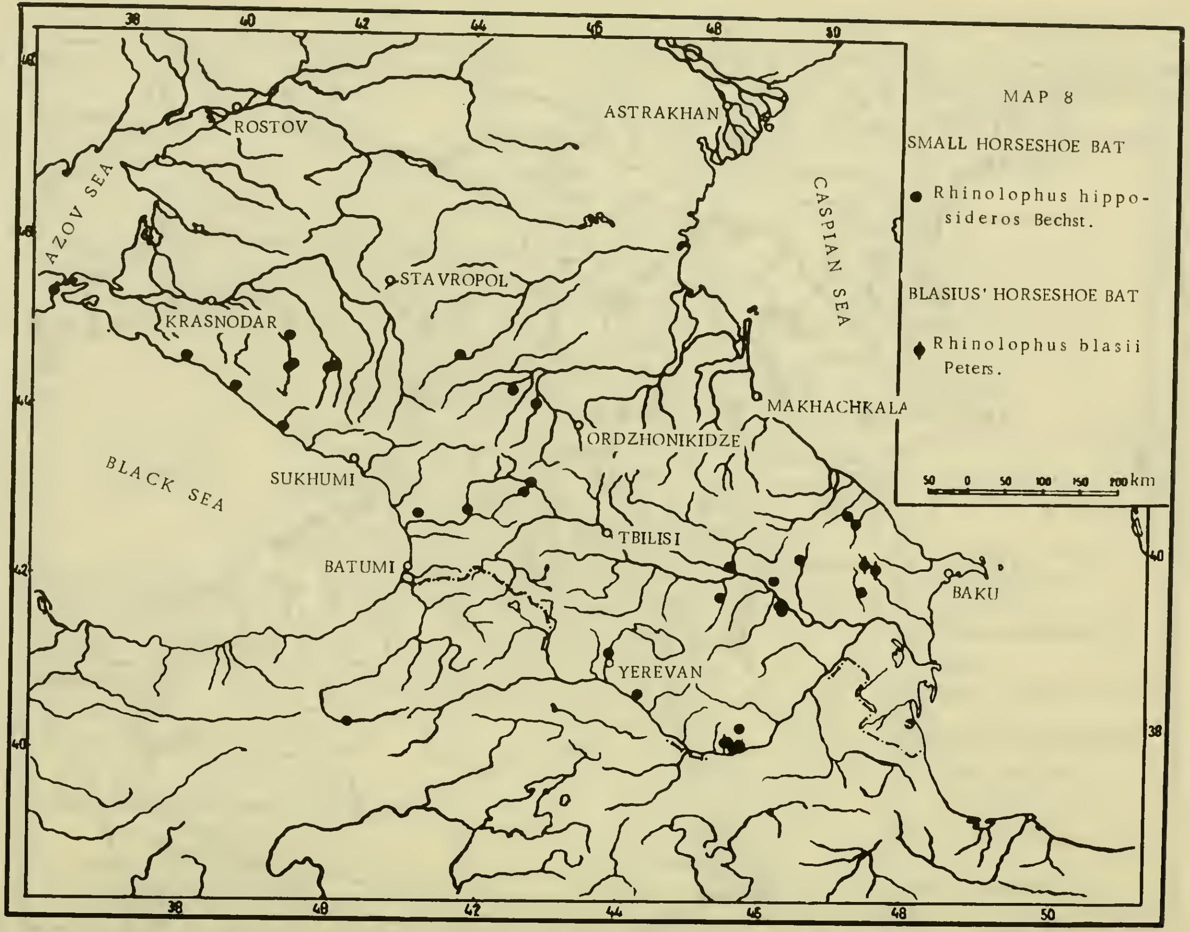

MAP 8

SMALL HORSESHOE BAT
● Rhinolophus hipposideros Bechst.
BLASIUS' HORSESHOE BAT
◆ Rhinolophus blasii Peters.
50 0 50 100 150 200 km
ASTRAKHAN
CASPIAN SEA
ROSTOV
AZOV SEA
STAVROPOL
KRASNODAR
MAKHACHKALA
ORDZHONIKIDZE
BLACK SEA
SUKHUMI
TBILISI
BATUMI
BAKU
YEREVAN
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48
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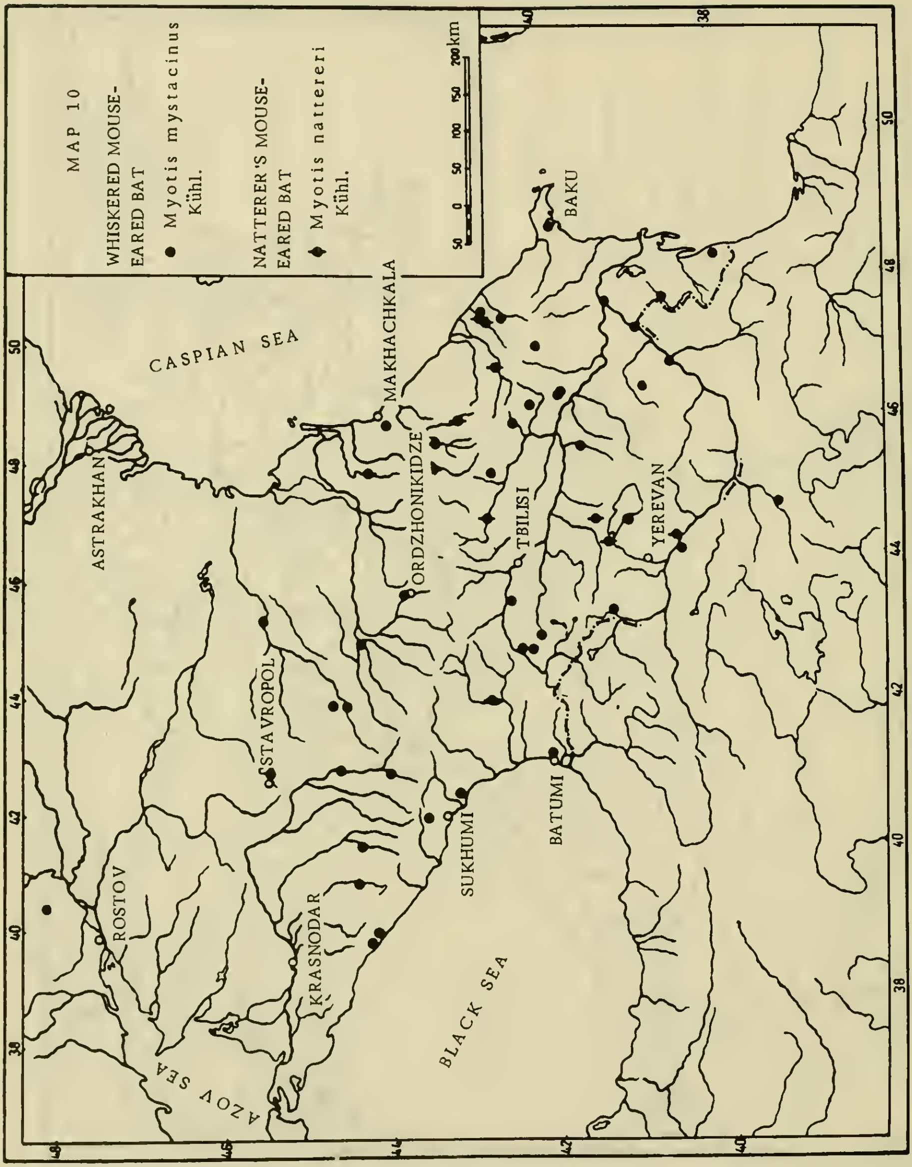
MAP 9
BECHSTEIN'S MOUSE-EARED BAT
● Myotis bechsteini Kühl.
SHARP-EARED MOUSE-EARED BAT
◆ Myotis oxygnathus Mont.
◐ Historical time
TRICOLOR MOUSE-EARED BAT
◆ Myotis emarginatus Geoffr.
50 0 50 100 150 200 km
38
40
42
44
46
48
50
ASTRAKHAN
ROSTOV
AZOV SEA
CASPIAN SEA
STAVROPOL
KRASNODAR
MAKHACHKALA
ORDZHONIKIDZE
BLACK SEA
SUKHUMI
TBILISI
BATUMI
BAKU
YEREVAN


MAP 10
WHISKERED MOUSE-EARED BAT
● Myotis mystacinus Kühl.
NATTERER'S MOUSE-EARED BAT
◆ Myotis nattereri Kühl.
50 0 50 100 150 200 km
CASPIAN SEA
BLACK SEA
AZOV SEA
ASTRAKHAN
MAKHACHKALA
ORDZHONIKIDZE
STAVROPOL
ROSTOV
KRASNODAR
SUKHUMI
BATUMI
TBILISI
YEREVAN
BAKU
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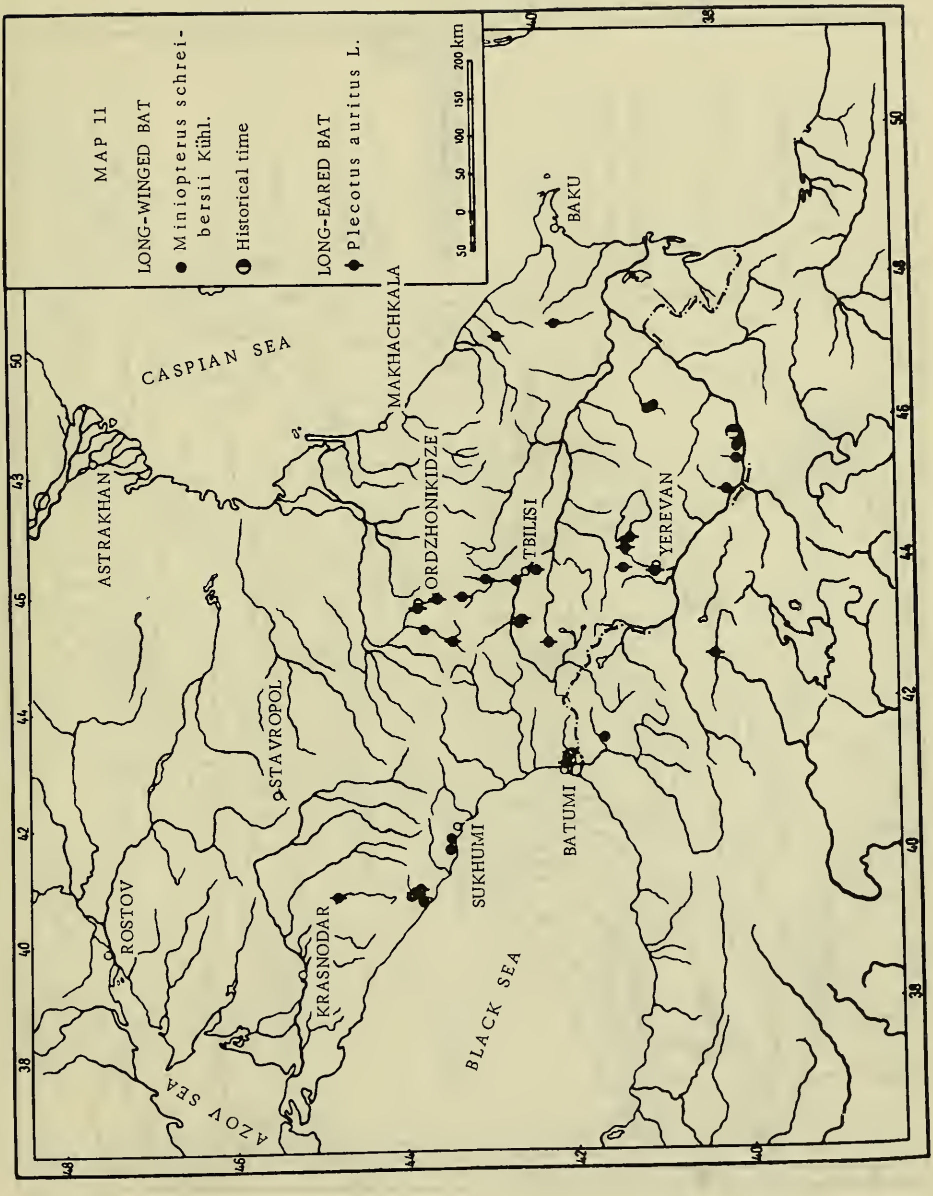
MAP 11
LONG-WINGED BAT
● Miniopterus schreibersii Kühl.
◐ Historical time
LONG-EARED BAT
◆ Plecotus auritus L.
50 0 50 100 150 200 km
CASPIAN SEA
BLACK SEA
AZOV SEA
ASTRAKHAN
MAKHACHKALA
ORDZHONIKIDZE
TBILISI
BAKU
YEREVAN
STAVROPOL
ROSTOV
KRASNODAR
SUKHUMI
BATUMI
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48
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44
42
40
38


MAP 12
ASIATIC BARBASTEL
● Barbastella darjelingensis Dobs.
EUROPEAN BARBASTEL
♦ Barbastella barbastellus Schr.
50 0 50 100 150 200 km
ASTRAKHAN
ROSTOV
CASPIAN SEA
AZOV SEA
STAVROPOL
KRASNODAR
MAKHACHKALA
ORDZHONIKIDZE
SUKHUMI
BLACK SEA
TBILISI
BATUMI
BAKU
YEREVAN
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MAP 13
LEISLER'S NOCTULE
◆ Nyctalus leisleri Kühl.
GIANT NOCTULE
◆ Nyctalus siculus Palumbo
COMMON NOCTULE
● Nyctalus noctula Schr.
50 9 50 100 150 200 km
ASTRAKHAN
CASPIAN SEA
ROSTOV
AZOV SEA
STAVROPOL
KRASNODAR
MAKHACHKALA
ORDZHONIKIDZE
BLACK SEA
SUKHUMI
TBILISI
BATUMI
BAKU
YEREVAN
38
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48
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MAP 14
PIPISTREL
● Vespertilio pipistrellus Schr.
50 0 50 100 150 200km
ASTRAKHAN
CASPIAN SEA
ROSTOV
AZOV SEA
STAVROPOL
KRASNODAR
MAKHACHKLA
ORDZHONIKIDZE
SUKHUMI
BLACK SEA
TBILISI
BATUMI
BAKU
YEREVAN
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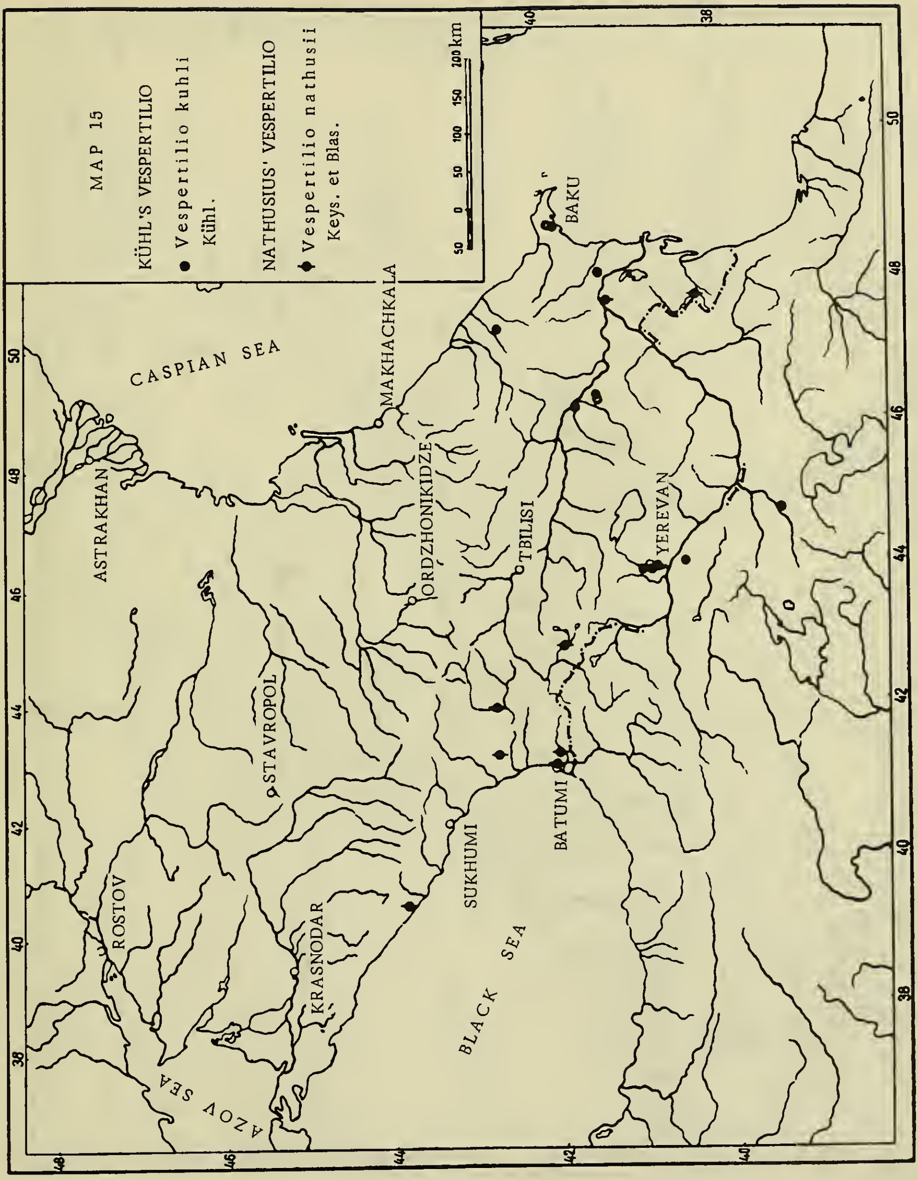
MAP 15
KÜHL'S VESPERTILIO
● Vespertilio kuhli Kühl.
NATHUSIUS' VESPERTILIO
◆ Vespertilio nathusii Keys. et Blas.
50
0
50
100
150
200 km
CASPIAN SEA
ASTRAKHAN
MAKHACHKALA
BAKU
ORDZHONIKIDZE
TBILISI
YEREVAN
STAVROPOL
ROSTOV
KRASNODAR
SUKHUMI
BATUMI
BLACK SEA
AZOV SEA
38
40
42
44
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48
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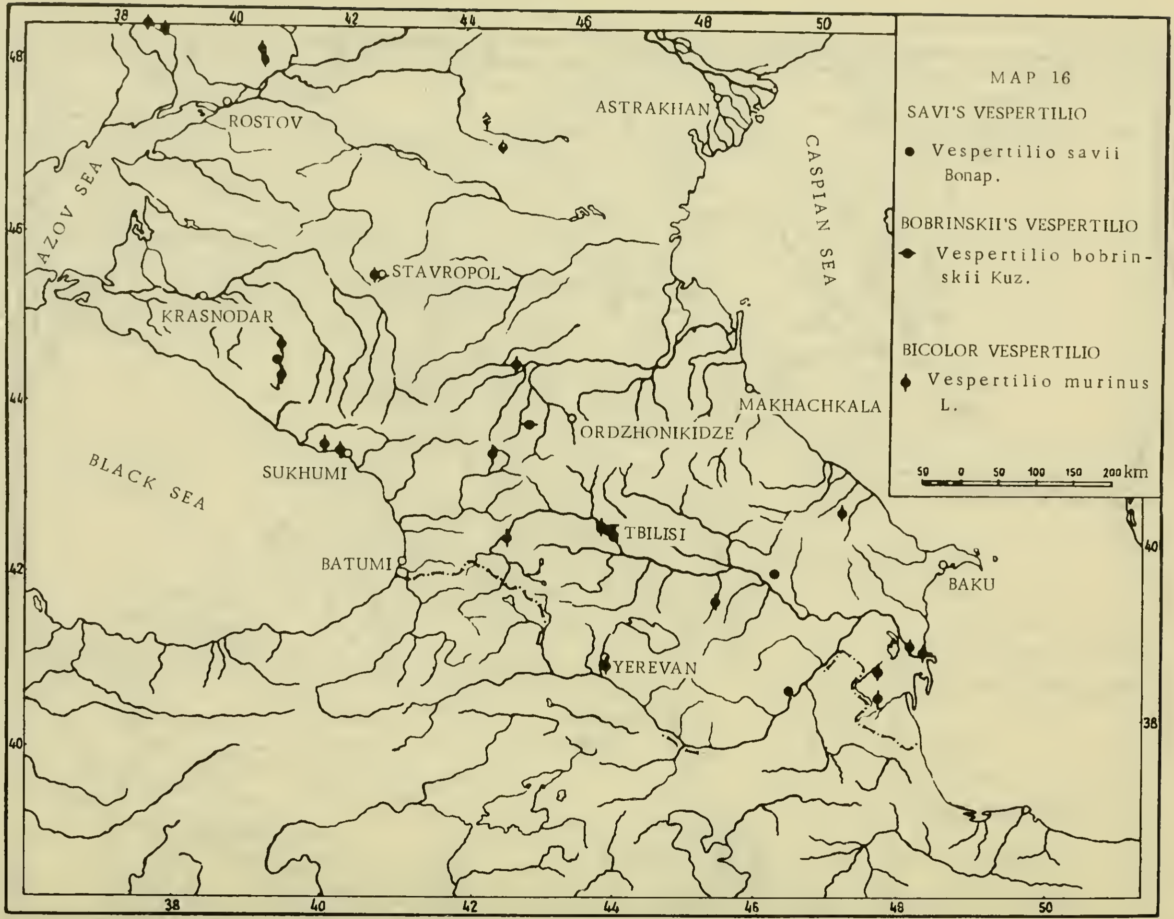
MAP 16
SAVI'S VESPERTILIO
● Vespertilio savii Bonap.
BOBRINSKII'S VESPERTILIO
◆ Vespertilio bobrinskii Kuz.
BICOLOR VESPERTILIO
◆ Vespertilio murinus L.
50 0 50 100 150 200 km
ROSTOV
ASTRAKHAN
CASPIAN SEA
AZOV SEA
STAVROPOL
KRASNODAR
MAKHACHKALA
ORDZHONIKIDZE
SUKHUMI
BLACK SEA
TBILISI
BATUMI
BAKU
YEREVAN
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MAP 17

SEROTINE VESPERTILIO
● Vespertilio serotinus Schr.
OGNEV'S VESPERTILIO
Vespertilio ognevi Bobr.
NORTHERN VESPERTILIO
Vespertilio nilssonii Keys. et Blas.
POCKETED BAT
Tadarida taeniotis Raf.
50 0 50 100 150 200 km
ROSTOV
ASTRAKHAN
AZOV SEA
CASPIAN SEA
STAVROPOL
KRASNODAR
MAKHACHKALA
ORDZHONIKIDZE
BLACK SEA
SUKHUMI
TBILISI
BATUMI'
BAKU
YEREVAN
38
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48
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MAP 18
JACKAL
Canis aureus L.
● Collected specimens
· 10 pelts
◑ Historical time
○ 2nd millennium B.C.
Probable route of penetration
SIBERIAN RED DOG
Cuon sp.
▲ Middle Pleistocene
50 0 50 100 150 200km
ROSTOV
ASTRAKHAN
AZOV SEA
STAVROPOL
KRASNODAR
MAKHACHKALA
ORDZHONIKIDZE
BLACK SEA
SUKHUMI
TBILISI
BATUMI
BAKU
CASPIAN SEA
YEREVAN
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MAP 19

WOLF
Canis lupus L.
● Collected specimens
• 10 pelts
○ 9-13th centuries A.D.
◑ 1st millennium B.C.
◓ Holocene
Canis aff. lupus L.
⊕ Upper Pleistocene
Canis lupus apscheronicus N. Ver.
⦶ Middle Pleistocene
TAMAN WOLF
Canis tamanensis N.Ver.
▲ Lower Pleistocene — Upper Pliocene
Canis sp.
△ Upper Pliocene
50 0 50 100 150 200 km
38
40
42
44
46
48
50
ASTRAKHAN
ROSTOV
AZOV SEA
STAVROPOL
KRASNODAR
MAKHACHKALA
ORDZHONIKIDZE
BLACK SEA
SUKHUMI
TBILISI
CASPIAN SEA
BATUMI
BAKU
YEREVAN


