N. K. Vereshchagin

THE MAMMALS OF THE CAUCASUS

A History of the Evolution of the Fauna

TRANSLATED FROM RUSSIAN

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Academy of Sciences of the USSR. Zoological Institute. Academy of Sciences of the Azerbaidzhan SSR

N. K. VERESHCHAGIN

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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.

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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

* [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
Leventsovka
Khapry
Novocherkassk
Aksai
ROSTOV
Morskaya
ASTRAKHAN
SEA OF AZOV
CASPIAN SEA
BLACK SEA
Petrovskoe
Blagodarnoe
Burlatskoe
Tsimbal quarry
Sinyaya gulley
Armavir
STAVROPOL
Kosyakin quarry
Belomechetskaya
KRASNODAR
Bakinskaya
Malgobek
Grozny
Achaluki
Ordzhonikidze
MAKHACHKALA
SUKHUMI
Arkneti
Dzhaparidze
Shiraki
TBILISI
Benara
BATUMI
Udabno
El'dar
Kushchi
BAKU
Lok-Batan
Naftalan
Nurnus
YEREVAN
Maragheh

FIGURE 1

(9)

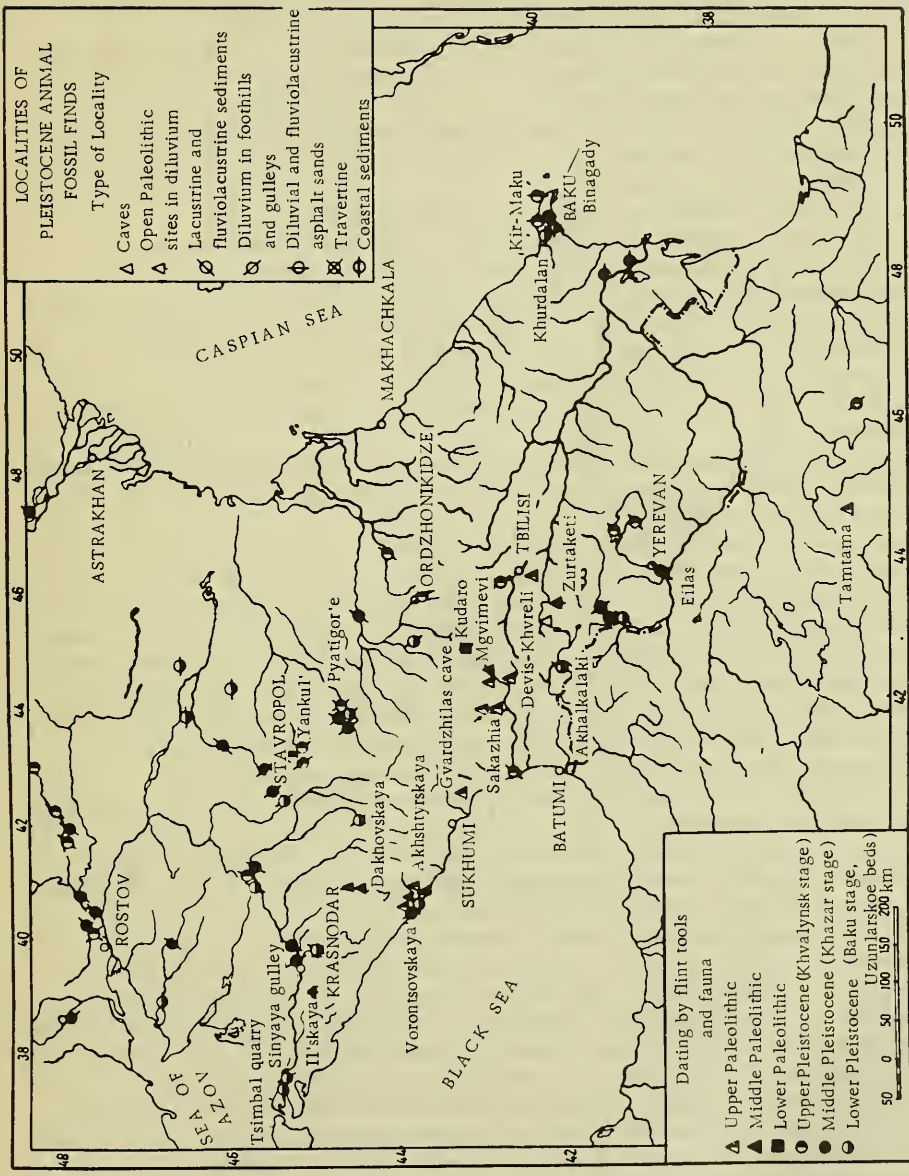

LOCALITIES OF PLEISTOCENE ANIMAL FOSSIL FINDS
Type of Locality
Caves
Open Paleolithic sites in diluvium
Lacustrine and fluviolacustrine sediments
Diluvium in foothills and gulleys
Diluvial and fluviolacustrine asphalt sands
Travertine
Coastal sediments
Dating by flint tools and fauna
Upper Paleolithic
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
ROSTOV
STAVROPOL
Yankul'
Pyatigor'e
KRASNODAR
Il'skaya
Tsimbal quarry
Sinyaya gulley
Voronstovskaya
Akhshtyrskaya
Dakhovskaya
Gvardzhilas cave
Kudaro
Mgvimevi
Sakazhia
Devis-Khvreli
SUKHUMI
BATUMI
Akhalkalaki
Zurtaketi
TBILISI
ORDZHONIKIDZE
MAKHACHKALA
Kir-Maku
Khurdalan
BAKU
Binagady
YEREVAN
Eilas
Tamtama
48
46
44
42
38
40
50

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.

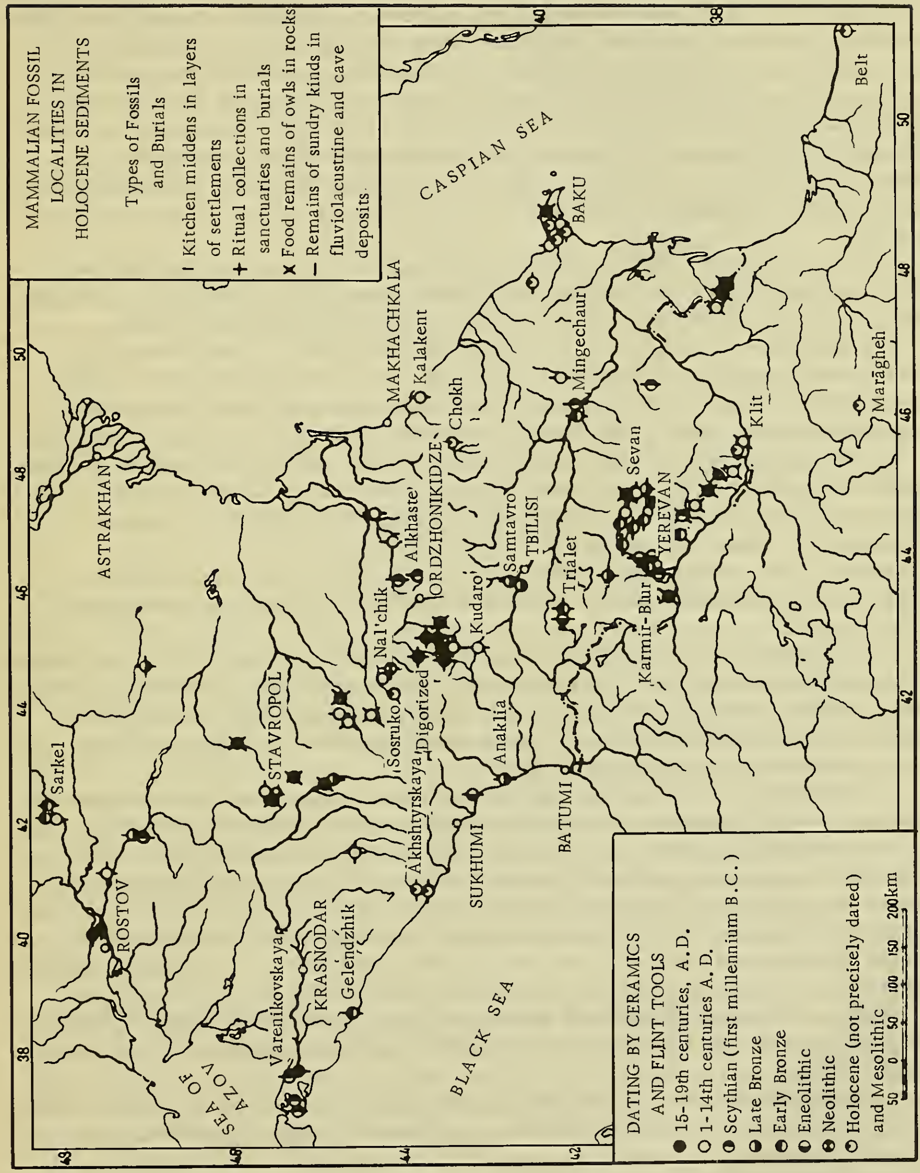
Caves containing bones of Tertiary age have not yet been found in the Caucasus. This is probably accounted for by the changes in the relief and river network which destroyed the older karst.