MAP 20
FOX
Vulpes vulpes L. (s. lato)
● Collected specimens
• 100 pelts
○ 9-13th centuries A.D.
1st millennium B.C.
2nd millennium B.C.
Holocene
Vulpes aff. vulpes L.
⊕ Upper Pleistocene
⊖ Middle Pleistocene
ASTRAKHAN
ROSTOV
AZOV SEA
STAVROPOL
KRASNODAR
MAKHACHKALA
ORDZHONIKIDZE
SUKHUMI
BLACK SEA
TBILISI
BATUMI
BAKU
CASPIAN SEA
YEREVAN
Vulpes vulpes aff. alpherakyi Sat.
Middle Pleistocene
Vulpes khomenkoi, V. Bog.
▲ Middle Pliocene
50 0 50 100 150 200 km
38
40
42
44
46
48
50


Map 21
CORSAC FOX
Vulpes corsac L.
● Collected specimens
• 1 pelt
◑ 9-13th centuries A.D.
Vulpes aff. corsac L.
⦶ Middle Pleistocene
Probable range in Pleistocene
STRIPED HYENA
Hyaena hyaena L.
Beginning of 20th century
Holocene
50 0 50 100 150 200km
CAVE HYENA
Crocuta crocuta spelaea Goldf.
⊕ Upper Pleistocene
⊙ Middle Pleistocene
Crocuta sp.
▲ Pliocene
ELDAR HYENA
Crocuta eldarica V. Bog.
△ Upper Miocene
ASTRAKHAN
CASPIAN SEA
ROSTOV
AZOV SEA
STAVROPOL
KRASNODAR
BLACK SEA
SUKHUMI
MAKHACHKALA
ORDZHONIKIDZE
TBILISI
BATUMI
BAKU
YEREVAN
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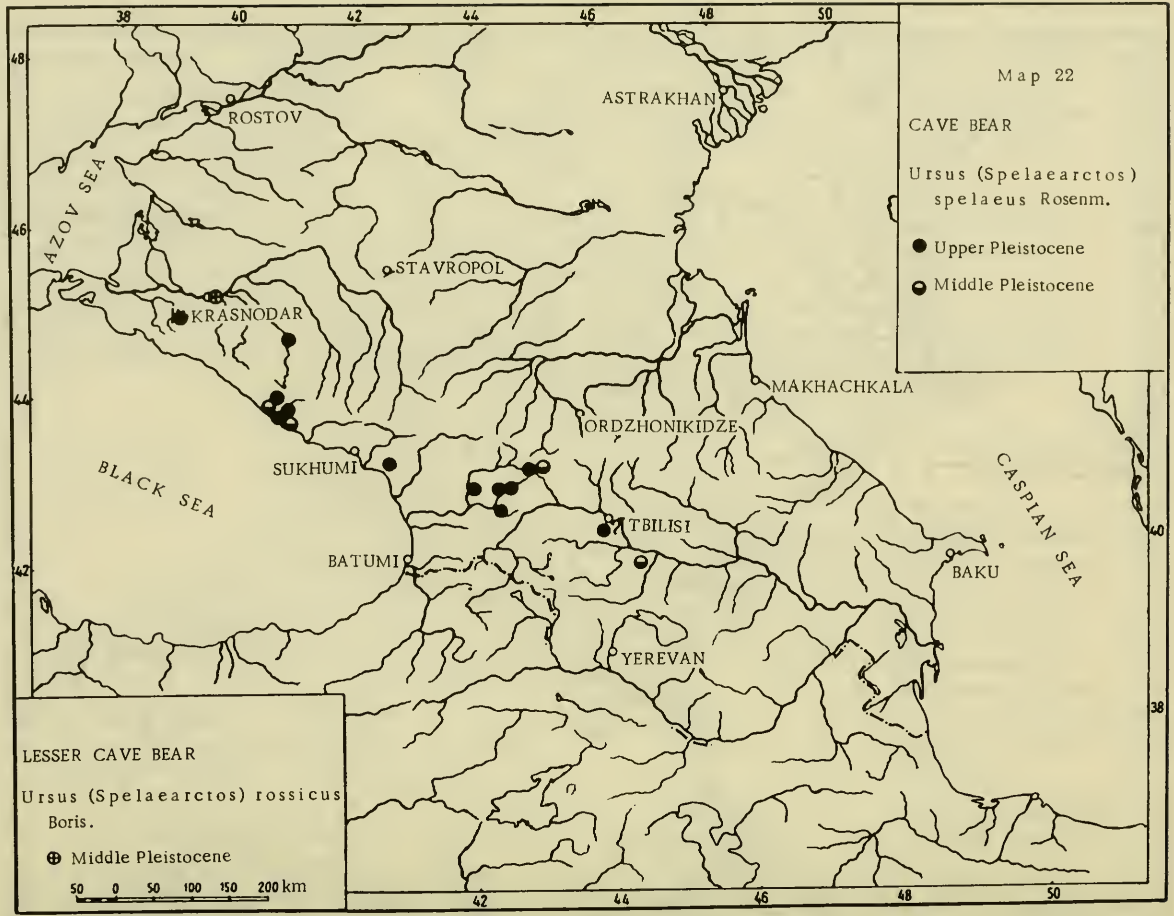

Map 22

CAVE BEAR

Ursus (Spelaearctos) spelaeus Rosenm.

● Upper Pleistocene

◒ Middle Pleistocene

LESSER CAVE BEAR

Ursus (Spelaearctos) rossicus Boris.

⊕ Middle Pleistocene

MAP 23

EUROPEAN BROWN BEAR

Ursus arctos L. (s. lato)


MAP 24
STONE MARTEN
Martes foina Erxl.
● Collected specimens
• 5 pelts
◐ 1st millennium B.C.
Martes cf. foina Erxl.
◐ Middle Pleistocene
Probable route of penetration
50 0 50 100 150 200 km
ROSTOV
ASTRAKHAN
AZOV SEA
STAVROPOL
KRASNODAR
MAKHACHKALA
ORDZHONIKIDZE
SUKHUMI
BLACK SEA
TBILISI
BATUMI
BAKU
CASPIAN SEA
YEREVAN
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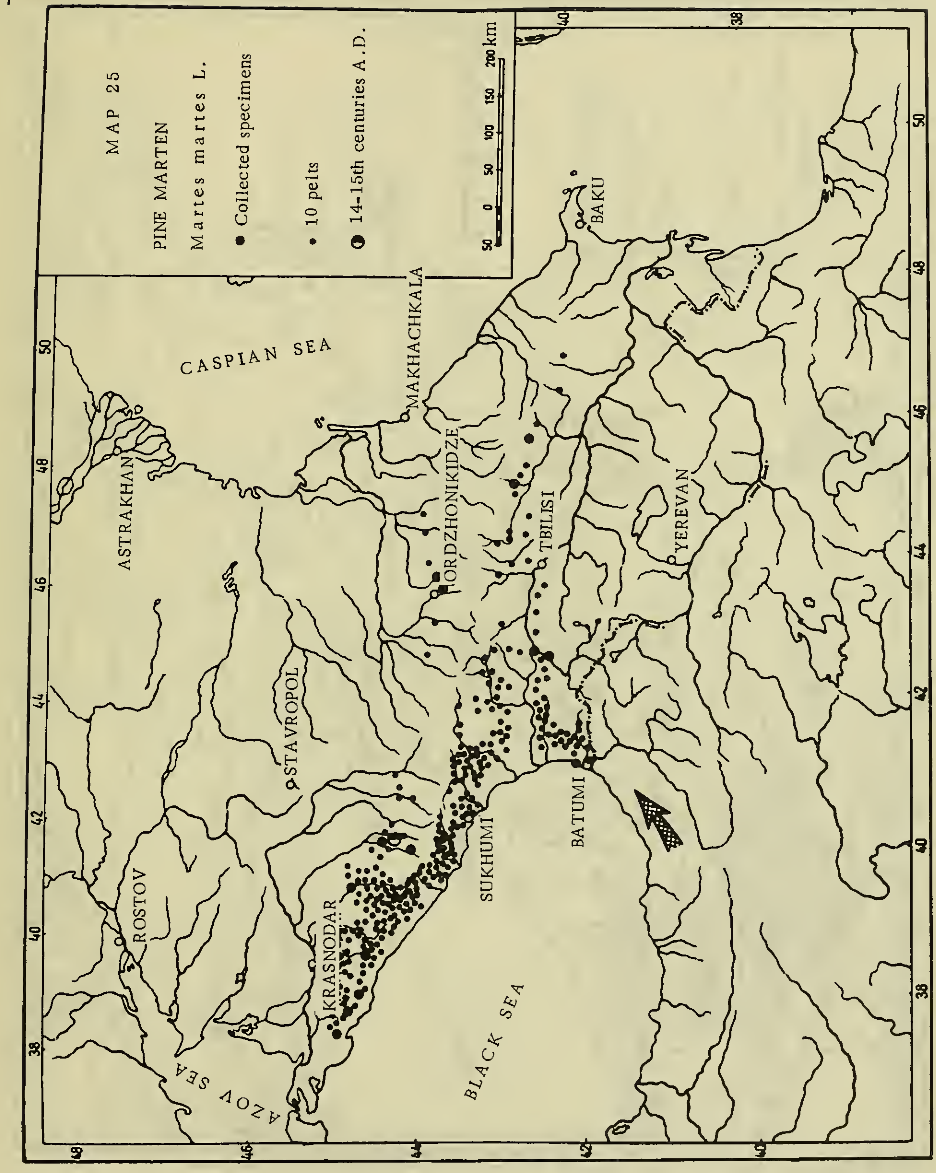


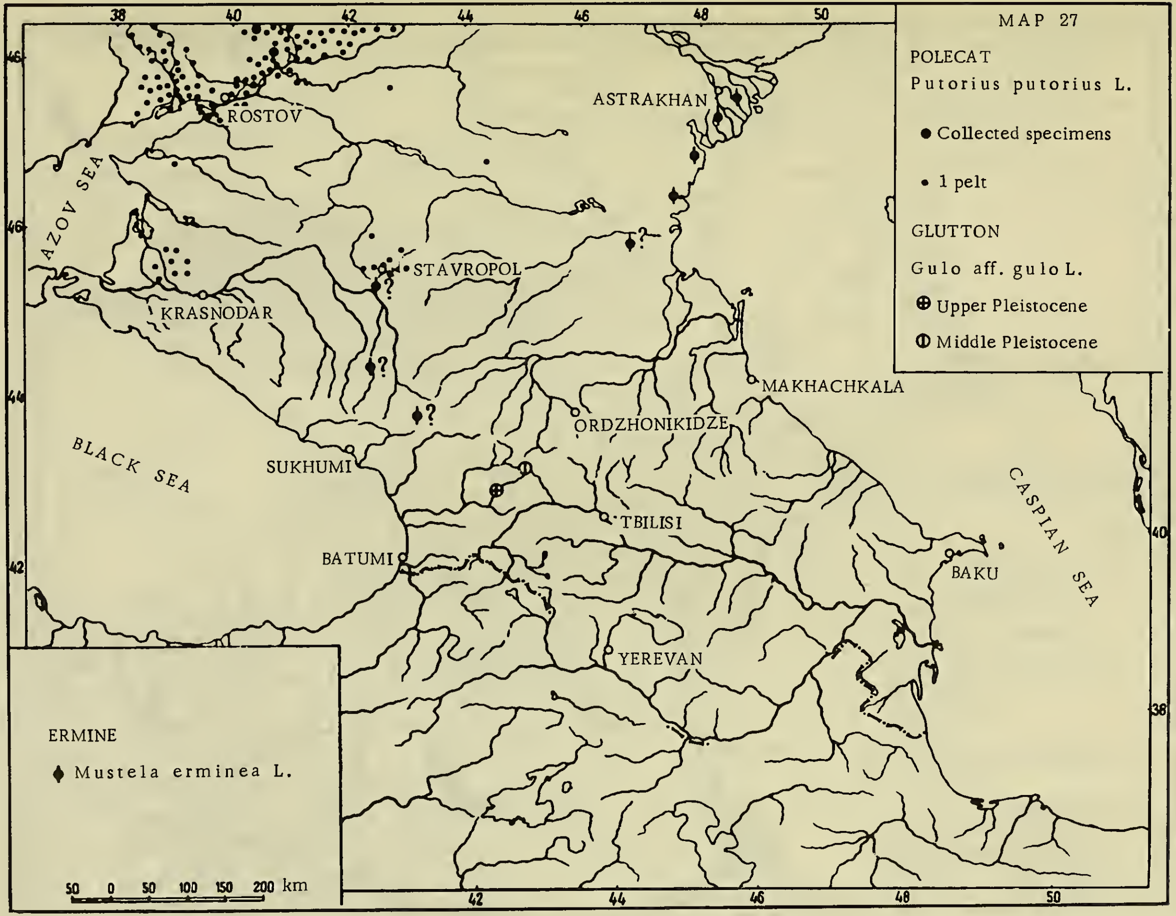
MAP 25

PINE MARTEN

Martes martes L.

MAP 26

TIGER POLECAT
Vormela peregusna
Güld.
- ● Collected specimens
- • 10 pelts
- ◐ Historical time
- ◐ Middle Pleistocene


MAP 27
POLECAT
Putorius putorius L.
● Collected specimens
• 1 pelt
GLUTTON
Gulo aff. gulo L.
⊕ Upper Pleistocene
⦶ Middle Pleistocene
ERMINE
♦ Mustela erminea L.
50 0 50 100 150 200 km
ROSTOV
ASTRAKHAN
AZOV SEA
STAVROPOL
KRASNODAR
MAKHACHKALA
ORDZHONIKIDZE
BLACK SEA
SUKHUMI
TBILISI
BATUMI
BAKU
CASPIAN SEA
YEREVAN
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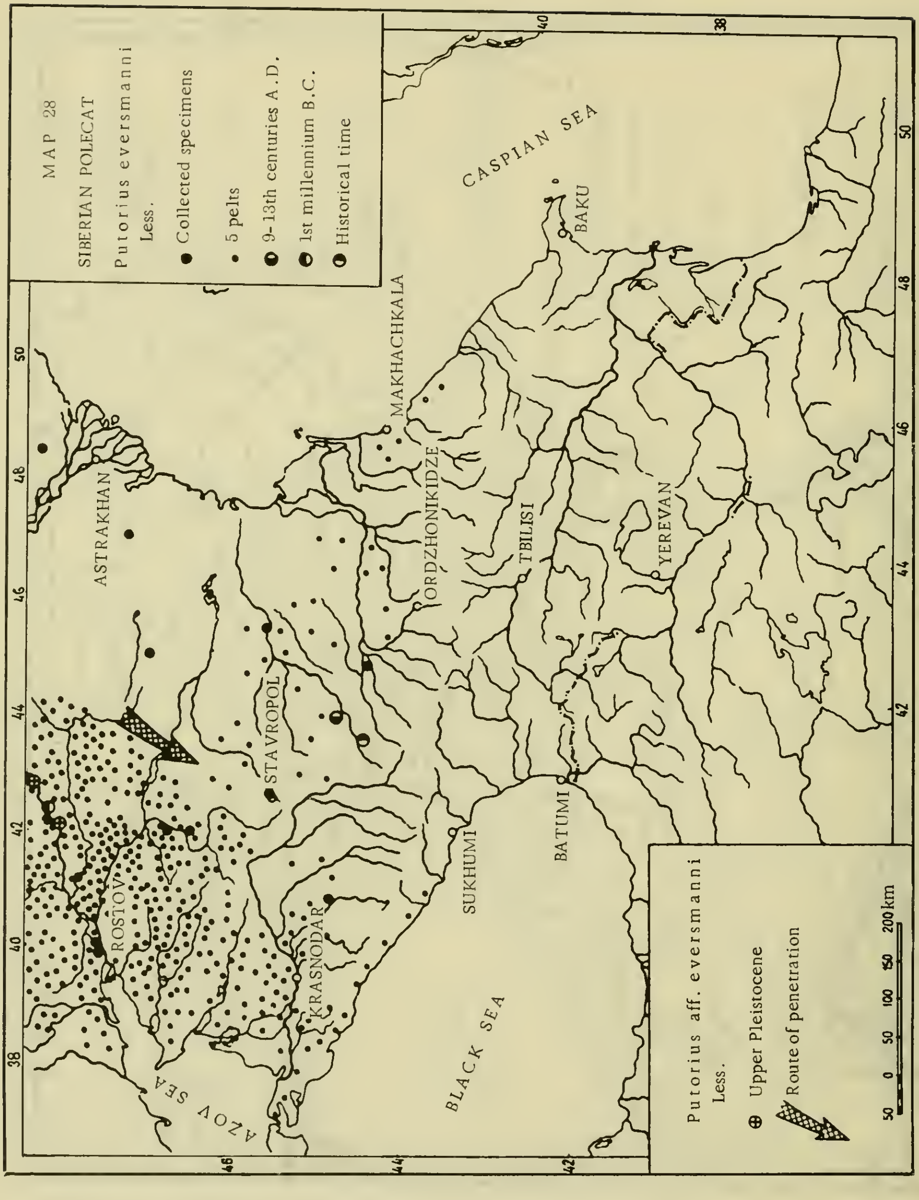
MAP 28
SIBERIAN POLECAT
Putorius eversmanni Less.
● Collected specimens
• 5 pelts
9-13th centuries A.D.
1st millennium B.C.
Historical time
Putorius aff. eversmanni Less.
⊕ Upper Pleistocene
Route of penetration
50 0 50 100 150 200 km
CASPIAN SEA
BLACK SEA
AZOV SEA
ASTRAKHAN
MAKHACHKALA
BAKU
ORDZHONIKIDZE
TBILISI
YEREVAN
STAVROPOL
ROSTOV
KRASNODAR
SUKHUMI
BATUMI
38
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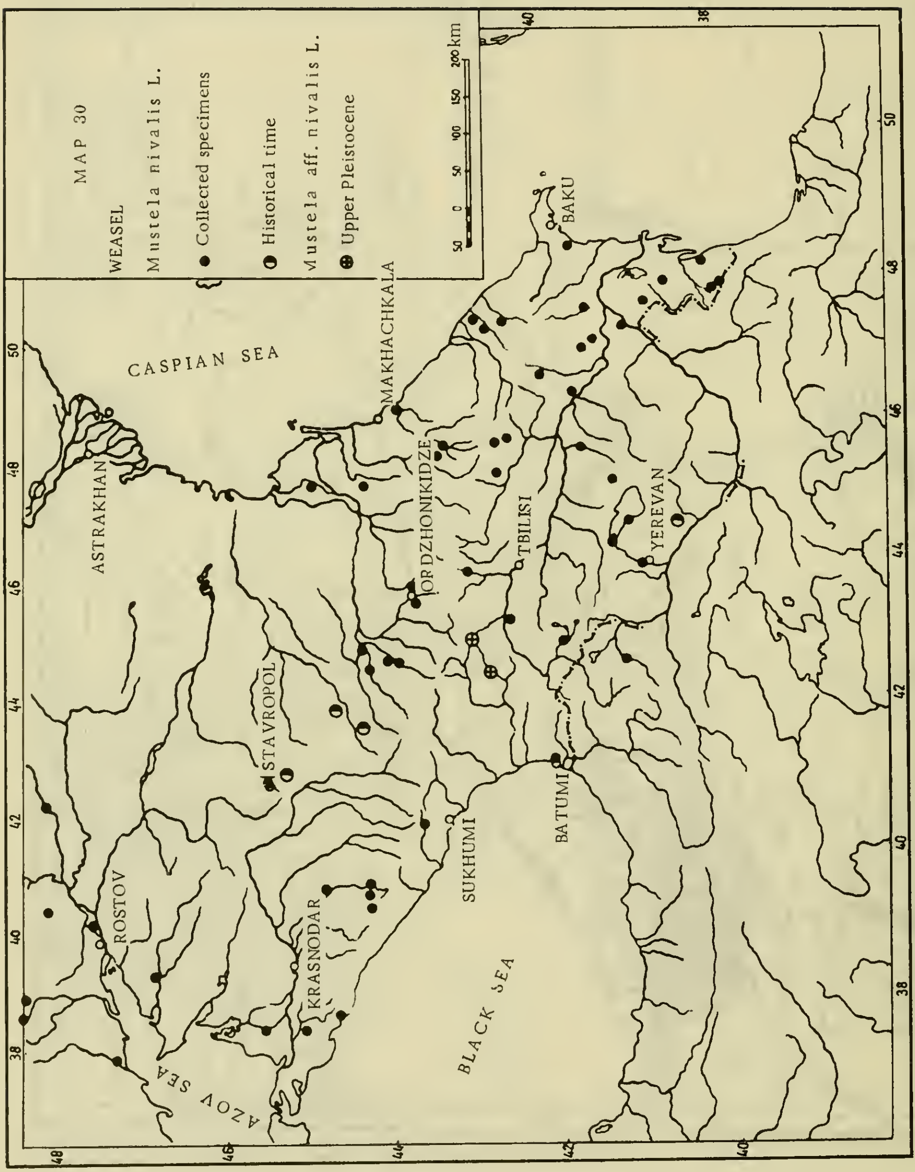
MAP 29

MINK

Lutreola lutreola Schr.



MAP 30

WEASEL

Mustela nivalis L.

● Collected specimens

◑ Historical time

Mustela aff. nivalis L.

⊕ Upper Pleistocene

MAP 31

BADGERS


MAP 32
OTTER
Lutra lutra L.
■ Occurrence of tracks
● Collected specimens
◑ 9-13th centuries A.D.
◐ 3rd-2nd centuries B.C.
◒ Holocene
Lutra aff. lutra L.
⊕ Upper Pleistocene
50 0 50 100 150 200 km
ASTRAKHAN
ROSTOV
AZOV SEA
CASPIAN SEA
STAVROPOL
KRASNODAR
MAKHACHKALA
ORDZHONIKIDZE
BLACK SEA
SUKHUMI
TBILISI
BATUMI
BAKU
YEREVAN
38
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MAP 33
TIGER
Panthera tigris L.
Range in the 1950's
● Last locations of yield
CAVE LION
Panthera spelaea Goldf.
⊕ Upper Pleistocene
⦶ Middle Pleistocene
Panthera sp.
▲ Upper Pliocene
LION
Panthera leo L.
Probable range in Holocene
50 0 50 00 150 200 km
ASTRAKHAN
ROSTOV
AZOV SEA
STAVROPOL
KRASNODAR
MAKHACHKALA
ORDZHONIKIDZE
SUKHUMI
BLACK SEA
BATUMI
TBILISI
1922
YEREVAN
BAKU
CASPIAN SEA
1896
1890
1932
38
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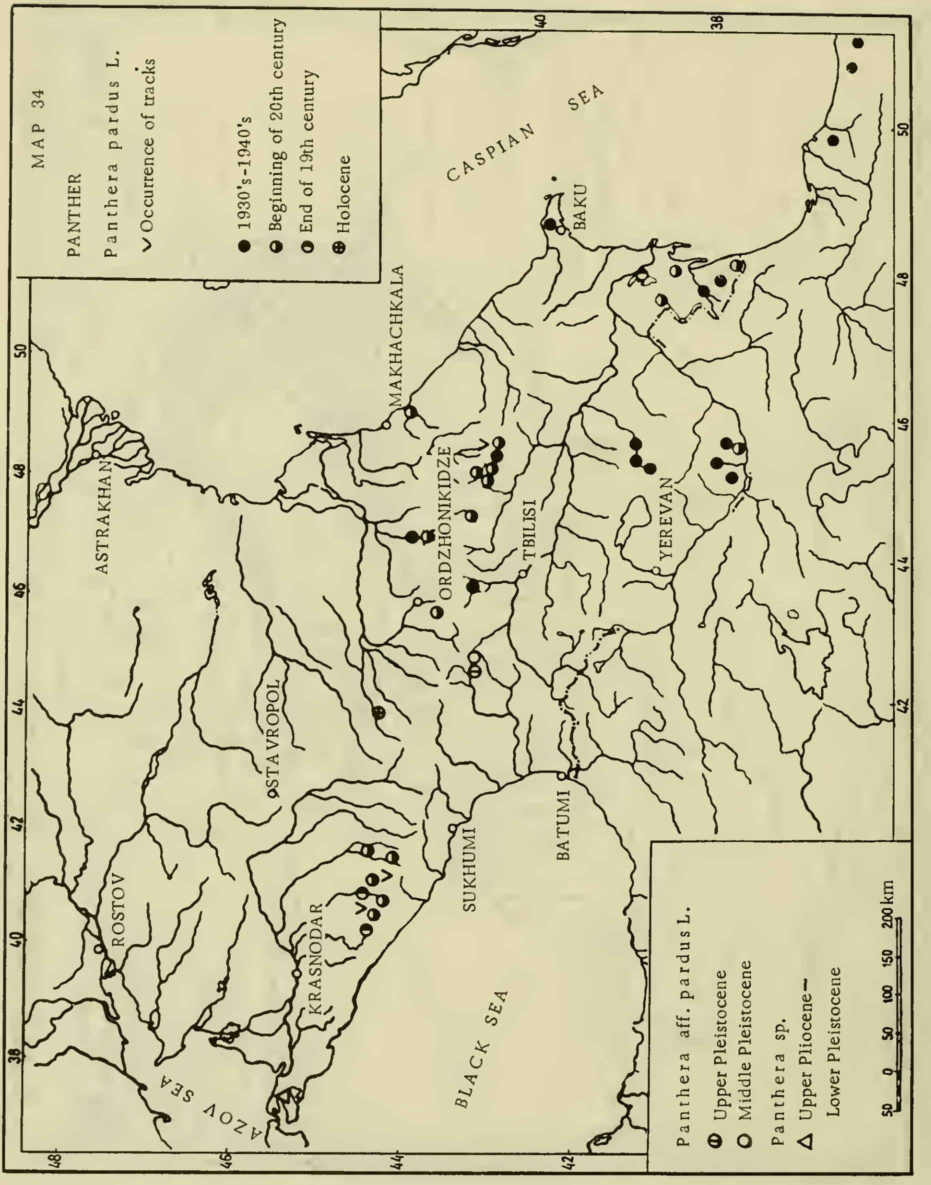
MAP 34
PANTHER
Panthera pardus L.
✓ Occurrence of tracks
● 1930's-1940's
◒ Beginning of 20th century
◐ End of 19th century
⊕ Holocene
Panthera aff. pardus L.
◐ Upper Pleistocene
○ Middle Pleistocene
Panthera sp.
△ Upper Pliocene—
Lower Pleistocene
50 0 50 100 150 200 km
CASPIAN SEA
BAKU
MAKHACHKALA
ASTRAKHAN
ORDZHONIKIDZE
TBILISI
YEREVAN
STAVROPOL
ROSTOV
KRASNODAR
SUKHUMI
BATUMI
BLACK SEA
AZOV SEA
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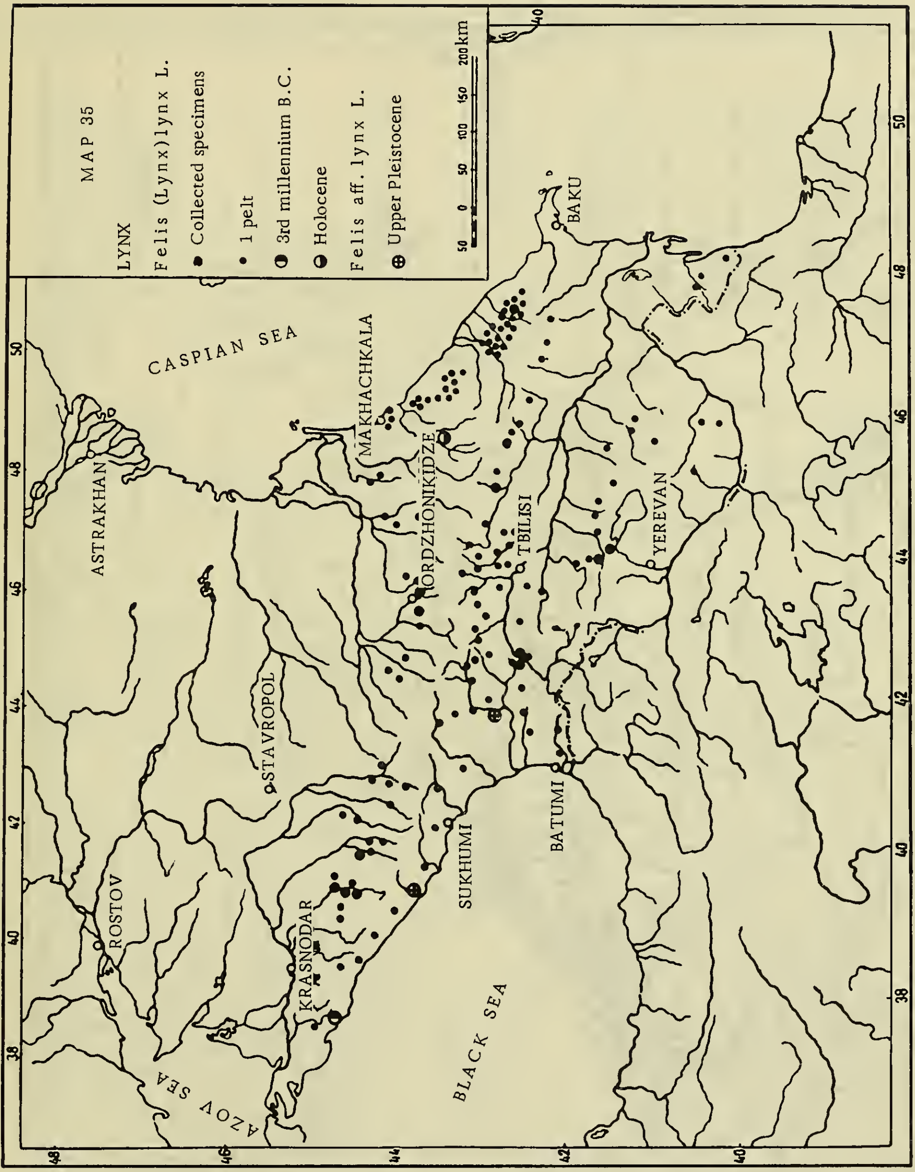

MAP 35

LYNX

Felis (Lynx) lynx L.
● Collected specimens
• 1 pelt
◑ 3rd millennium B.C.
◐ Holocene
Felis aff. lynx L.
⊕ Upper Pleistocene
50 0 50 100 150 200 km
CASPIAN SEA
BLACK SEA
AZOV SEA
ASTRAKHAN
MAKHACHKALA
ORDZHONIKIDZE
TBILISI
BAKU
YEREVAN
STAVROPOL
ROSTOV
KRASNODAR
SUKHUMI
BATUMI
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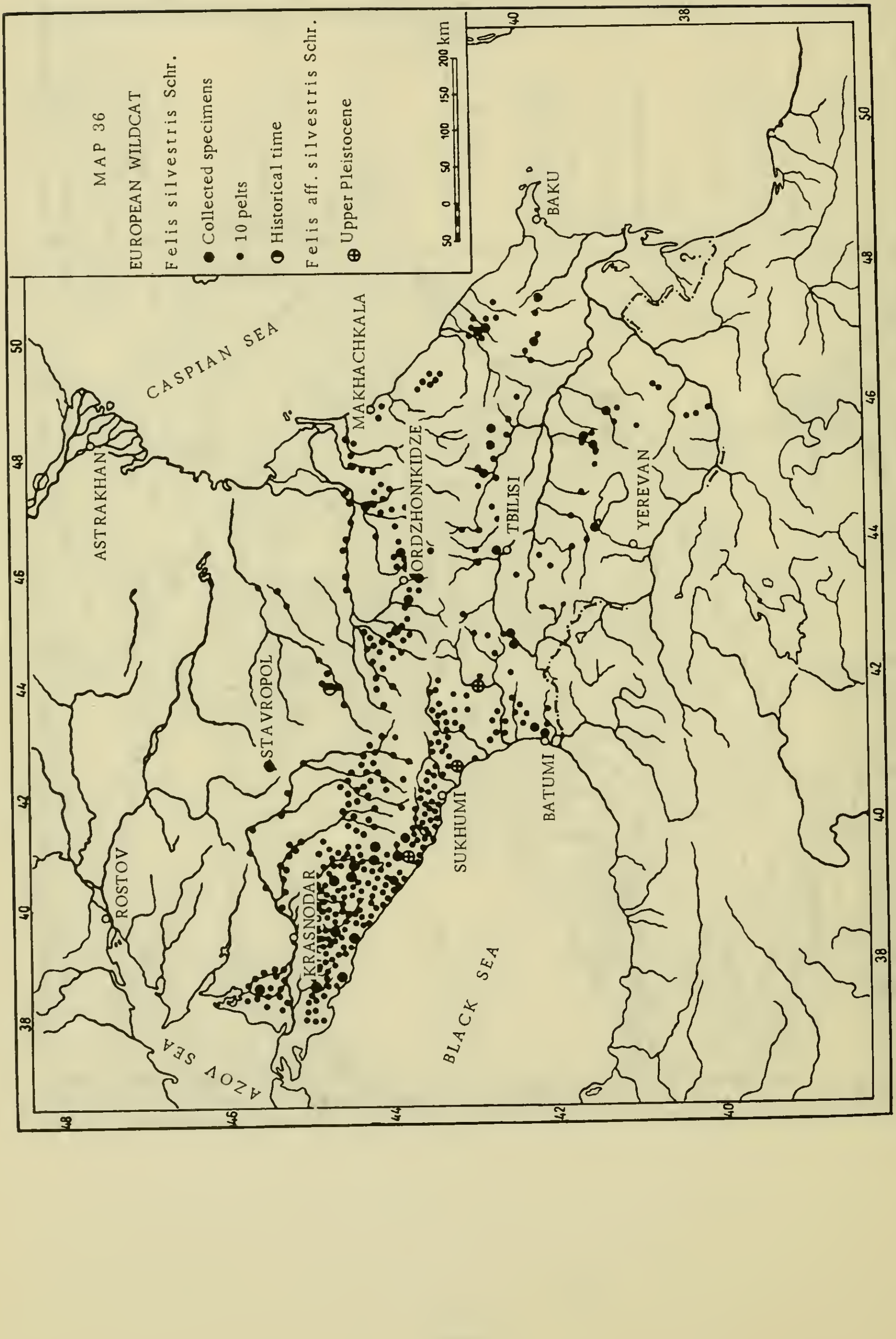


MAP 36

EUROPEAN WILDCAT

Felis silvestris Schr.

● Collected specimens

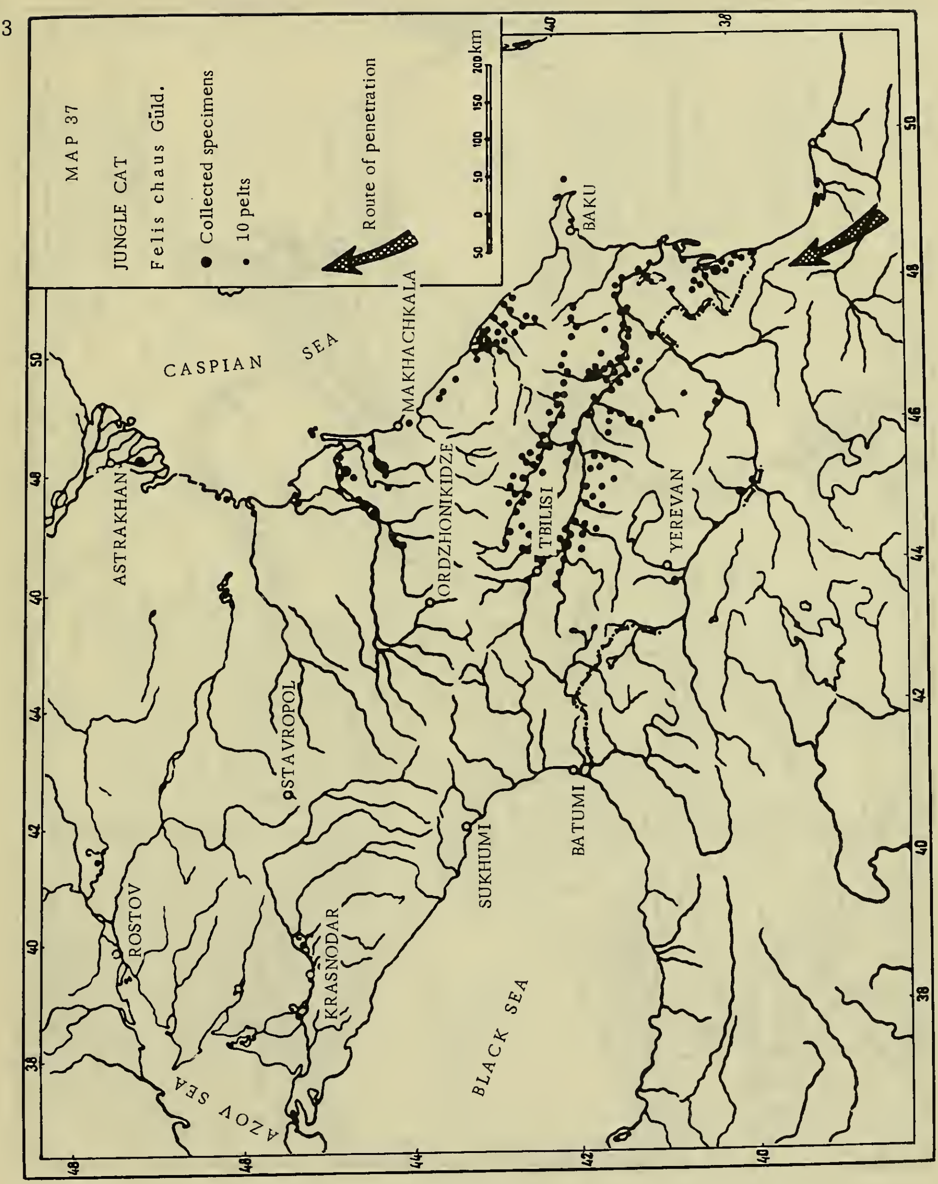
• 10 pelts

◐ Historical time

Felis aff. silvestris Schr.

⊕ Upper Pleistocene

663


MAP 37
JUNGLE CAT
Felis chaus Güld.
● Collected specimens
• 10 pelts
Route of penetration
50 0 50 100 150 200 km
CASPIAN SEA
ASTRAKHAN
MAKHACHKALA
BAKU
ORDZHONIKIDZE
TBILISI
YEREVAN
STAVROPOL
ROSTOV
KRASNODAR
SUKHUMI
BATUMI
BLACK SEA
AZOV SEA
38
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48
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MAP 38
AFRICAN WILDCAT
Felis lybica Forster
● Collected specimens
• 1 pelt
◐ 8-13th centuries A.D.
◒ 2nd-1st millennia B.C.
Felis cf. lybica Forster
⊕ Upper Pleistocene
⦶ Middle Pleistocene
MANUL
Otocolobus manul Pall.
♦ Collected specimens
CHEETAH
Acinonyx jubatus Schr.
Probable range in Holocene
Acinonyx aff. jubatus Schr.
○ Middle Pleistocene
50 0 50 100 150 200 km
ASTRAKHAN
ROSTOV
AZOV SEA
STAVROPOL
KRASNODAR
MAKHACHKALA
ORDZHONIKIDZE
SUKHUMI
BLACK SEA
TBILISI
BATUMI
BAKU
CASPIAN SEA
YEREVAN
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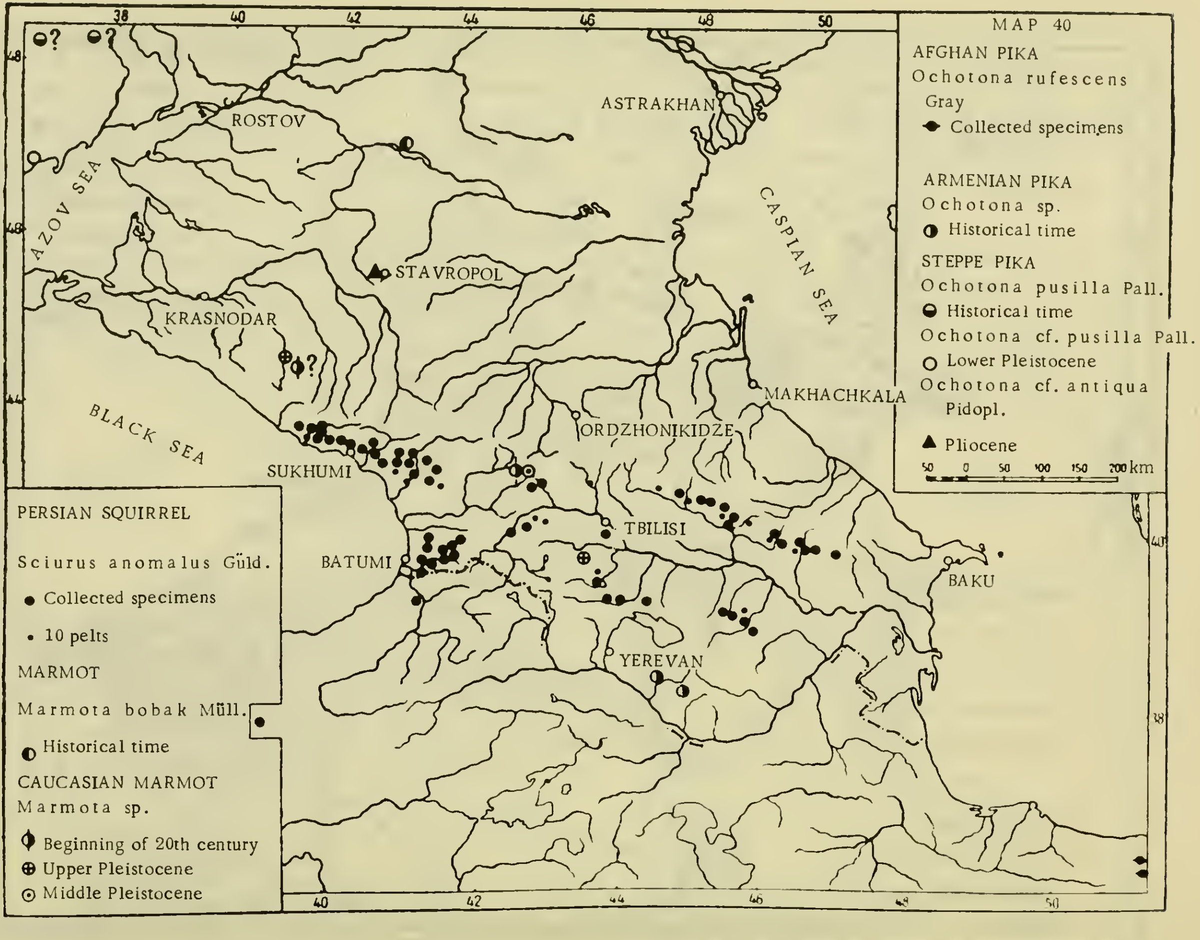
MAP 39