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
Kitchen middens in layers of settlements
Ritual collections in sanctuaries and burials
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
MAKHACHKALA
Kalakent
Chokh
BAKU
Mingechaur
Belt
Marāgheh
Klit
Sevan
YEREVAN
Karmir-Blur
Trialet
TBILISI
Samtavro
Kudaro
ORDZHONIKIDZE
Alkhaste
Nal'chik
Sosruko
Digorized
Akhshtyrskaya
Anaklia
SUKHUMI
BATUMI
STAVROPOL
Sarkel
ROSTOV
Varenikovskaya
KRASNODAR
Gelendzhik

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

* [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 P r o m e t h e o m y s) 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)

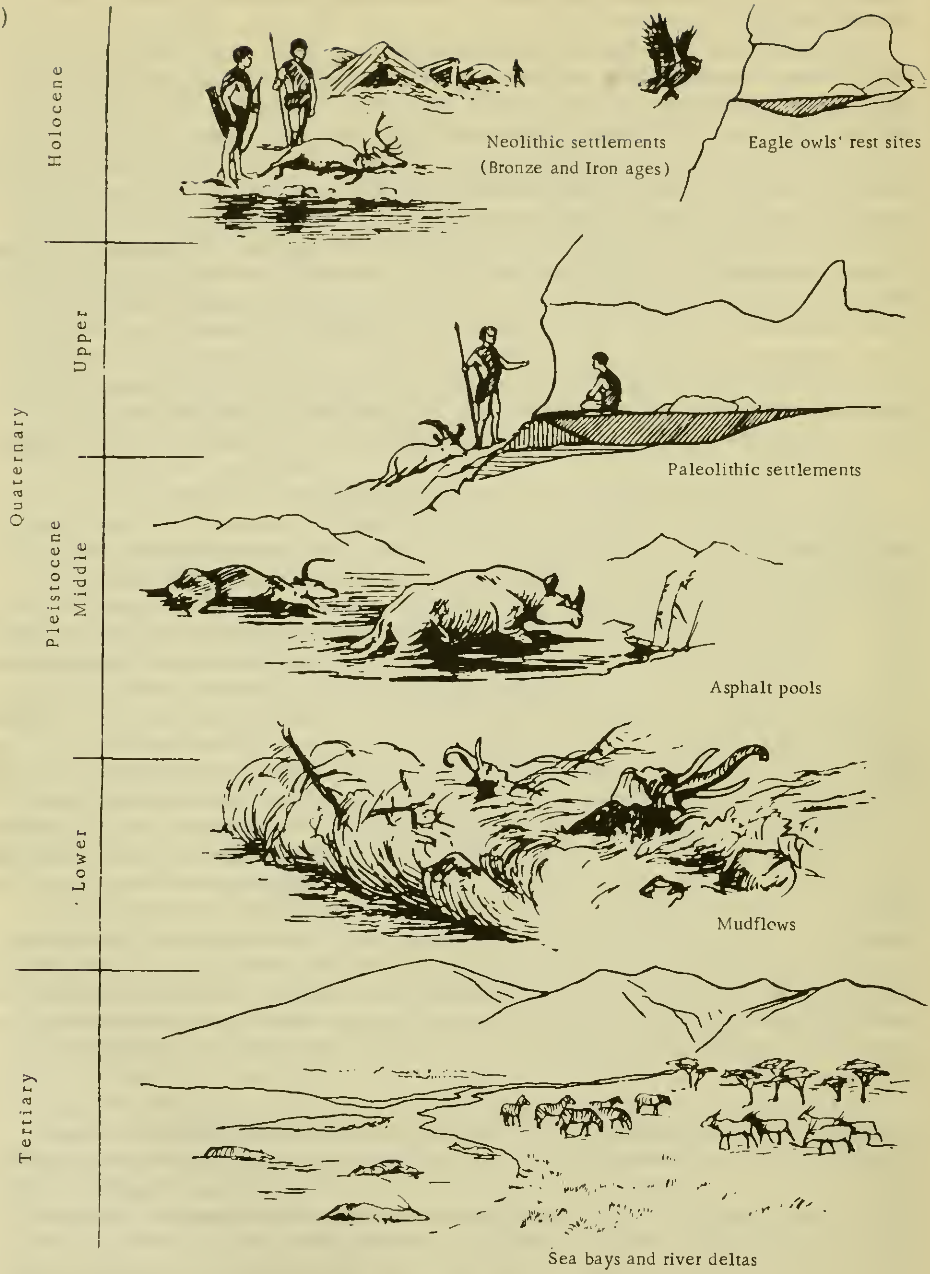


FIGURE 4. Predominant circumstances of animal death and types of fossil burials in the Cenozoic of the Caucasian Isthmus

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)
Fieldwork centers
50 0 50 100 150 200 km
BLACK SEA
CASPIAN SEA
SEA OF AZOV
Amvrosievka
Taganrog
Zhdanov
ROSTOV
Don R.
Tsimlyanskaya
Sal'sk
Divnoe
Stepnoi [Elista)
Potevoe [Utta]
ASTRAKHAN
Volga R.
Arzgir
Kuma R.