EUROPEAN HARE


MAP 40
AFGHAN PIKA
Ochotona rufescens Gray
◆ Collected specimens
ARMENIAN PIKA
Ochotona sp.
◑ Historical time
STEPPE PIKA
Ochotona pusilla Pall.
◒ Historical time
Ochotona cf. pusilla Pall.
○ Lower Pleistocene
Ochotona cf. antiqua Pidopl.
▲ Pliocene
50 0 50 100 150 200 km
PERSIAN SQUIRREL
Sciurus anomalus Güld.
● Collected specimens
• 10 pelts
MARMOT
Marmota bobak Müll.
◐ Historical time
CAUCASIAN MARMOT
Marmota sp.
⏀ Beginning of 20th century
⊕ Upper Pleistocene
⊙ Middle Pleistocene
ROSTOV
ASTRAKHAN
AZOV SEA
CASPIAN SEA
STAVROPOL
KRASNODAR
BLACK SEA
MAKHACHKALA
ORDZHONIKIDZE
SUKHUMI
TBILISI
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YEREVAN
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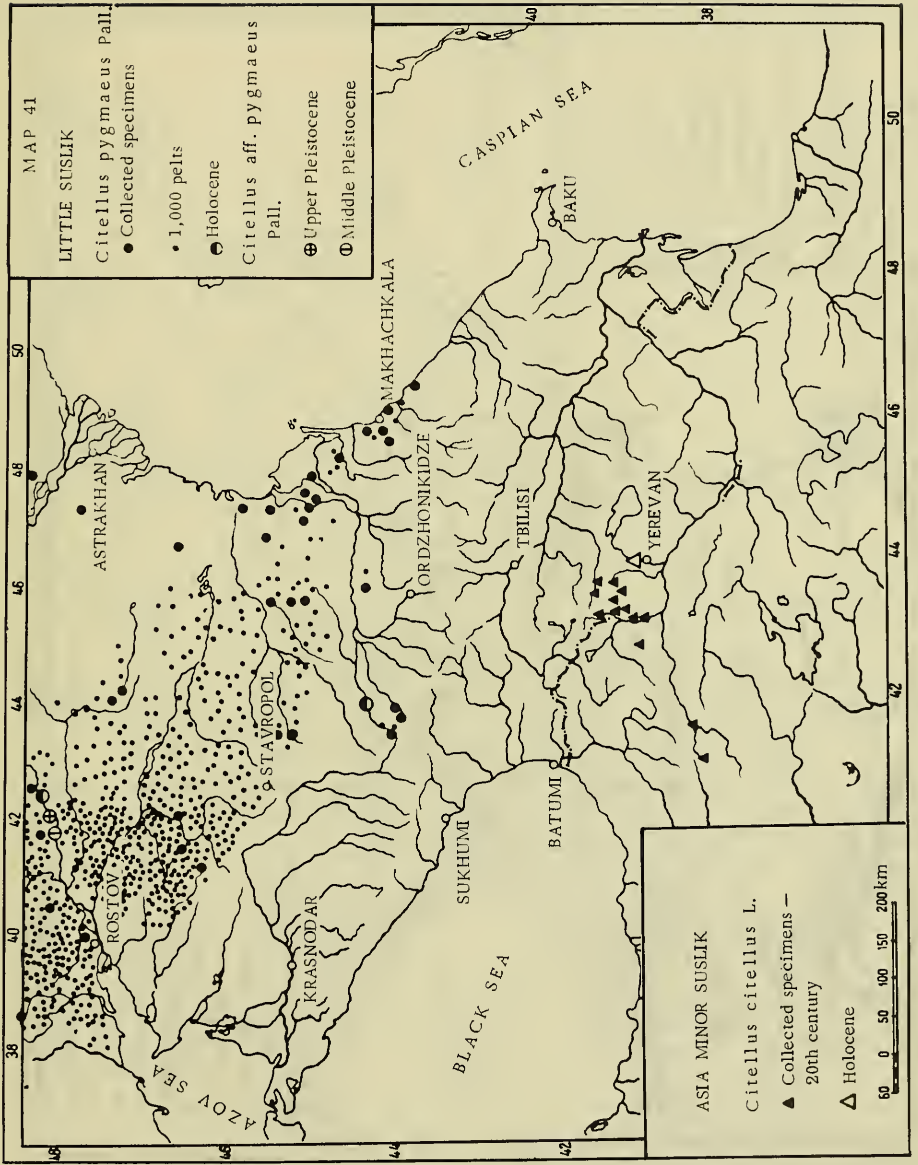
MAP 41
LITTLE SUSLIK
Citellus pygmaeus Pall.
● Collected specimens
• 1,000 pelts
◐ Holocene
Citellus aff. pygmaeus Pall.
⊕ Upper Pleistocene
⦶ Middle Pleistocene
ASIA MINOR SUSLIK
Citellus citellus L.
▲ Collected specimens – 20th century
△ Holocene
50 0 50 100 150 200 km
CASPIAN SEA
BLACK SEA
AZOV SEA
ASTRAKHAN
MAKHACHKALA
BAKU
ORDZHONIKIDZE
TBILISI
YEREVAN
STAVROPOL
ROSTOV
KRASNODAR
SUKHUMI
BATUMI
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MAP 42
EUROPEAN BEAVER
Castor fiber L.
■ Present breeding locations
Probable range in historical time
● 8-13th centuries A.D.
◐ First millennium B.C.
⊕ Upper Pleistocene
TAMAN BEAVER
Castor tamanensis N. Ver.
○ Lower Pleistocene — Upper Pliocene
TROGONTHERIUM BEAVER
Trogontherium cuvieri Fisch.
▲ Lower Pleistocene —Upper Pliocene
AMBLYCASTOR BEAVER
Amblycastor caucasicus Arg.
▲ Pliocene
Steneofiber sp.
△ Pliocene
50 0 50 100 150 200 km
ROSTOV
ASTRAKHAN
AZOV SEA
STAVROPOL
KRASNODAR
MAKHACHKALA
ORDZHONIKIDZE
BLACK SEA
SUKHUMI
TBILISI
BATUMI
BAKU
CASPIAN SEA
YEREVAN
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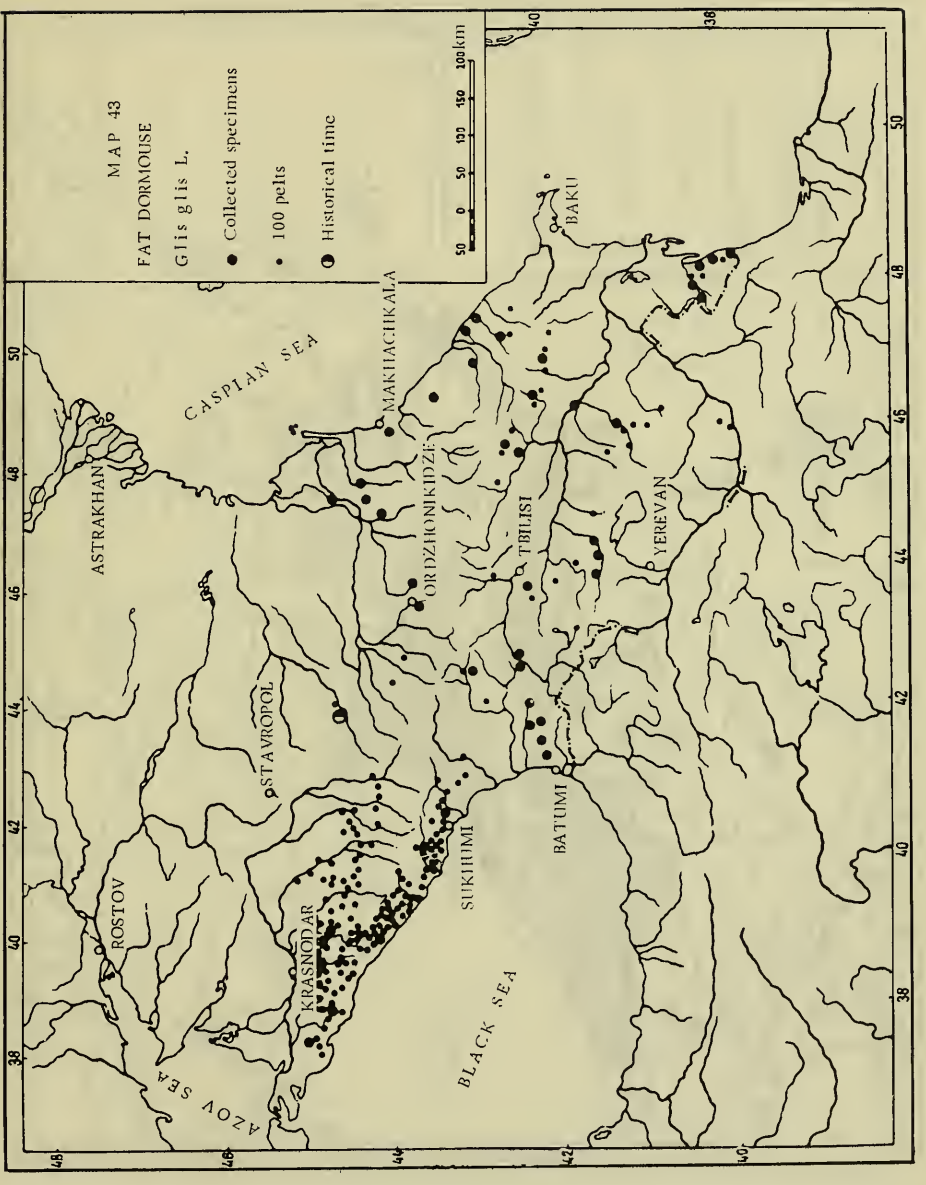
MAP 43
FAT DORMOUSE
Glis glis L.
● Collected specimens
• 100 pelts
◐ Historical time
50 0 50 100 150 100km
ASTRAKHAN
CASPIAN SEA
MAKHACHKALA
BAKU
ORDZHONIKIDZE
TBILISI
YEREVAN
STAVROPOL
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BLACK SEA
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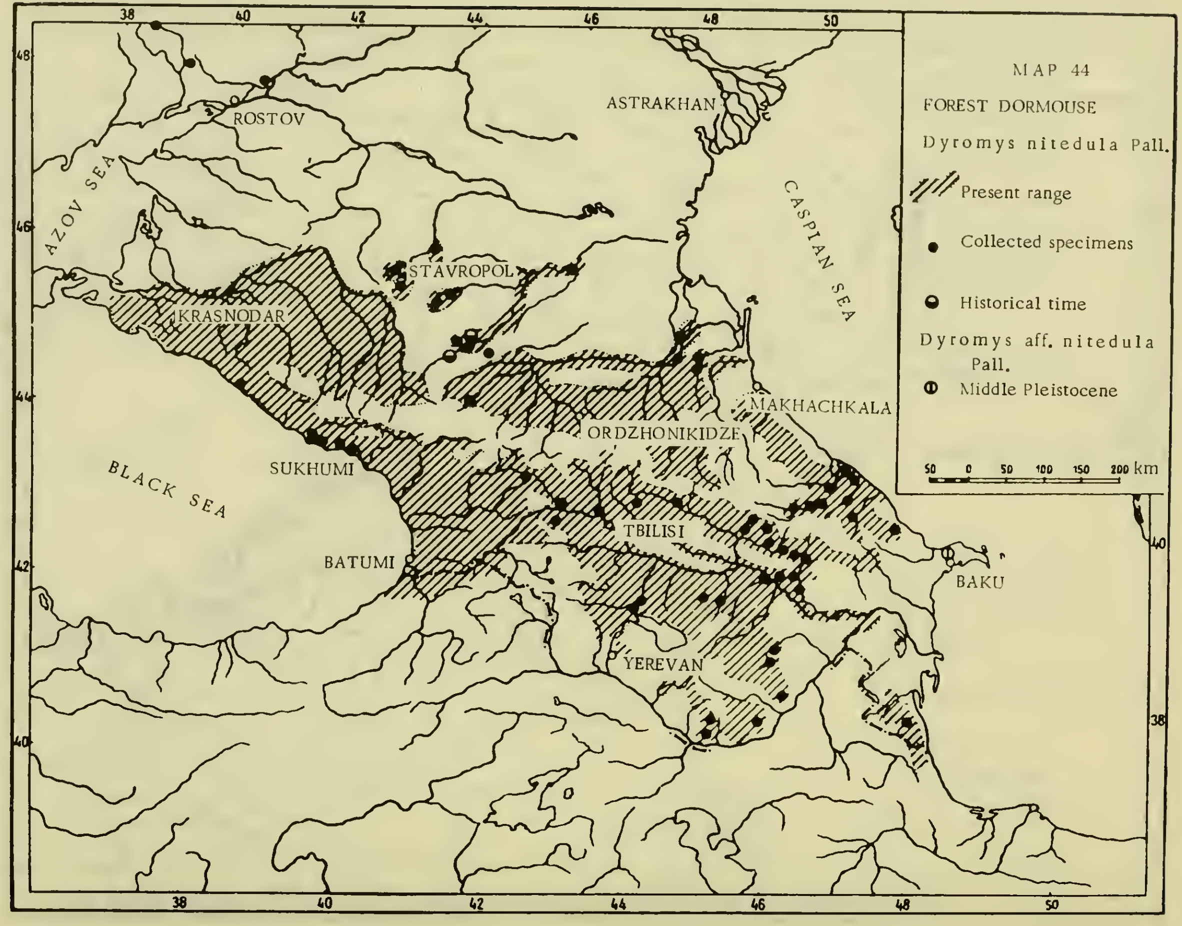
MAP 44
FOREST DORMOUSE
Dyromys nitedula Pall.
▨ Present range
● Collected specimens
◐ Historical time
Dyromys aff. nitedula Pall.
⦶ Middle Pleistocene
50 0 50 100 150 200 km
ASTRAKHAN
ROSTOV
AZOV SEA
STAVROPOL
KRASNODAR
CASPIAN SEA
MAKHACHKALA
ORDZHONIKIDZE
SUKHUMI
BLACK SEA
TBILISI
BATUMI
BAKU
YEREVAN
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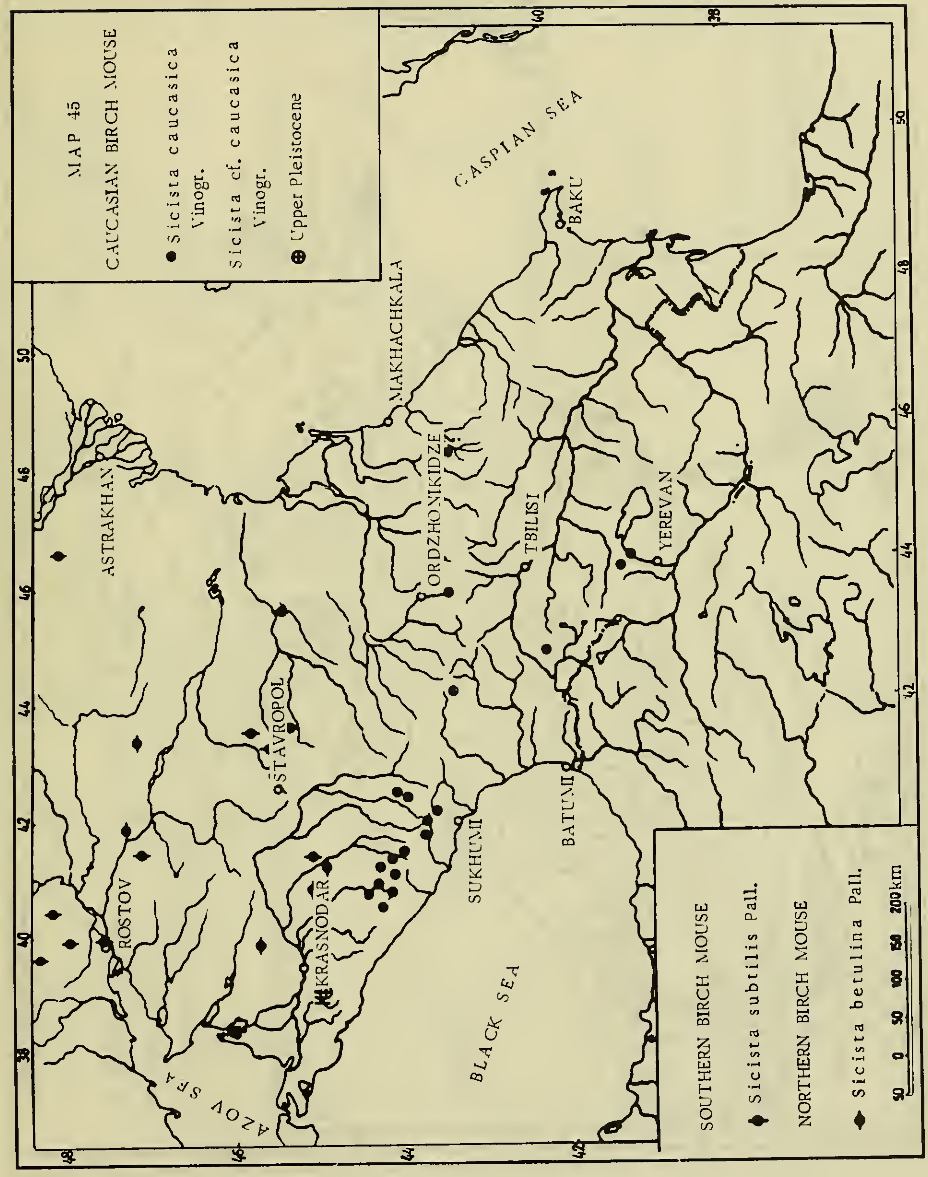
MAP 45
CAUCASIAN BIRCH MOUSE
● Sicista caucasica Vinogr.
Sicista cf. caucasica Vinogr.
⊕ Upper Pleistocene
SOUTHERN BIRCH MOUSE
Sicista subtilis Pall.
NORTHERN BIRCH MOUSE
Sicista betulina Pall.
50 0 50 100 150 200km
CASPIAN SEA
BLACK SEA
AZOV SEA
ASTRAKHAN
MAKHACHKALA
BAKU
ORDZHONIKIDZE
TBILISI
YEREVAN
STAVROPOL
ROSTOV
KRASNODAR
SUKHUMI
BATUMI
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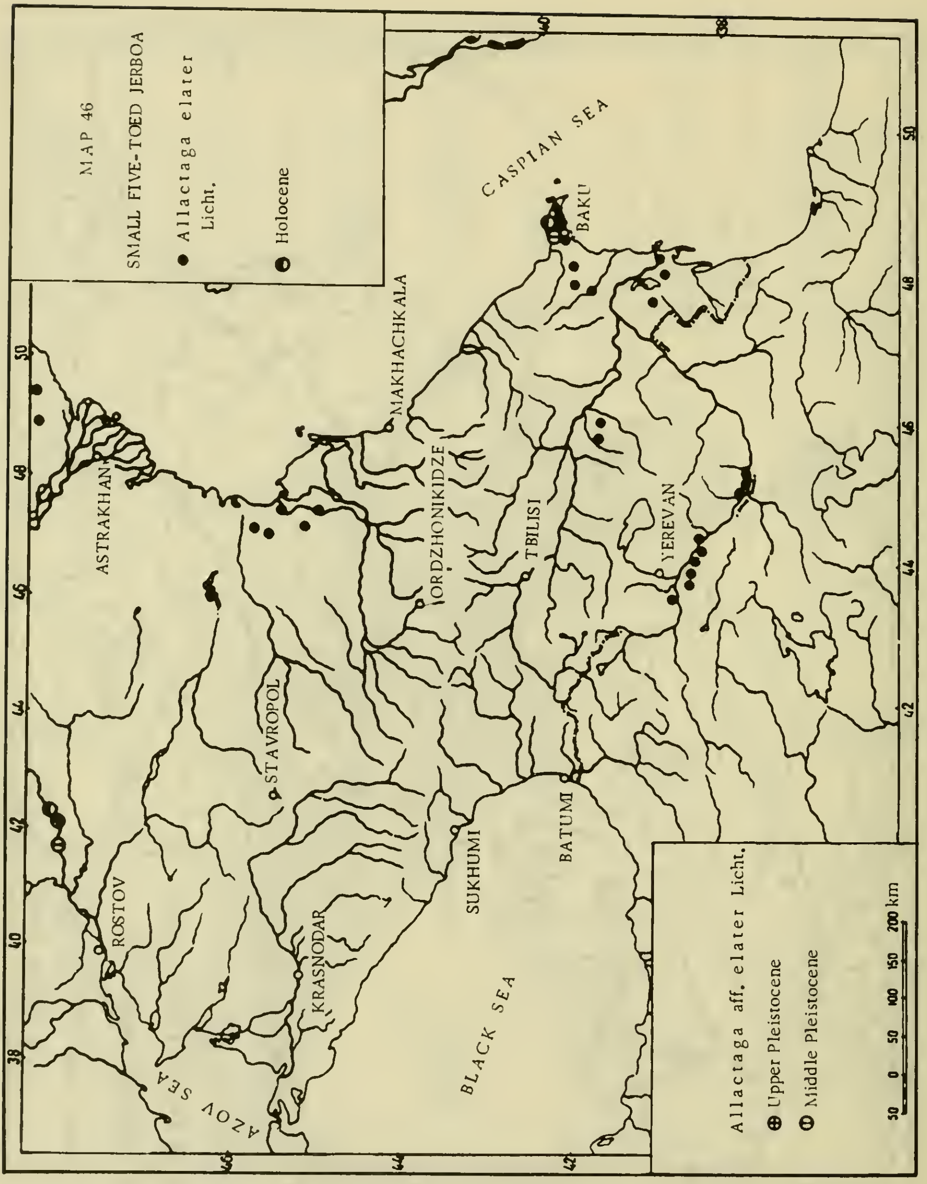

MAP 46

SMALL FIVE-TOED JERBOA

MAP 47

GREAT JERBOA

Allactaga jaculus Pall.


MAP 48
WILLIAM'S MOUNTAIN JERBOA
● Allactaga williamsi Thos.
◑ Historical time
Allactaga williamsi dzhafarovi J. Grom.
◑ Middle Pleistocene
LITTLE EARTH HARE
♦ Alactagulus acontion Pall.
Alactagulus aff. acontion Pall.
⊕ Upper Pleistocene
50 0 50 100 150 200 km
ROSTOV
ASTRAKHAN
STAVROPOL
KRASNODAR
MAKHACHKALA
ORDZHONIKIDZE
SUKHUMI
TBILISI
BATUMI
BAKU
YEREVAN
AZOV SEA
BLACK SEA
CASPIAN SEA
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MAP 49

THICK-TAILED THREE-TOED JERBOA
● Scirtopoda telum Licht.
◒ Holocene
Scirtopoda aff. telum Licht.
⊕ Upper Pleistocene
⦶ Middle Pleistocene
NORTHERN THREE-TOED JERBOA
♦ Dipus sagitta Pall.
◑ Holocene
Dipus aff. sagitta Pall.
▲ Upper Pleistocene
△ Middle Pleistocene
50 0 50 100 150 200 km
ROSTOV
ASTRAKHAN
STAVROPOL
KRASNODAR
AZOV SEA
BLACK SEA
SUKHUMI
BATUMI
ORDZHONIKIDZE
MAKHACHKALA
TBILISI
YEREVAN
BAKU
CASPIAN SEA
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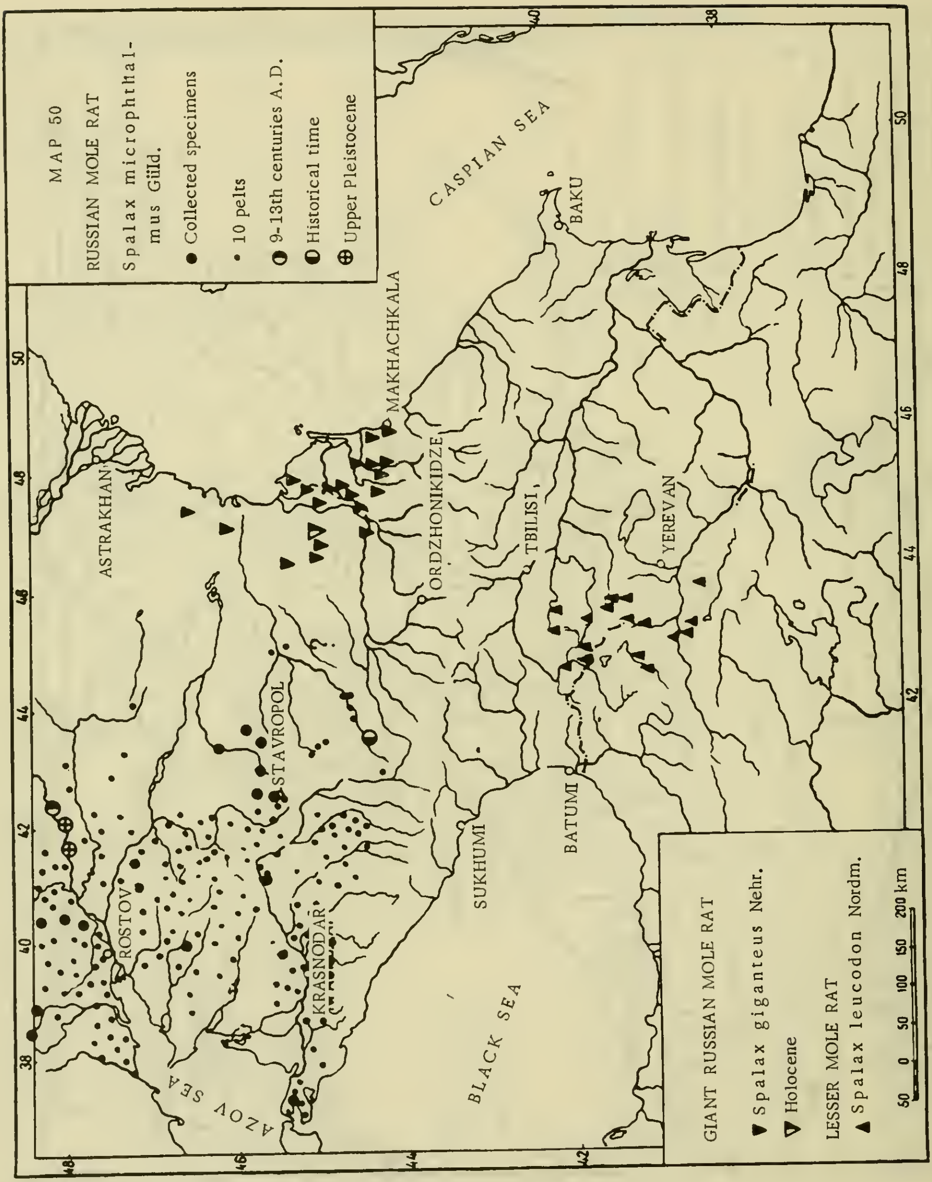
MAP 50
RUSSIAN MOLE RAT
Spalax microphthalmus Güld.
● Collected specimens
• 10 pelts
◐ 9-13th centuries A.D.
◑ Historical time
⊕ Upper Pleistocene
GIANT RUSSIAN MOLE RAT
▼ Spalax giganteus Nehr.
▽ Holocene
LESSER MOLE RAT
▲ Spalax leucodon Nordm.
50 0 50 100 150 200 km
CASPIAN SEA
BLACK SEA
AZOV SEA
ASTRAKHAN
MAKHACHKALA
BAKU
ORDZHONIKIDZE
TBILISI
YEREVAN
STAVROPOL
ROSTOV
KRASNODAR
SUKHUMI
BATUMI
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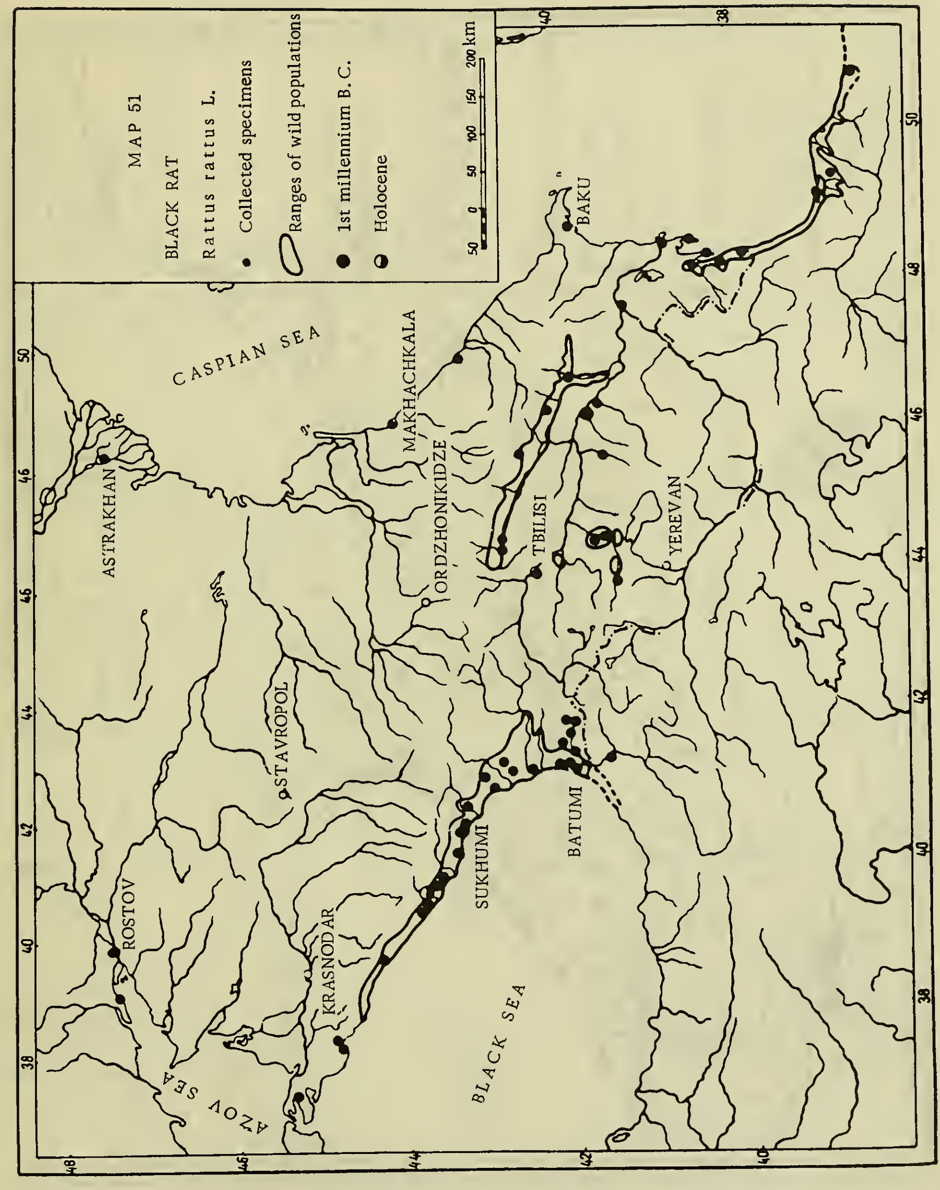

MAP 51

BLACK RAT

Rattus rattus L.

MAP 52

NORWAY RAT

Rattus norvegicus Berck.


MAP 53
FIELD MOUSE
Mus musculus L.
● Mus musculus hortulanus Nordm.
Mus musculus tataricus Sat.
Mus musculus formosovi Hept.
Mus aff. musculus L.
Upper Pleistocene
Middle Pleistocene
Mus sp.
▲ Pliocene
50 0 50 100 150 200 km
HOUSE MOUSE
▼ Mus musculus L.
ASTRAKHAN
CASPIAN SEA
ROSTOV
AZOV SEA
STAVROPOL
KRASNODAR
MAKHACHKALA
ORDZHONIKIDZE
BLACK SEA
SUKHUMI
TBILISI
BATUMI
BAKU
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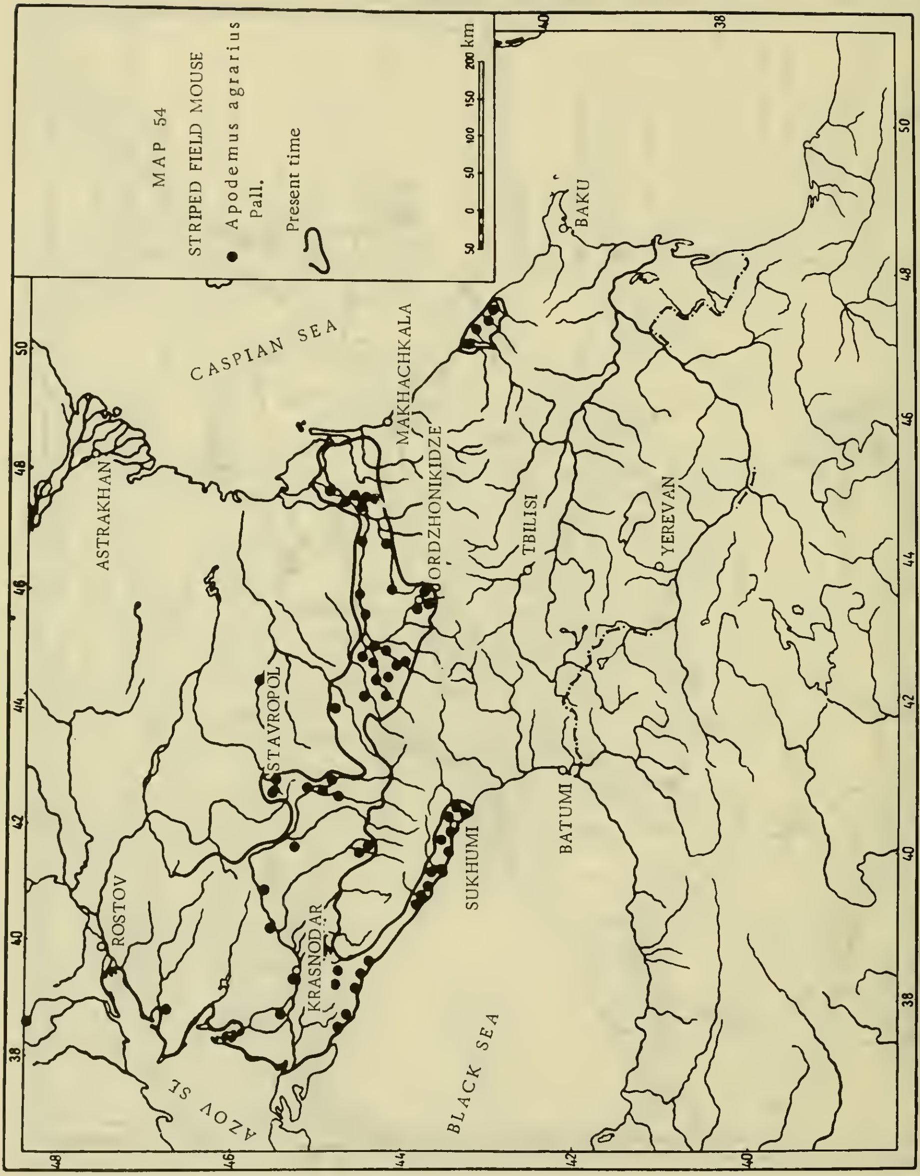
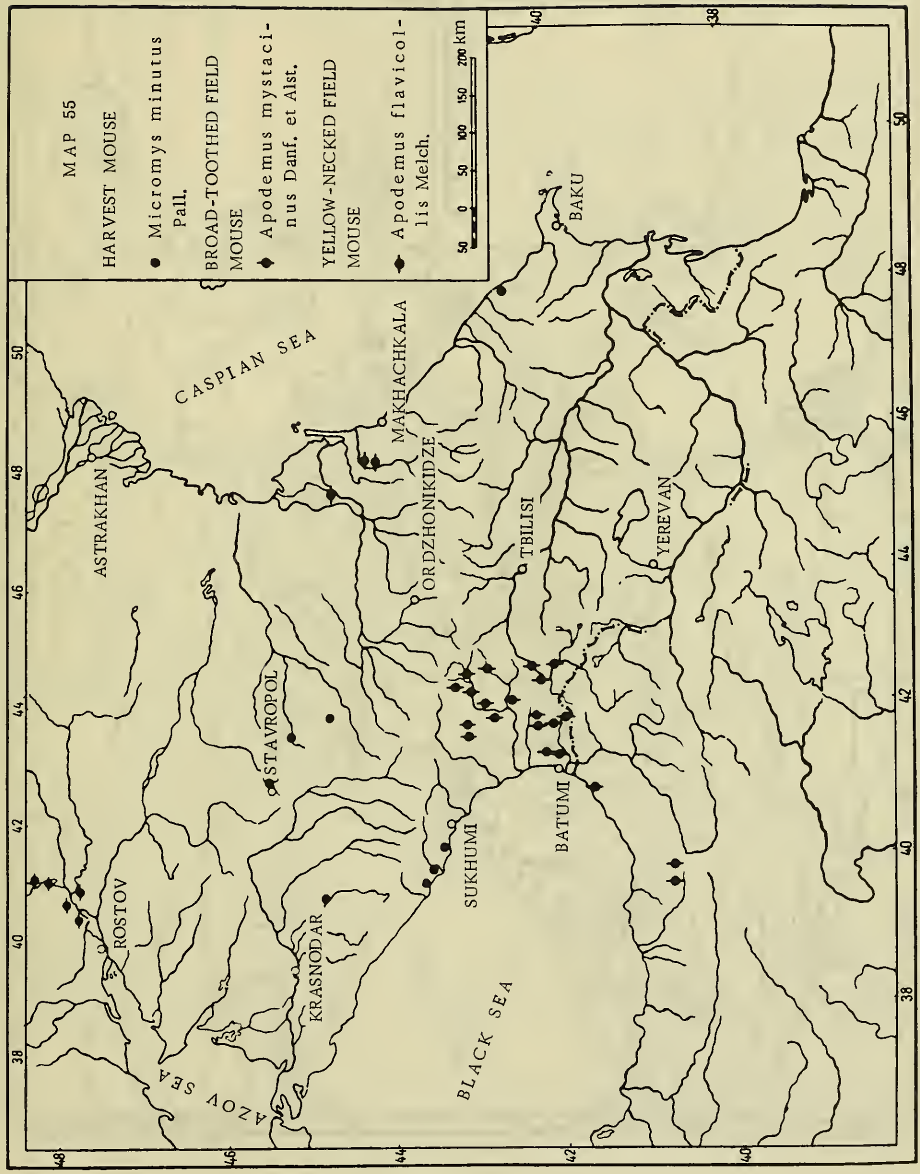


MAP 54

STRIPED FIELD MOUSE

● Apodemus agrarius Pall.

Present time



MAP 55

HARVEST MOUSE
● Micromys minutus Pall.
BROAD-TOOTHED FIELD MOUSE
◆ Apodemus mystacinus Danf. et Alst.
YELLOW-NECKED FIELD MOUSE
◆ Apodemus flavicollis Melch.
50 0 50 100 150 200 km
CASPIAN SEA
BLACK SEA
AZOV SEA
ASTRAKHAN
MAKHACHKALA
ORDZHONIKIDZE
TBILISI
BAKU
YEREVAN
STAVROPOL
ROSTOV
KRASNODAR
SUKHUMI
BATUMI
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MAP 56

CAUCASIAN YELLOW-SPOTTED MOUSE


MAP 57
COMMON FIELD MOUSE
● Apodemus sylvaticus L.
Boundaries of present range
◑ Historical time
◒ Holocene
Apodemus aff. sylvaticus L.
⦶ Middle Pleistocene
50 0 50 100 150 200 km
ASTRAKHAN
ROSTOV
STAVROPOL
KRASNODAR
CASPIAN SEA
MAKHACHKALA
ORDZHONIKIDZE
SUKHUMI
BLACK SEA
TBILISI
BATUMI
BAKU
YEREVAN
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MAP 58

ASIA MINOR (GOLDEN) HAMSTER


MAP 59
COMMON HAMSTER
Cricetus cricetus L.
● Collected specimens
• 100 pelts
◑ Historical time
Cricetus aff. cricetus L.
⊕ Upper Pleistocene
⦶ Middle Pleistocene
Cricetus sp.
▲ Pliocene
PROTO-HAMSTER
Paleocricetus caucasicus Arg.
△ Middle Miocene
50 0 50 100 150 200 km
ROSTOV
ASTRAKHAN
AZOV SEA
KRASNODAR
STAVROPOL
MAKHACHKALA
ORDZHONIKIDZE
BLACK SEA
SUKHUMI
TBILISI
CASPIAN SEA
BATUMI
BAKU
YEREVAN
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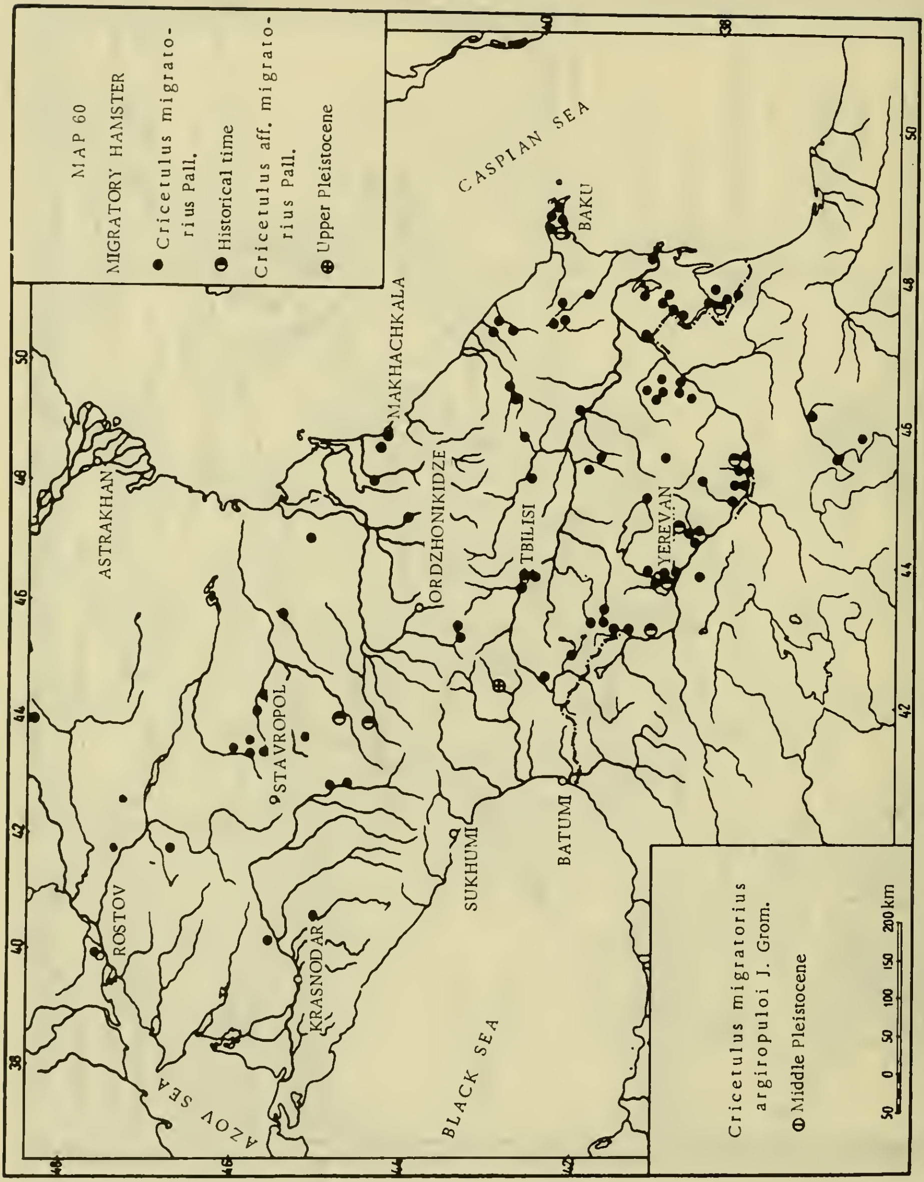

MAP 60
MIGRATORY HAMSTER


MAP 61
MOUSE-LIKE HAMSTER
● Calomyscus bailwardi Thos.
GREAT GERBIL
♦ Rhombomys opimus Licht.
◒ Holocene
MIDDAY GERBIL
◆ Meriones meridianus Pall.
RED-TAILED LIBYAN GERBIL
✖ Meriones erythrourus Gray
Meriones erythrourus intermedius J. Grom.
Φ Middle Pleistocene
50 0 50 100 150 200km
ASTRAKHAN
ROSTOV
AZOV SEA
STAVROPOL
KRASNODAR
MAKHACHKALA
ORDZHONIKIDZE
BLACK SEA
SUKHUMI
TBILISI
BATUMI
BAKU
CASPIAN SEA
YEREVAN
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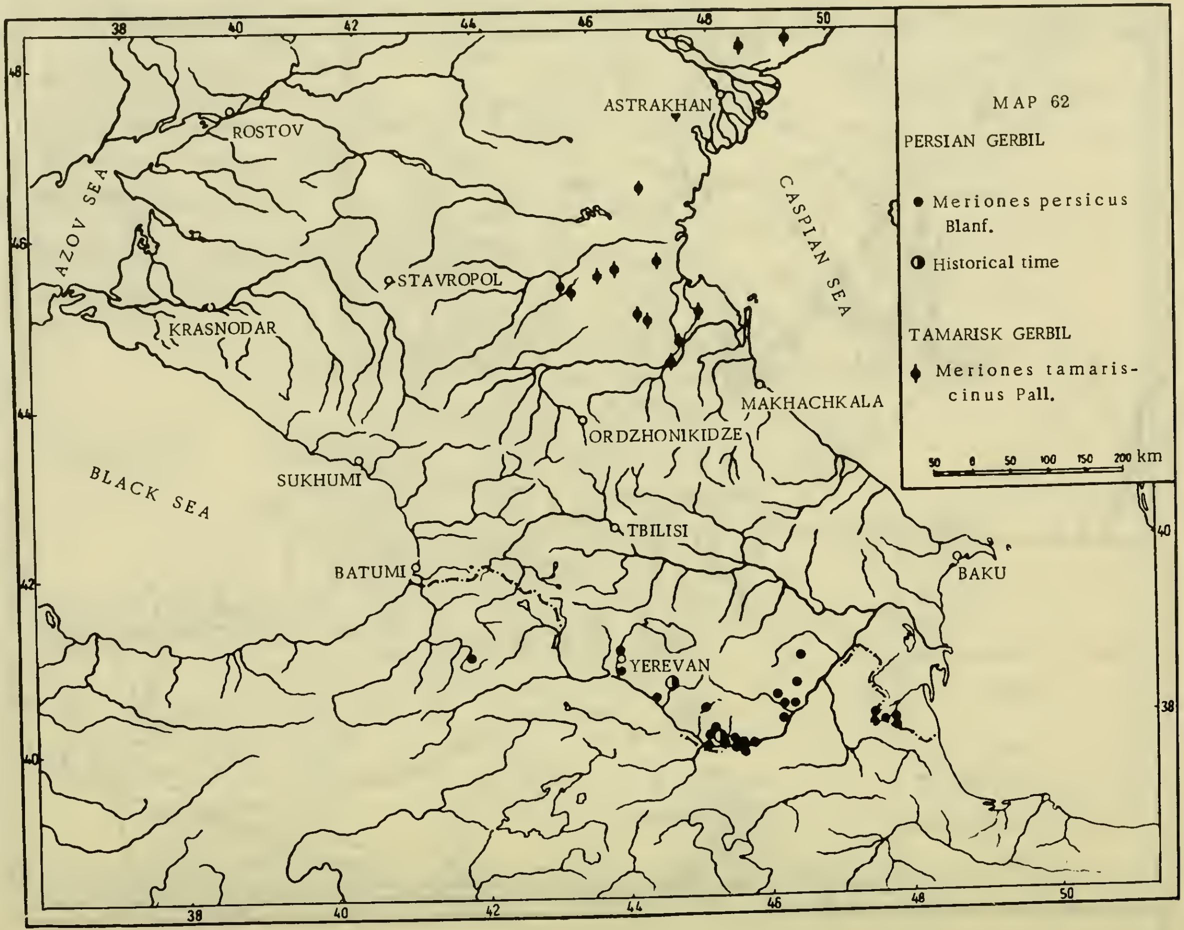
MAP 62
PERSIAN GERBIL
● Meriones persicus Blanf.
◑ Historical time
TAMARISK GERBIL
♦ Meriones tamariscinus Pall.
50 0 50 100 150 200 km
ASTRAKHAN
ROSTOV
AZOV SEA
CASPIAN SEA
STAVROPOL
KRASNODAR
MAKHACHKALA
ORDZHONIKIDZE
SUKHUMI
BLACK SEA
TBILISI
BATUMI
BAKU
YEREVAN
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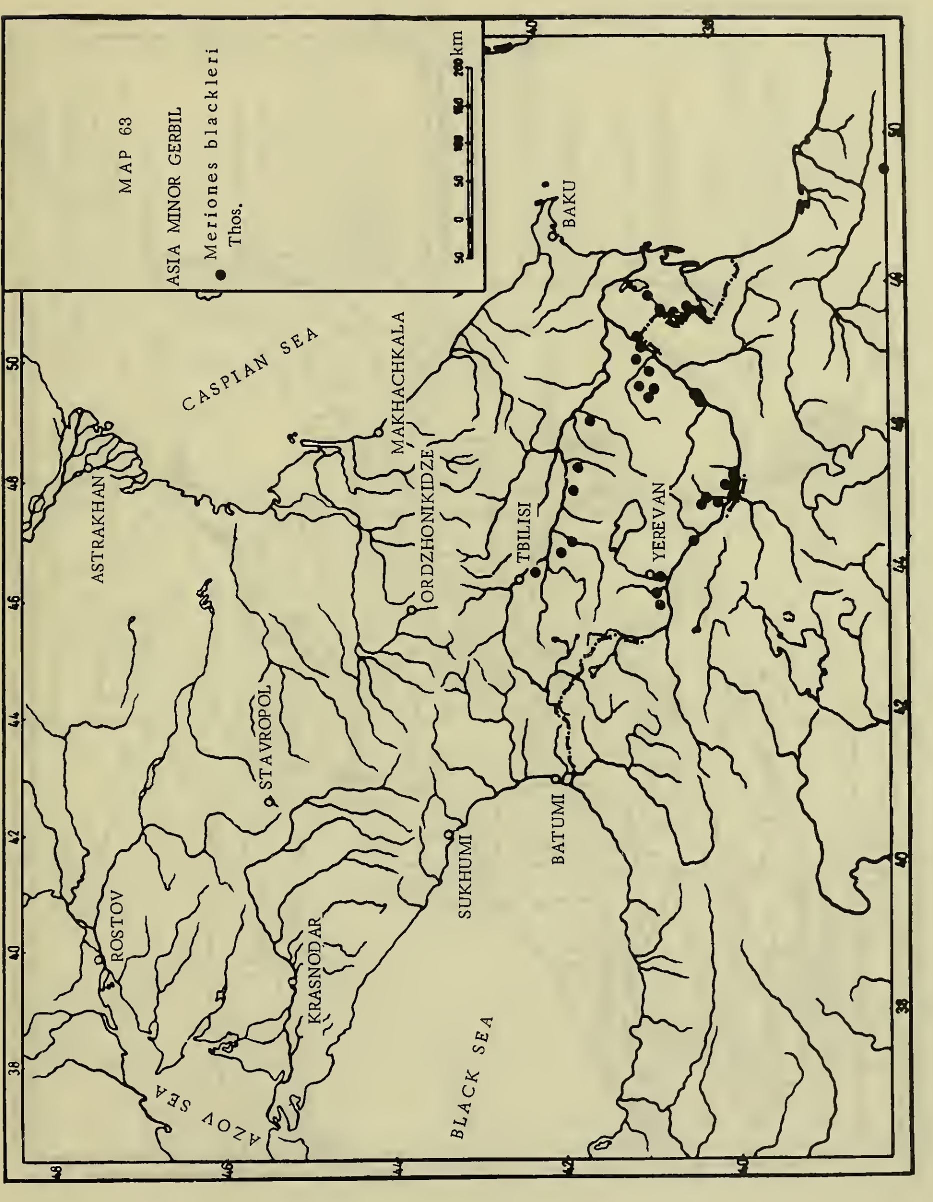
MAP 63
ASIA MINOR GERBIL
● Meriones blackleri Thos.
50 0 50 100 150 200 km
CASPIAN SEA
BLACK SEA
AZOV SEA
ASTRAKHAN
MAKHACHKALA
ORDZHONIKIDZE
BAKU
TBILISI
YEREVAN
STAVROPOL
ROSTOV
KRASNODAR
SUKHUMI
BATUMI
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MAP 64