Kropotkin
Kuban R.
Laba R.
Kerch
KRASNODAR
Maikop
Novorossiisk
STAVROPOL
Budennovsk
Cherkessk
Terekli-Mekteb
Chechen I.
Terek R.
Kizlyar
Pyatigorsk
Mozdok
Khasavyurt
MAKHACHKALA
GROZNY
ORDZHONIKIDZE
Tuapse
Sochi
Chugush Mt.
Mt. Elburz
Mestia
Gagry
SUKHUMI
Mt. Kazbek
Gunib
Derbent
Rion R.
Alazan R.
Zakataly
Kuba
Kutaisi
Gori
Poti
Borzhomi
TBILISI
Akhaltsykh
Dyubrar Mt.
Shemakha
Artem I.
Zhiloi I.
BAKU
BATUMI
Kura R.
Bulla I.
Svinoi I.
Samsun
Ordu
Trebizond
Artvin
Kirovakan
Kirovabad
Mt. Aragats
Kars
L. Sevan
Sabirabad
Shusha
YEREVAN
Karyagino
Araks
Mt. Ararat
Nakhichevan
Lenkoran
Astara
Erzurum
Kafan
Maku
Megri
Ardebil
Khoi
L. Van
Bitlis
Siirt
Tabriz
Kuh-e-Sahand
Marāgheh
Mianeh
Resht
L. Urmia
Rezaiyeh
38
40
42
44
46
48
50

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 anti-plague 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.

* 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.

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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.

Bogáchev (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.

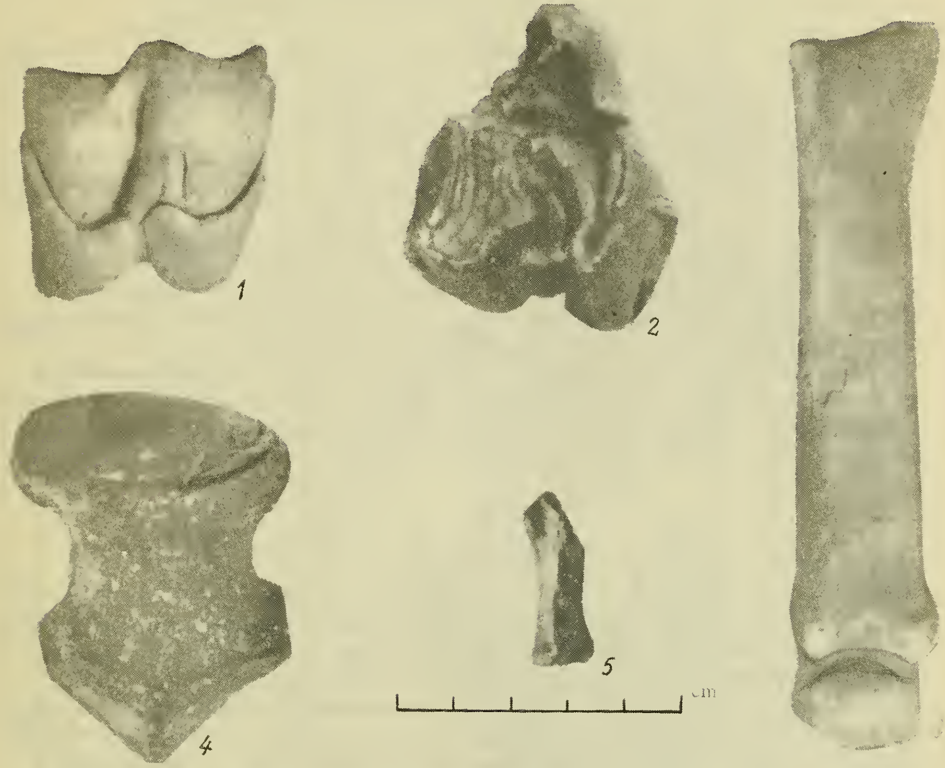
The marine (Middle Oligocene) Maikop beds of Cis- and Transcaucasia contain abundant remains of cod and herring. Occurrences of *Halitherium* cf. *schinzi* Kaup. and other, unidentified, sirenian species (possibly the ancestors of dugongs) are known from the Chiaturi manganese basin of Georgia, on the 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		Number of bones
Camivora		Anchitherium aurelianense Cuv.	4
		Dicerorhinus caucasicus Boris.	172
Amphicyon sp.	9	Chalicotheriidae gen.	3
Hyaena sp.	6	Fam. gen.	1
Ursavus sp.	4		
		Artiodactyla	
Tubulidentata		Kubanochoerus robustus Gab.	1
Orycteropus sp.	1	Hippopotamidae (?) gen.	1
Rodentia		Micromeryx flourensianus Lartet	7
		Dicrocerus elegans Lartet	3
Palaeocricetus caucasicus Arg.	6	Paratragocerus caucasicus Soc.	8
		Eotragus cf. martinianus Lartet	12
Proboscidea		Hypsodontus miocenicus Soc.	1
Platybelodon danovi Boris.	4	Fam. gen.	52
Mastodon sp.	131		
		Cetacea	
Perissodactyla		Fam. gen.	34
Paranchitherium karpinskii Boris	20		

* 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)