VINOGRADOV'S GERBIL
● Meriones vinogradovi Heptn.
ARAZDAYAN GERBIL
♦ Meriones sp.
STEPPE LEMMING
▲ Lagurus lagurus Pall.
50 0 50 100 150 200 km
ASTRAKHAN
CASPIAN SEA
ROSTOV
AZOV SEA
STAVROPOL
KRASNODAR
MAKHACHKALA
ORDZHONIKIDZE
BLACK SEA
SUKHUMI
TBILISI
BATUMI
BAKU
YEREVAN
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MAP 65
NORTHERN MOLE VOLE
● Ellobius talpinus Pall.
Historical time
Holocene
Ellobius aff. talpius Pall.
Upper Pleistocene
Middle Pleistocene
TRANSCAUCASIAN MOLE VOLE
Ellobius lutescens Thos.
Historical time
Ellobius aff. lutescens Thos.
Middle Pleistocene
50 0 50 100 150 200km
PROMETHEAN VOLE
▼ Prometheomys schaposchnikovi Sat.
Prometheomys aff. schaposchnikovi Sat.
Upper Pleistocene
Middle Pleistocene
ROSTOV
ASTRAKHAN
AZOV SEA
STAVROPOL
CASPIAN SEA
KRASNODAR
MAKHACHKALA
ORDZHONIKIDZE
BLACK SEA
SUKHUMI
TBILISI
BATUMI
BAKU
YEREVAN
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MAP 66
WATER VOLE
Arvicola terrestris L.
● Collected specimens
• 100 pelts
◐ Historical time
◒ Holocene
Arvicola aff. terrestris L.
⊕ Upper Pleistocene
Arvicola sp.
⦶ Middle Pleistocene
50 0 50 100 150 200 km
ROSTOV
ASTRAKHAN
AZOV SEA
STAVROPOI
KRASNODAR
BLACK SEA
SUKHUMI
ORDZHONIKIDZE
MAKHACHKALA
TBILISI
BATUMI
YEREVAN
BAKU
CASPIAN SEA
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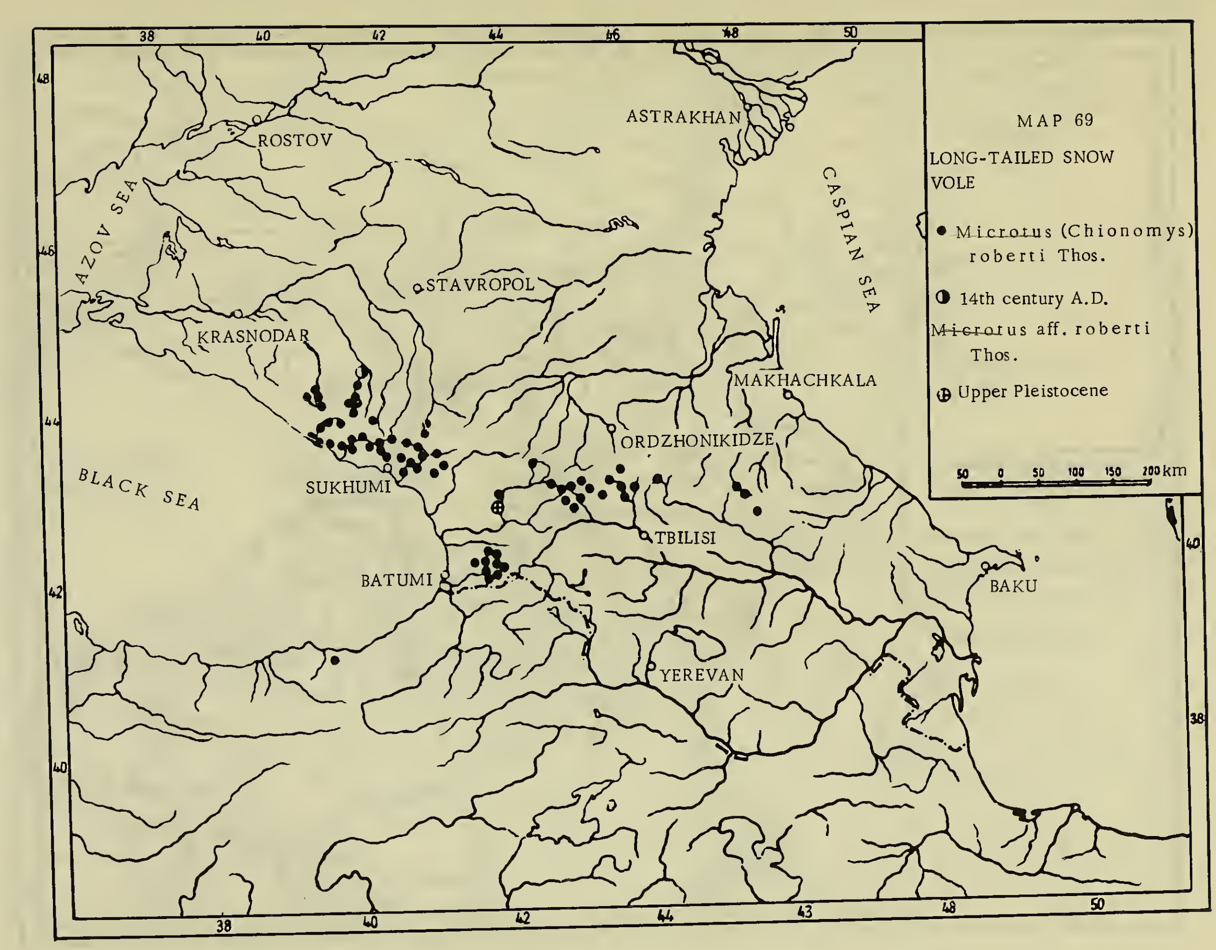
MAP 67

ASIA MINOR SNOW VOLE

MAP 68

CAUCASIAN SNOW VOLE


MAP 69
LONG-TAILED SNOW VOLE
● Microtus (Chionomys) roberti Thos.
◐ 14th century A.D. ~~Microtus~~ aff. roberti Thos.
⊕ Upper Pleistocene
50 0 50 100 150 200 km
ASTRAKHAN
ROSTOV
AZOV SEA
CASPIAN SEA
STAVROPOL
KRASNODAR
MAKHACHKALA
ORDZHONIKIDZE
SUKHUMI
BLACK SEA
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BATUMI
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YEREVAN
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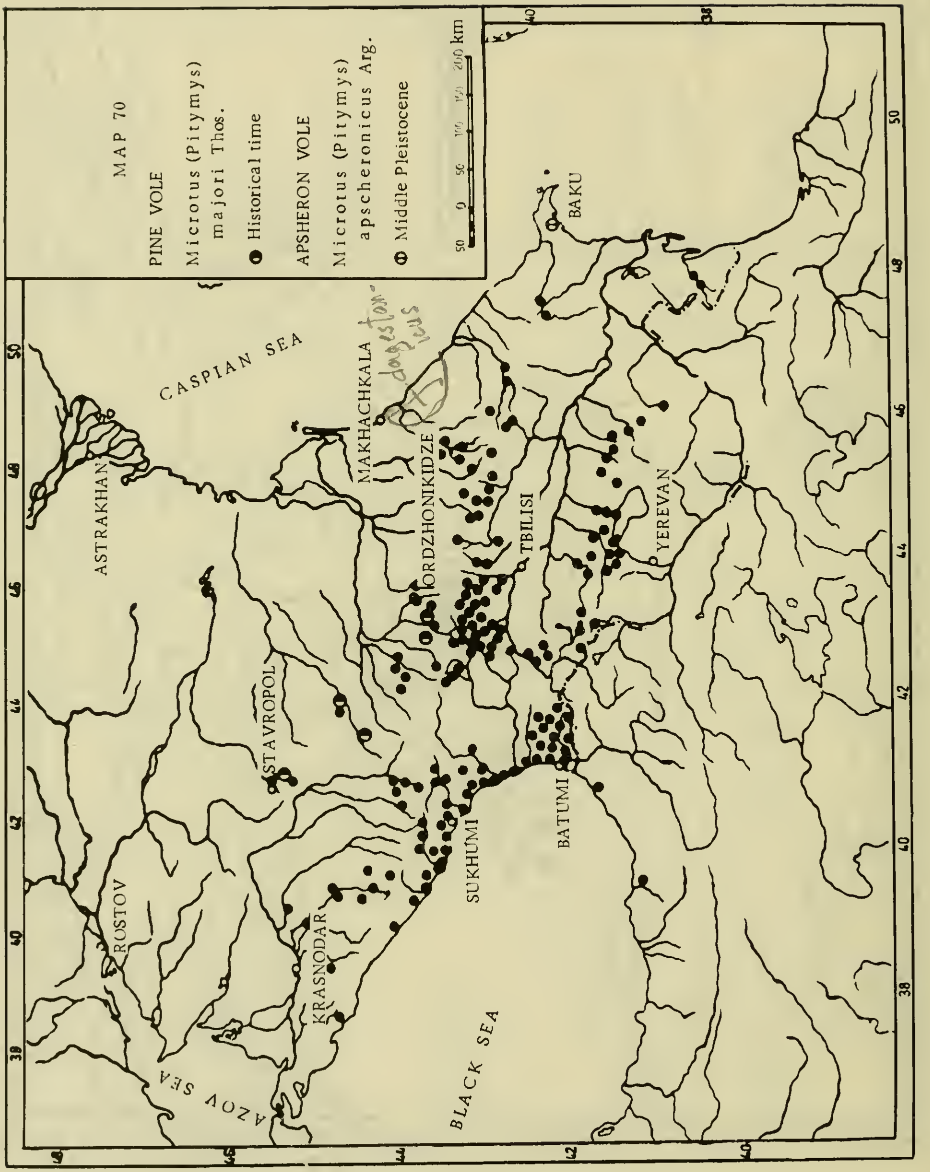


MAP 70

PINE VOLE

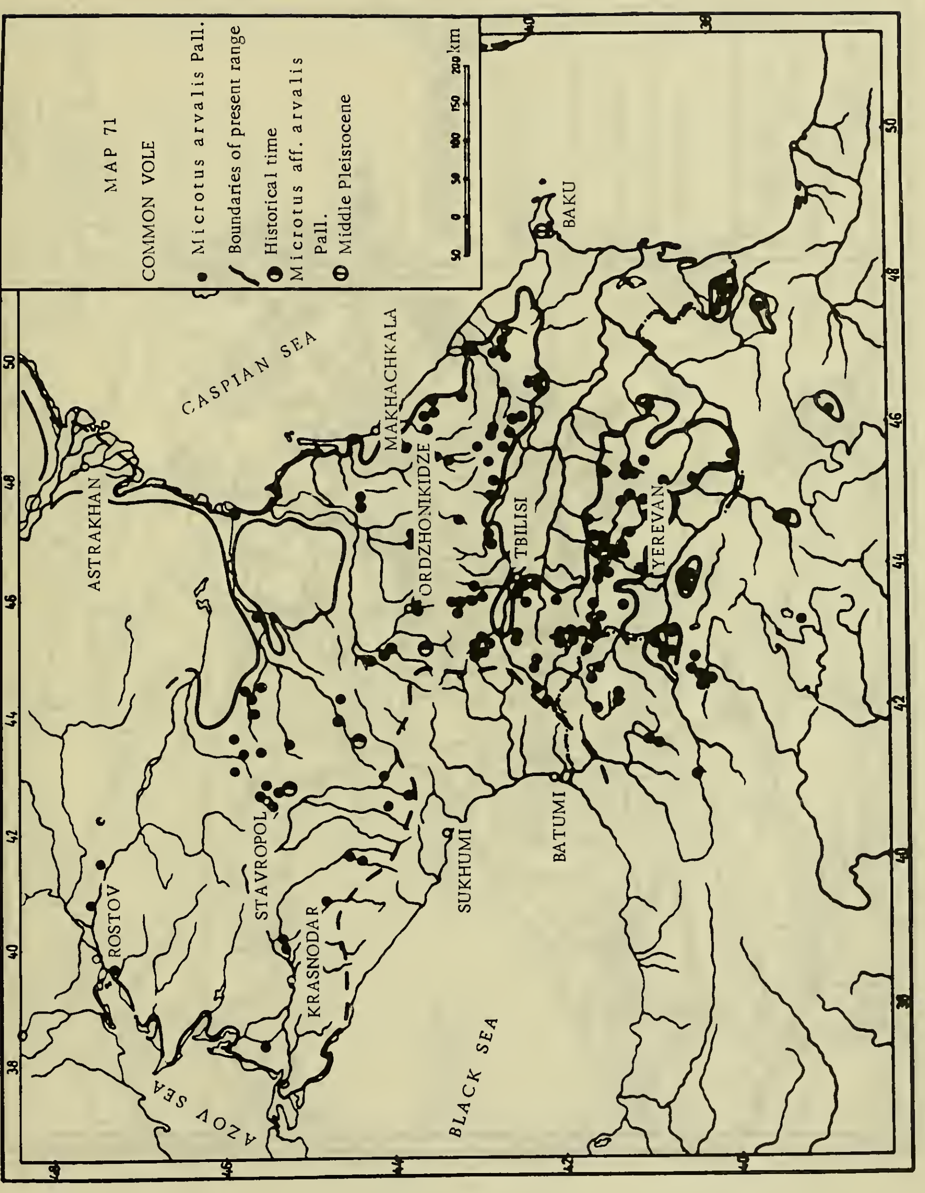
Microtus (Pitymys) majori Thos.

● Historical time

APSHERON VOLE

Microtus (Pitymys) apscheronicus Arg.

⦶ Middle Pleistocene


MAP 71
COMMON VOLE
● Microtus arvalis Pall.
Boundaries of present range
Historical time
Microtus aff. arvalis Pall.
Middle Pleistocene
50 0 50 100 150 200 km
CASPIAN SEA
BLACK SEA
AZOV SEA
ASTRAKHAN
MAKHACHKALA
ORDZHONIKIDZE
TBILISI
BAKU
YEREVAN
BATUMI
SUKHUMI
STAVROPOL
KRASNODAR
ROSTOV
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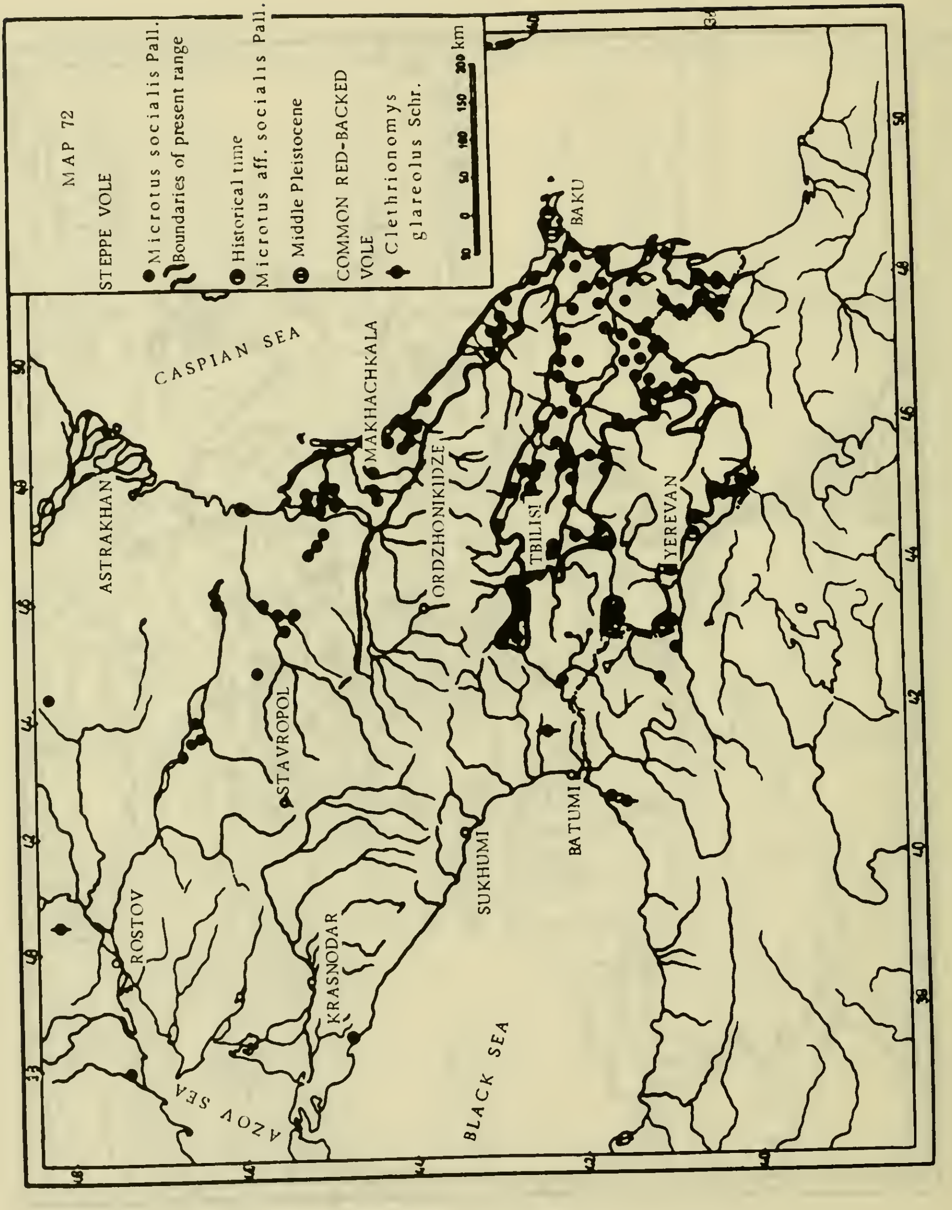
MAP 72
STEPPE VOLE
● Microtus socialis Pall.
Boundaries of present range
Historical time
Microtus aff. socialis Pall.
Middle Pleistocene
COMMON RED-BACKED VOLE
Clethrionomys glareolus Schr.
50 0 50 100 150 200 km
CASPIAN SEA
ASTRAKHAN
MAKHACHKALA
ORDZHONIKIDZE
TBILISI
BAKU
YEREVAN
STAVROPOL
ROSTOV
KRASNODAR
SUKHUMI
BATUMI
AZOV SEA
BLACK SEA
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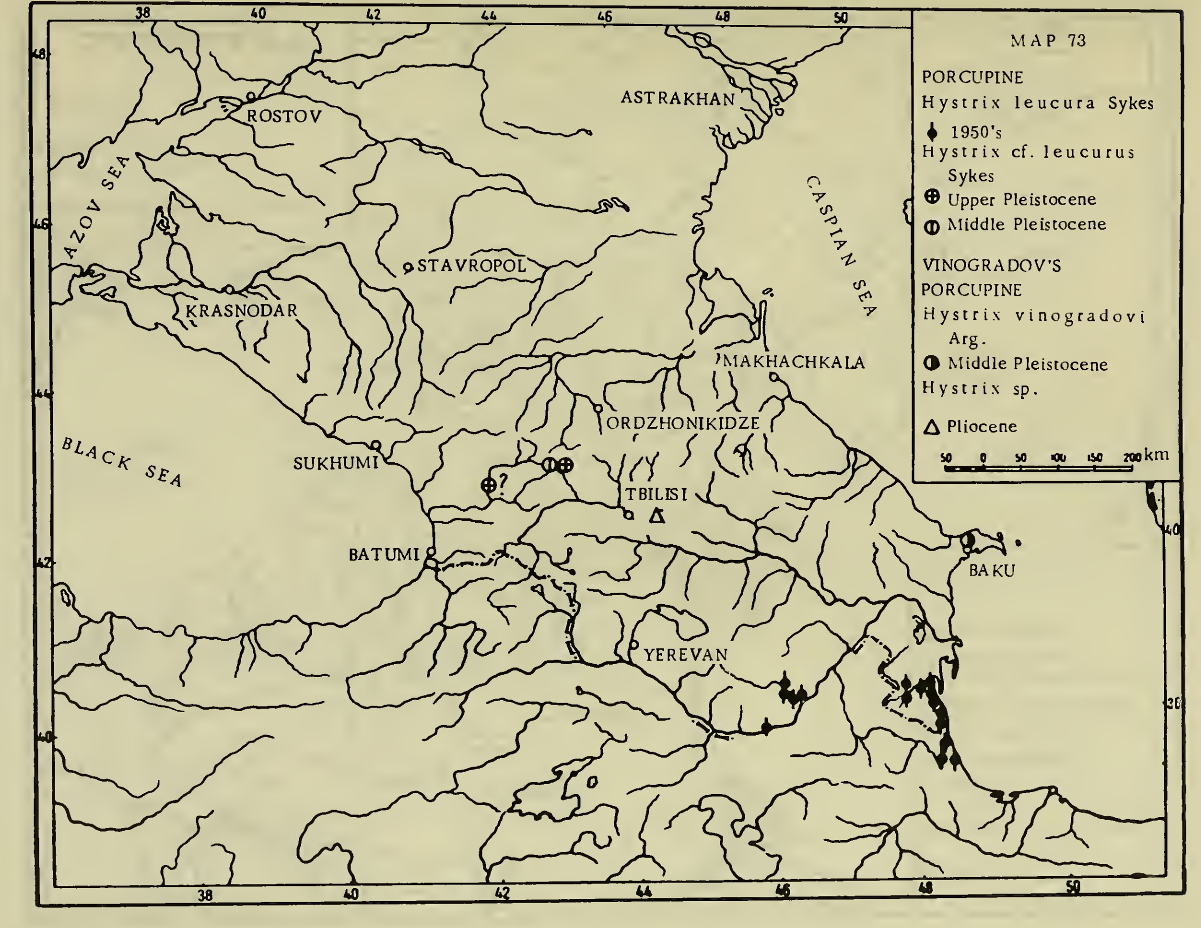
MAP 73

PORCUPINE
Hystrix leucura Sykes
♦ 1950's
Hystrix cf. leucurus Sykes
⊕ Upper Pleistocene
⦶ Middle Pleistocene
VINOGRADOV'S PORCUPINE
Hystrix vinogradovi Arg.
◐ Middle Pleistocene
Hystrix sp.
△ Pliocene
50 0 50 100 150 200 km
ROSTOV
ASTRAKHAN
AZOV SEA
CASPIAN SEA
STAVROPOL
KRASNODAR
MAKHACHKALA
ORDZHONIKIDZE
BLACK SEA
SUKHUMI
TBILISI
BATUMI
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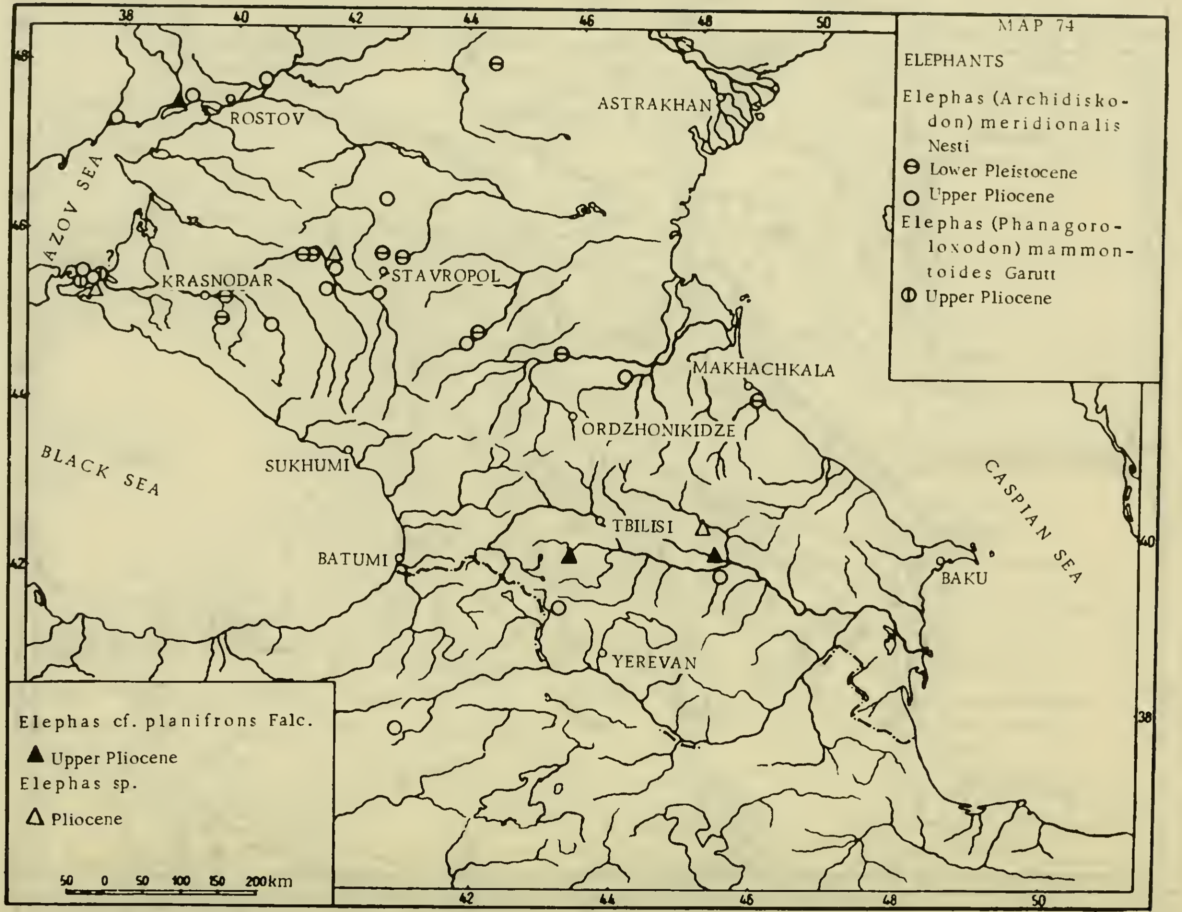

MAP 74

ELEPHANTS

MAP 75

ELEPHANT

Elephas (Parelephas) trogontherii Pohl.

⊕ Middle Pleistocene

⊖ Lower Pleistocene — Upper Pliocene


MAP 76
MAMMOTH
Elephas (Mammonteus) primigenius Blum.
◐ Upper Pleistocene
⊕ Middle Pleistocene
Elephas (Hesperoloxodon) antiquus Falc.
⌘ Middle Pleistocene
⊖ Lower Pleistocene
Upper Pliocene
50 0 50 100 150 200 km
ASTRAKHAN
CASPIAN SEA
ROSTOV
AZOV SEA
KRASNODAR
STAVROPOL
MAKHACHKALA
ORDZHONIKIDZE
SUKHUMI
BLACK SEA
TBILISI
BATUMI
BAKU
YEREVAN
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MAP 77
ELASMOTHERES
Elasmotherium sibiricum Fisch.
⊖ Middle Pleistocene
○ Lower Pleistocene
Elasmotherium caucasicum Boris.
▲ Upper Pliocene
WOOLLY RHINOCEROS
Rhinoceros tichorhinus Fisch.
● Upper Pleistocene
◒ Middle Pleistocene
50 0 50 100 150 200 km
RHINOCEROSES
Rhinoceros cf. mercki Jaeg.
⦶ Middle Pleistocene
Rhinoceros binagadensis Dzjaf.
ϕ Middle Pleistocene
Rhinoceros cf. etruscus Falc.
△ Upper Pliocene
Dicerorhinus orientalis Schloss.
▲ Lower Pliocene
Dicerorhinus caucasicus Boris.
△ Middle Miocene
ROSTOV
AZOV SEA
KRASNODAR
BLACK SEA
STAVROPOL
ASTRAKHAN
CASPIAN SEA
MAKHACHKALA
ORDZHONIKIDZE
SUKHUMI
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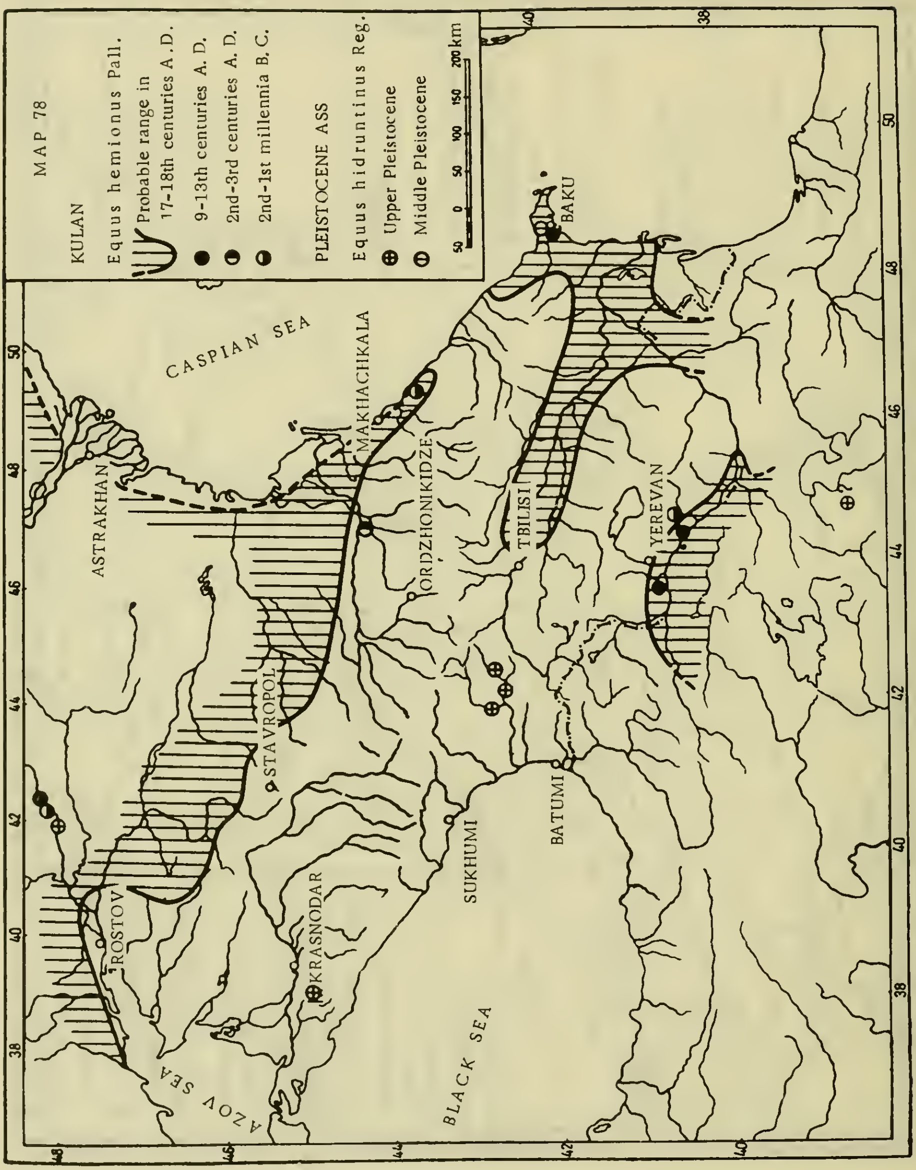
MAP 78
KULAN
Equus hemionus Pall.
Probable range in 17-18th centuries A.D.
9-13th centuries A. D.
2nd-3rd centuries A. D.
2nd-1st millennia B. C.
PLEISTOCENE ASS
Equus hidruntinus Reg.
Upper Pleistocene
Middle Pleistocene
50 0 50 100 150 200 km
CASPIAN SEA
ASTRAKHAN
MAKHACHKALA
BAKU
ORDZHONIKIDZE
TBILISI
YEREVAN
STAVROPOL
ROSTOV
KRASNODAR
SUKHUMI
BATUMI
BLACK SEA
AZOV SEA
38
40
42
44
46
48
50


MAP 79
TARPAN
Equus caballus gmelini Ant.
Probable range in 18th century A.D.
8-13th century A.D.
Holocene
SOUTHWEST ASIAN HORSE
Equus caballus L. (s. lato)
Upper Pleistocene
Middle Pleistocene
TAMAN HORSE
Equus aff. süssenbornensis Wüst.
Lower Pleistocene – Upper Pliocene
EARLY HORSE
Equus stenonis Cocchi
Upper Pliocene
50 0 50 100 150 200 km
ROSTOV
ASTRAKHAN
AZOV SEA
KRASNODAR
STAVROPOL
MAKHACHKALA
ORDZHONIKIDZE
BLACK SEA
SUKHUMI
TBILISI
BATUMI
YEREVAN
BAKU
CASPIAN SEA
38
40
42
44
46
48
50


MAP 80
BOAR
Sus scrofa L.
● Collected specimens and visual observations — 1950's
◒ Historical time
◑ 2nd-1st millennia B. C.
Sus aff. scrofa L.
⊕ Upper Pleistocene
⦶ Middle Pleistocene
APSHERON BOAR
Sus apscheronicus Burtsch. et Dzjaf.
⦶ Middle Pleistocene
TAMAN BOAR
Sus tamanensis N. Ver.
○ Lower Pleistocene — Upper Pliocene
50 0 50 100 150 200 km
ASTRAKHAN
ROSTOV
AZOV SEA
STAVROPOL
KRASNODAR
MAKHACHKALA
ORDZHONIKIDZE
BLACK SEA
SUKHUMI
TBILISI
CASPIAN SEA
BATUMI
BAKU
YEREVAN
38
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48
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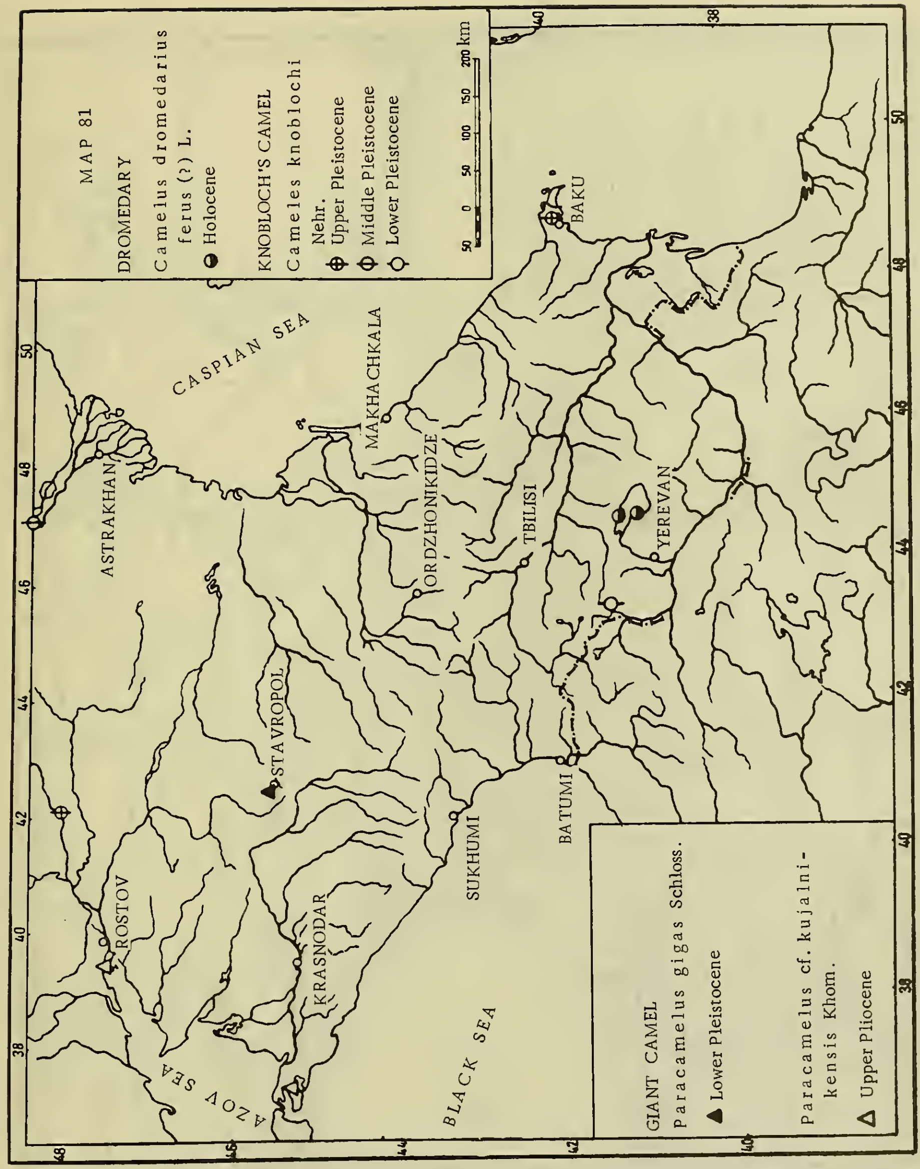
MAP 81
DROMEDARY
Camelus dromedarius ferus (?) L.
● Holocene
KNOBLOCH'S CAMEL
Cameles knoblochi Nehr.
⊕ Upper Pleistocene
Φ Middle Pleistocene
○ Lower Pleistocene
50 0 50 100 150 200 km
GIANT CAMEL
Paracamelus gigas Schloss.
▲ Lower Pleistocene
Paracamelus cf. kujalnikensis Khom.
△ Upper Pliocene
CASPIAN SEA
BLACK SEA
AZOV SEA
ASTRAKHAN
MAKHACHKALA
BAKU
ORDZHONIKIDZE
TBILISI
YEREVAN
STAVROPOL
ROSTOV
KRASNODAR
SUKHUMI
BATUMI
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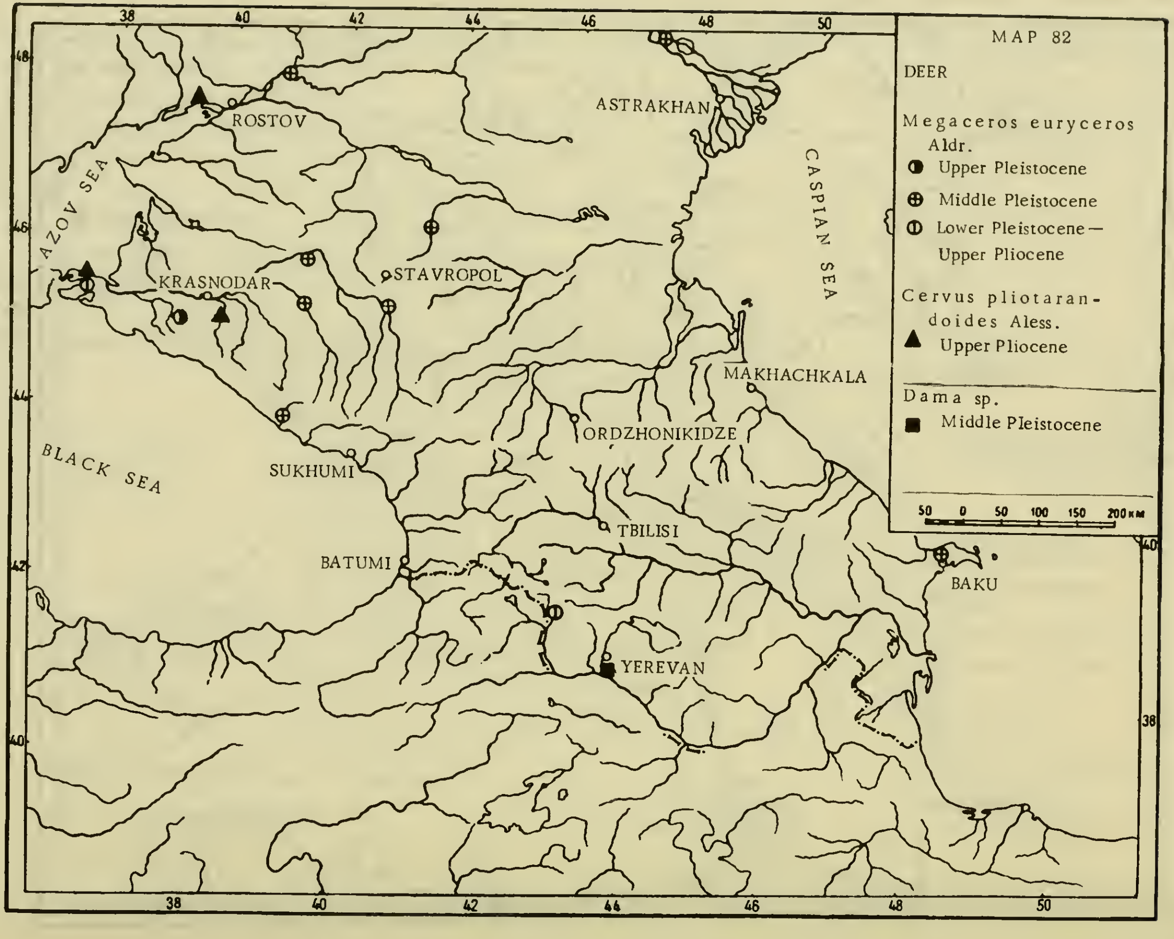
MAP 82
DEER
Megaceros euryceros Aldr.
◐ Upper Pleistocene
⊕ Middle Pleistocene
⦶ Lower Pleistocene — Upper Pliocene
Cervus pliotarandoides Aless.
▲ Upper Pliocene
Dama sp.
■ Middle Pleistocene
50 0 50 100 150 200 KM
ASTRAKHAN
CASPIAN SEA
ROSTOV
AZOV SEA
KRASNODAR
STAVROPOL
MAKHACHKALA
ORDZHONIKIDZE
BLACK SEA
SUKHUMI
TBILISI
BATUMI
BAKU
YEREVAN
38
40
42
44
46
48
50


MAP 83
RED DEER
Cervus elaphus L.
(s. lato)
• Collected specimens and visual observations, 1950's
◐ 15-19th centuries, A. D.
◐ 8-13th centuries A. D.
◒ 1st millennium B.C.
◒ Holocene
Cervus aff. elaphus L.
⊕ Upper Pleistocene
⦶ Middle Pleistocene
○ Lower Pleistocene
Cervus sp.
▲ Lower Pleistocene
△ Upper Pliocene
50 0 50 100 150 200 km
ROSTOV
ASTRAKHAN
AZOV SEA
STAVROPOL
KRASNODAR
BLACK SEA
SUKHUMI
BATUMI
ORDZHONIKIDZE
MAKHACHKALA
TBILISI
YEREVAN
BAKU
CASPIAN SEA
38
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42
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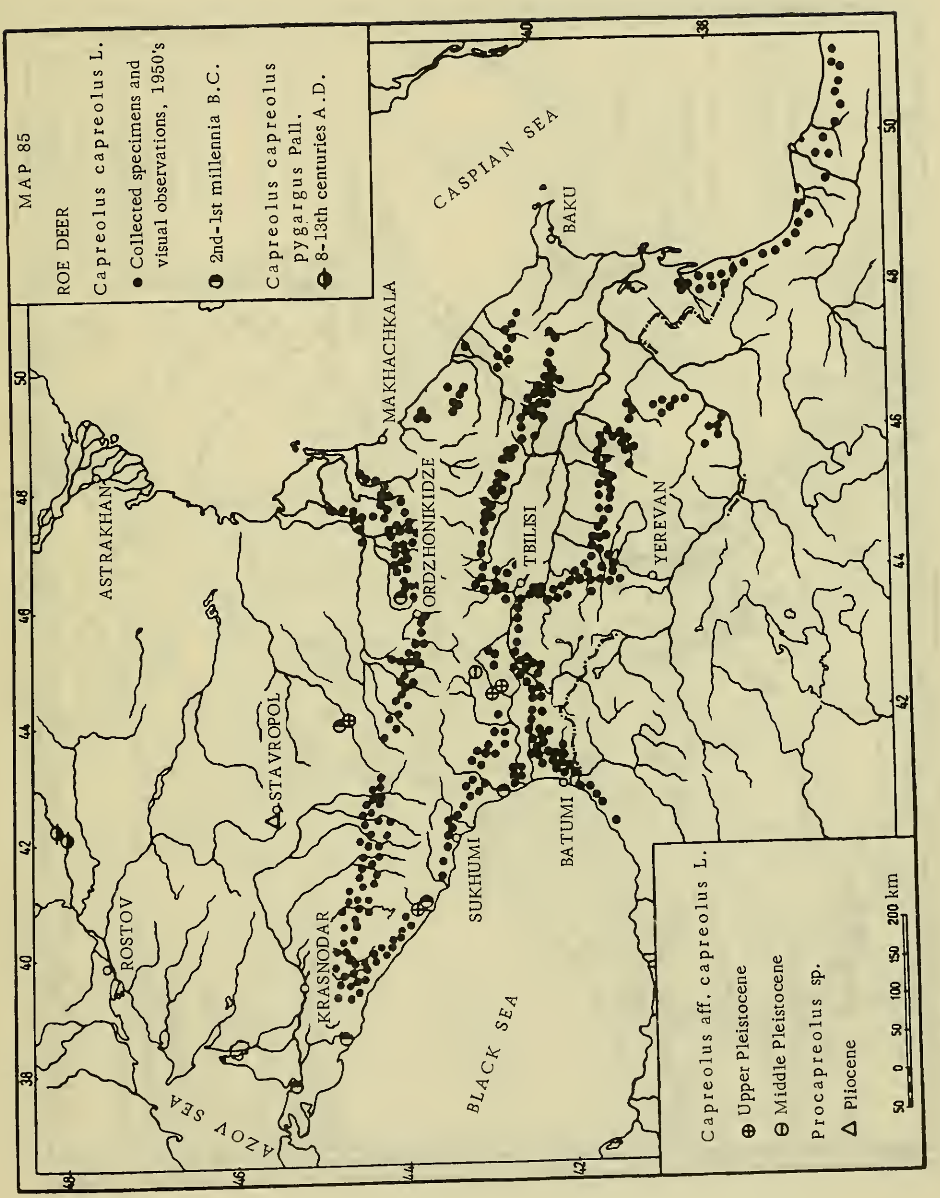
MAP 84

CAUCASIAN ELK


MAP 85
ROE DEER
Capreolus capreolus L.
● Collected specimens and visual observations, 1950's
◑ 2nd-1st millennia B.C.
Capreolus capreolus pygargus Pall.
⊖ 8-13th centuries A.D.
Capreolus aff. capreolus L.
⊕ Upper Pleistocene
⊖ Middle Pleistocene
Procapreolus sp.
△ Pliocene
50 0 50 100 150 200 km
ASTRAKHAN
MAKHACHKALA
CASPIAN SEA
BAKU
ORDZHONIKIDZE
TBILISI
YEREVAN
STAVROPOL
ROSTOV
KRASNODAR
SUKHUMI
BATUMI
BLACK SEA
AZOV SEA
38
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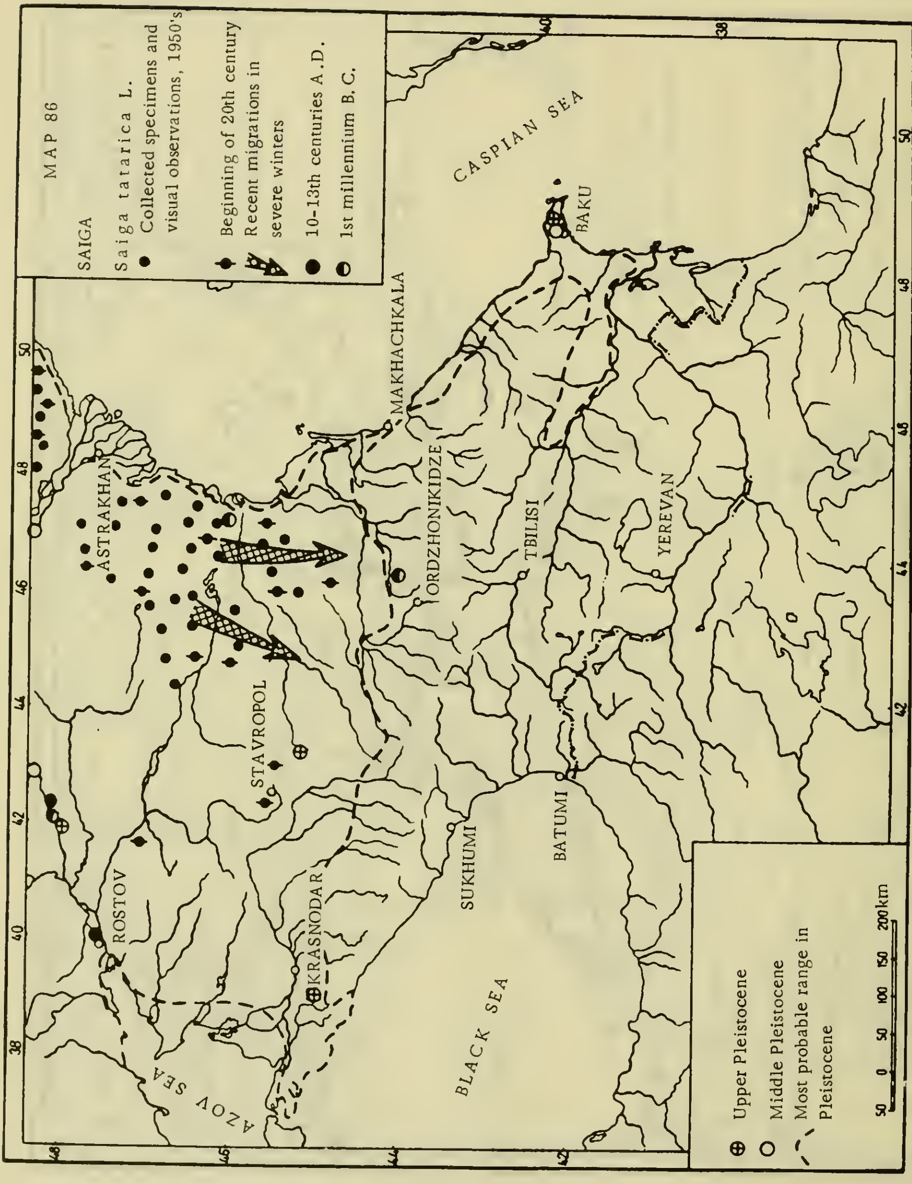
MAP 86
SAIGA
Saiga tatarica L.
● Collected specimens and visual observations, 1950's
Beginning of 20th century
Recent migrations in severe winters
● 10-13th centuries A.D.
◐ 1st millennium B.C.
⊕ Upper Pleistocene
○ Middle Pleistocene
Most probable range in Pleistocene
50 0 50 100 150 200 km
CASPIAN SEA
BLACK SEA
AZOV SEA
ASTRAKHAN
MAKHACHKALA
BAKU
ORDZHONIKIDZE
TBILISI
YEREVAN
STAVROPOL
ROSTOV
KRASNODAR
SUKHUMI
BATUMI
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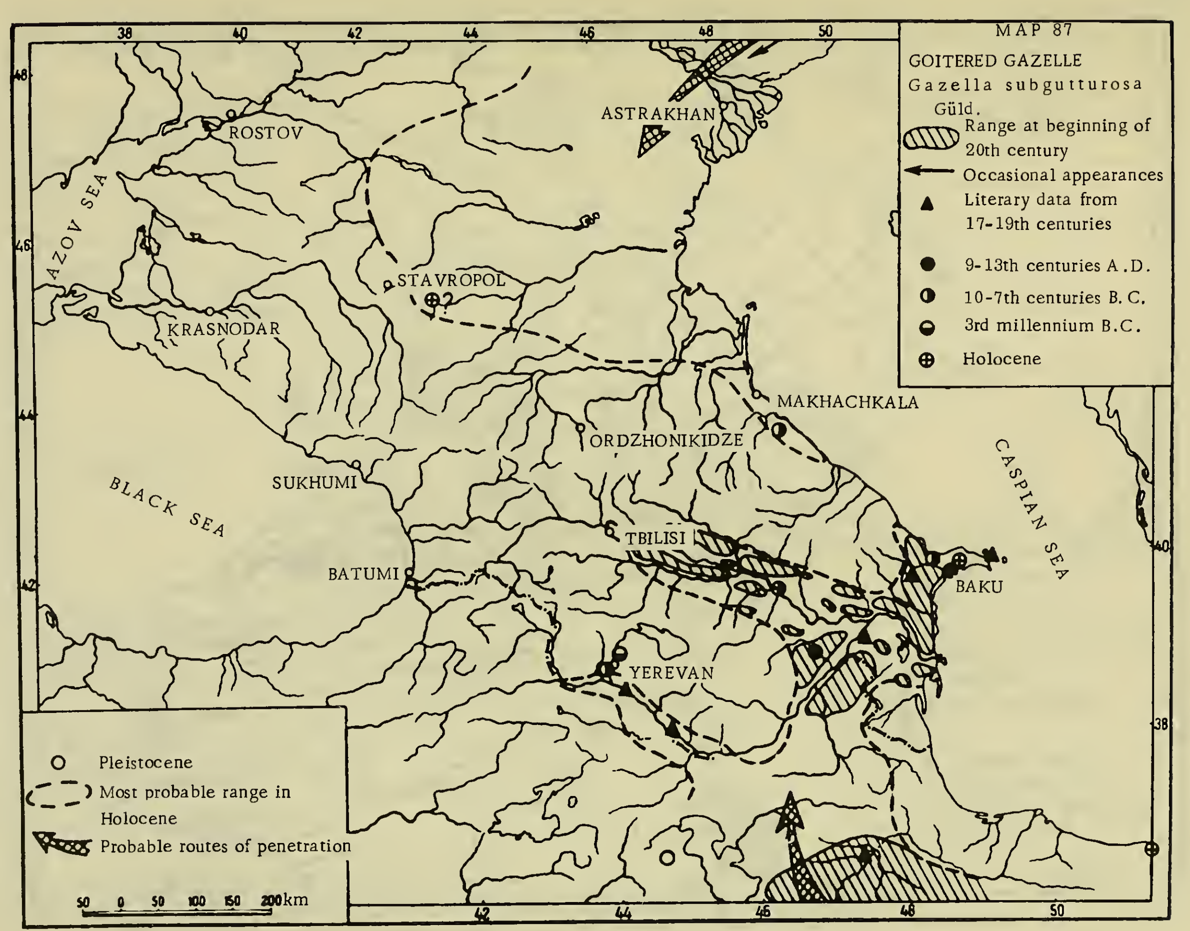
MAP 87
GOITERED GAZELLE
Gazella subgutturosa Güld.
Range at beginning of 20th century
Occasional appearances
▲ Literary data from 17-19th centuries
● 9-13th centuries A.D.
◑ 10-7th centuries B.C.
⊖ 3rd millennium B.C.
⊕ Holocene
○ Pleistocene
Most probable range in Holocene
Probable routes of penetration
50 0 50 100 150 200km
ASTRAKHAN
ROSTOV
AZOV SEA
STAVROPOL
KRASNODAR
MAKHACHKALA
ORDZHONIKIDZE
SUKHUMI
BLACK SEA
CASPIAN SEA
TBILISI
BAKU
BATUMI
YEREVAN
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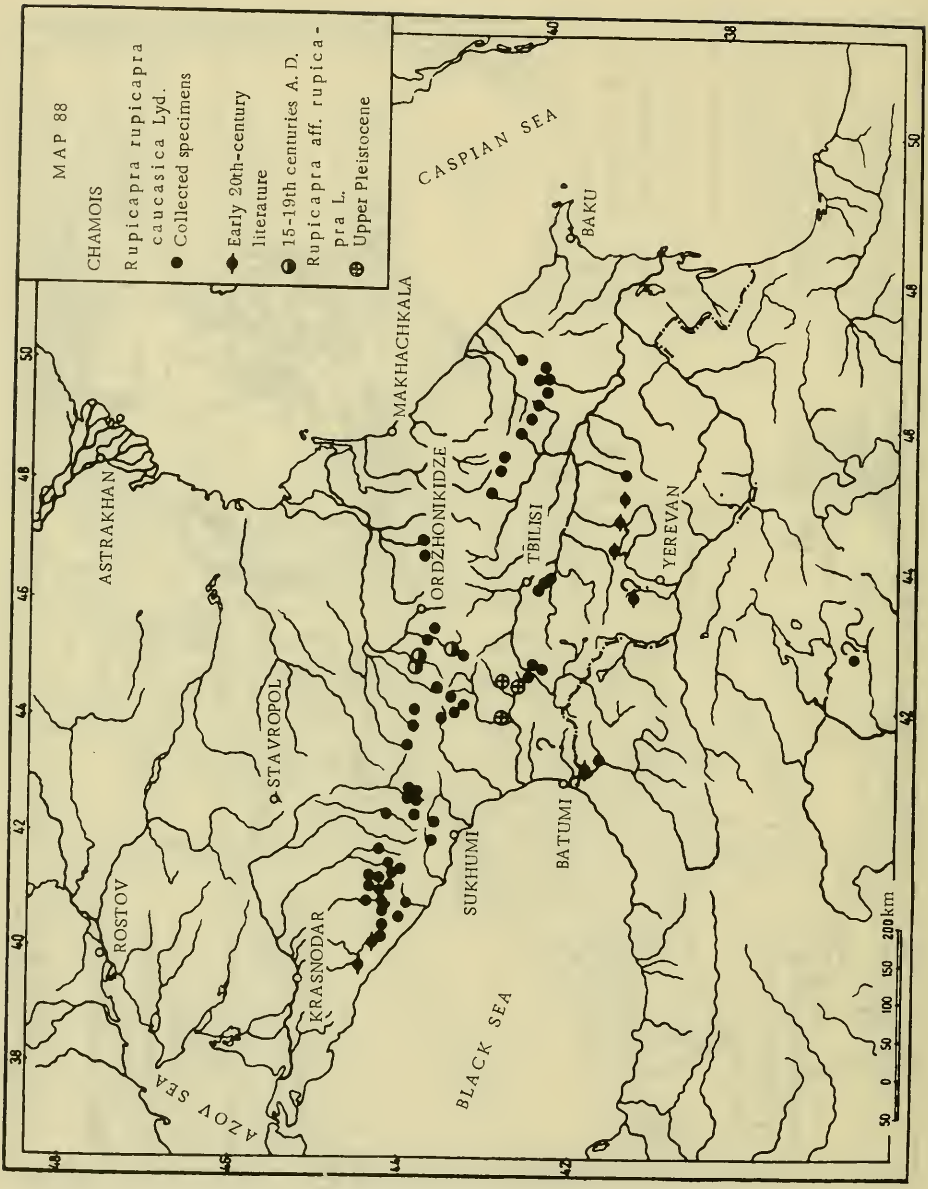
MAP 88
CHAMOIS
Rupicapra rupicapra caucasica Lyd.
● Collected specimens
◆ Early 20th-century literature
◐ 15-19th centuries A. D.
Rupicapra aff. rupicapra L.
⊕ Upper Pleistocene
CASPIAN SEA
BAKU
MAKHACHKALA
ASTRAKHAN
ORDZHONIKIDZE
TBILISI
YEREVAN
STAVROPOL
ROSTOV
KRASNODAR
SUKHUMI
BATUMI
BLACK SEA
AZOV SEA
50 0 50 100 150 200 km


MAP 89
EAST CAUCASIAN GOAT
• Capra cylindricornis Blyth
◒ 15-19th centuries A.D.
◐ Point of release
◑ Lower Holocene
WEST CAUCASIAN GOAT
▲ Capra caucasica Güld.
▲ 15-19th centuries A.D.
Capra cf. caucasica Güld.
▲ Holocene
△ Upper Pleistocene
△ Middle Pleistocene
50 0 50 100 150 200 km
ROSTOV
ASTRAKHAN
AZOV SEA
STAVROPOL
KRASNODAR
MAKHACHKALA
ORDZHONIKIDZE
BLACK SEA
SUKHUMI
TBILISI
CASPIAN SEA
BATUMI
BAKU
YEREVAN
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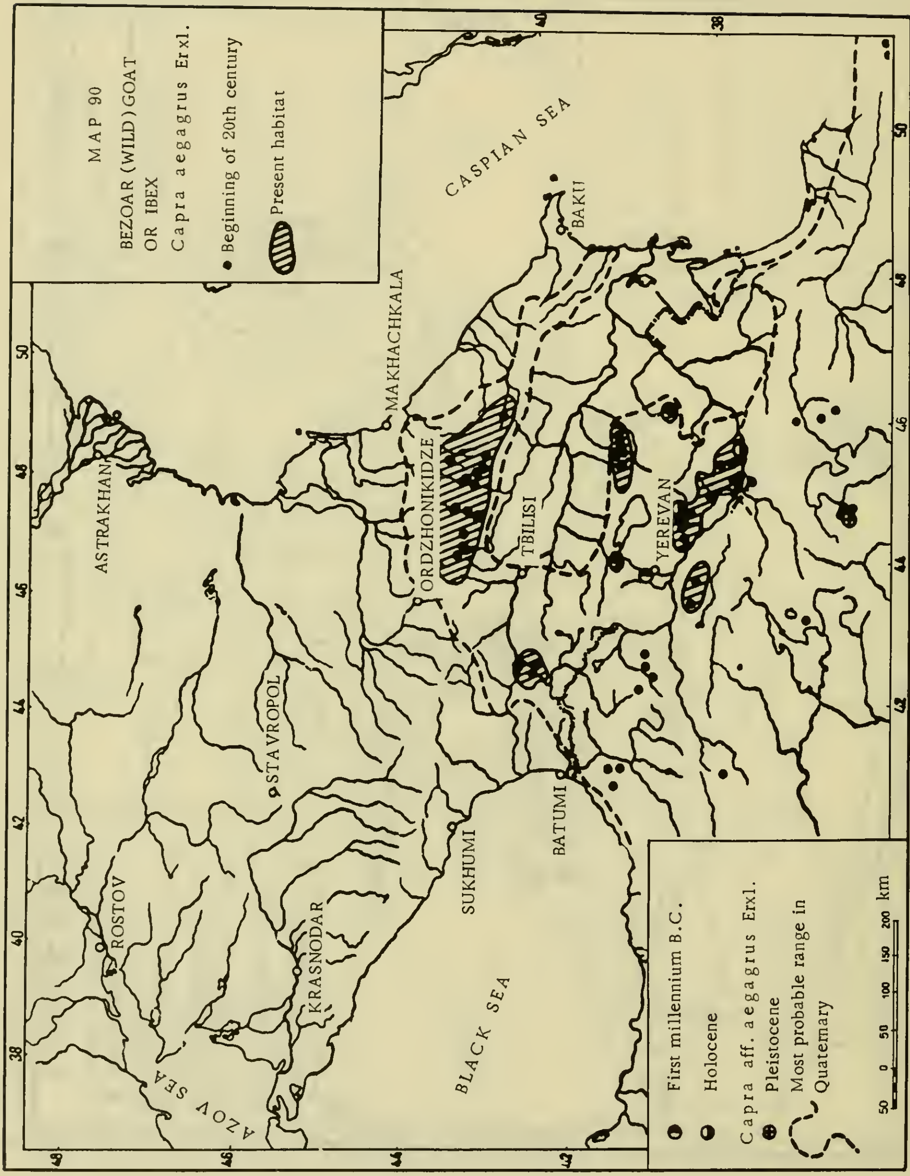

MAP 90

BEZOAR (WILD) GOAT OR IBEX

Capra aegagrus Erxl.


MAP 91
ARMENIAN MOUFLON
Ovis gmelini Blyth
Collected specimens and range in 19-20th centuries A.D.
2nd-1st millennia B.C.
Ovis cf. gmelini Blyth
Lower Holocene
ARGALI
Ovis cf. ammon L.
⊕ Upper Pleistocene
○ Middle Pleistocene
50 0 50 100 150 200km
ASTRAKHAN
ROSTOV
AZOV SEA
STAVROPOL
KRASNODAR
MAKHACHKALA
ORDZHONIKIDZE
SUKHUMI
BLACK SEA
TBILISI
BATUMI
BAKU
CASPIAN SEA
YEREVAN
38
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MAP 92
CAUCASIAN BISON
Bison bonasus caucasicus Sat.
● Beginning of 20th century
✝ Place of death of last bisons
◑ Collected specimens 14–18th centuries
◒ Literary data from 14—19th centuries
◓ Lower Holocene
PRIMITIVE BISON
Bison priscus Boj. (s. lato)
⊕ Upper Pleistocene
⦶ Middle Pleistocene
TAMAN BISON
Bison sp. (tamanensis N. Ver.)
△ Lower Pleistocene – Upper Pliocene
50 0 50 100 150 200 km
38
40
42
44
46
48
50
ASTRAKHAN
ROSTOV
AZOV SEA
STAVROPOL
KRASNODAR
MAKHACHKALA
ORDZHONIKIDZE
BLACK SEA
SUKHUMI
TBILISI
CASPIAN SEA
BATUMI
BAKU
YEREVAN
?

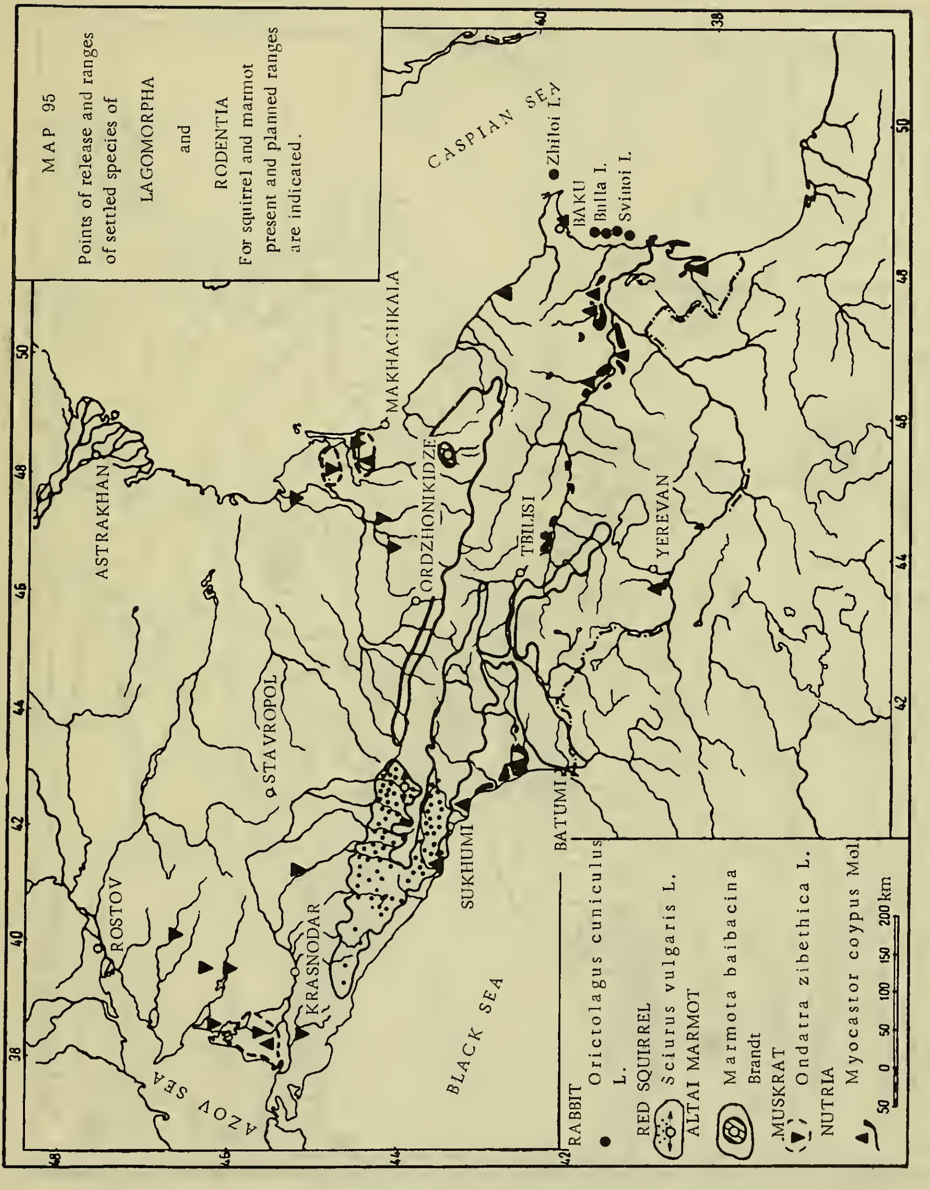
MAP 93

PRIMITIVE BULL

MAP 94

Point of release and ranges of settled species of CARNIVORA

For common raccoon the present and planned ranges are indicated



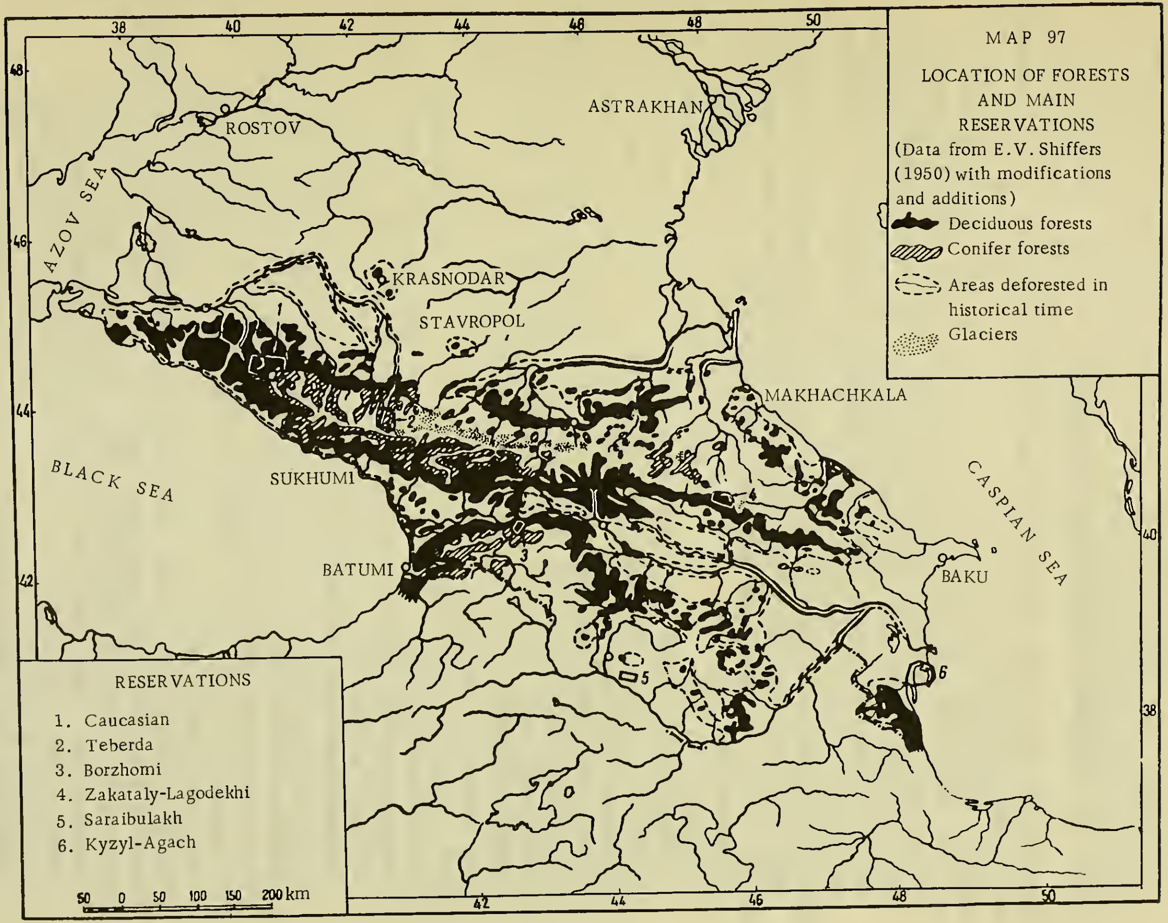
MAP 95

Points of release and ranges of settled species of LAGOMORPHA and RODENTIA

For squirrel and marmot present and planned ranges are indicated.

MAP 96

Points of release and ranges of settled species of ARTIODACTYLA



MAP 97

LOCATION OF FORESTS AND MAIN RESERVATIONS

(Data from E. V. Shiffers (1950) with modifications and additions)

INDEX OF COMMON NAMES OF MAMMALS

*INDEX OF LATIN NAMES OF MAMMALS**

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* [This index has been reproduced photographically from the Russian. The Russian page numbers referred to are at the left-hand side of the text. Asterisks denote appearance in figures, crosses in maps (Supplement, Part 2).]

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