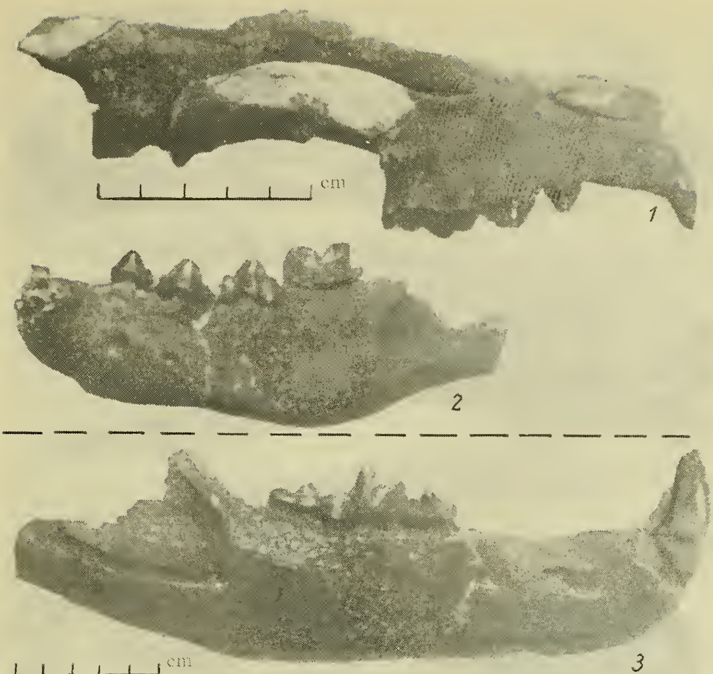


FIGURE 10. Bones of carnivores from Belomechetskaya

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.

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)

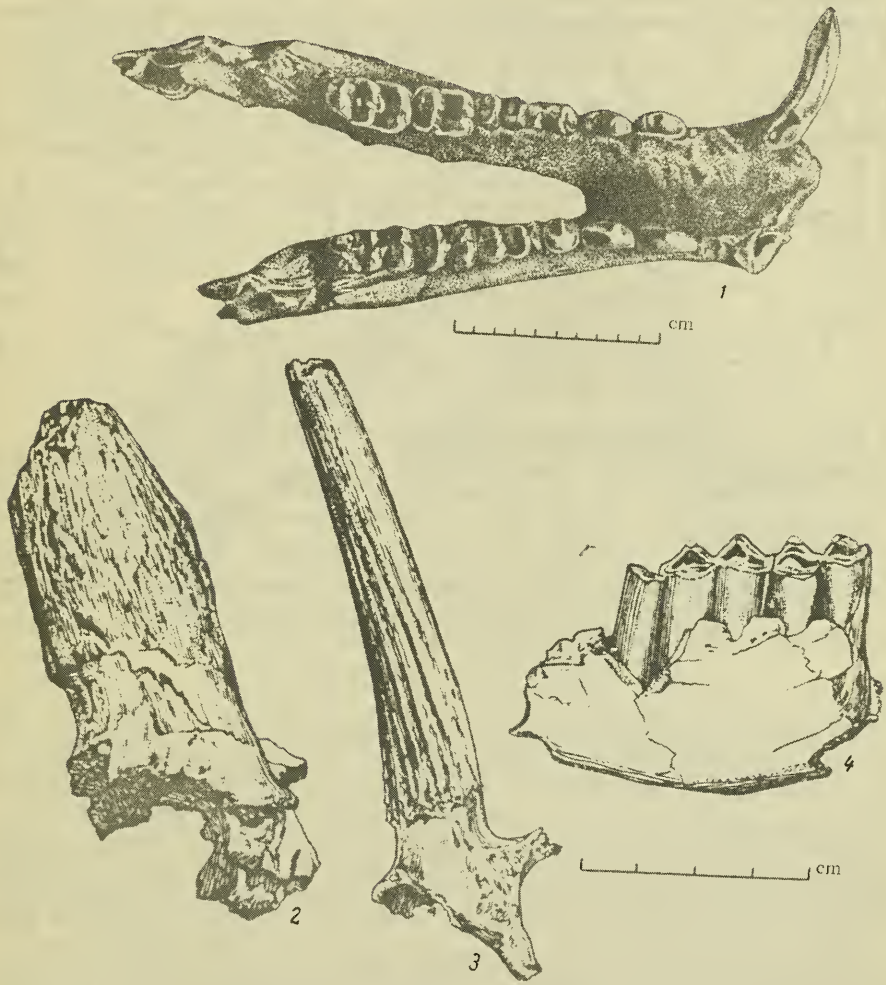


FIGURE 15.

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

(A b i e s sp.)*, pines (P i n u s sp.) and sequoia (S e q u o i a sp.) occur in the exposures along the Supsa River. Magnolia, laurel (L a u r u s p r i m i g e n i u s), cinnamon (C i n n a m o m u m p o l y m o r p h u m), elm, willow and pear trees have been identified from the Kakhetian Range and the Trans-Kuban Plain.

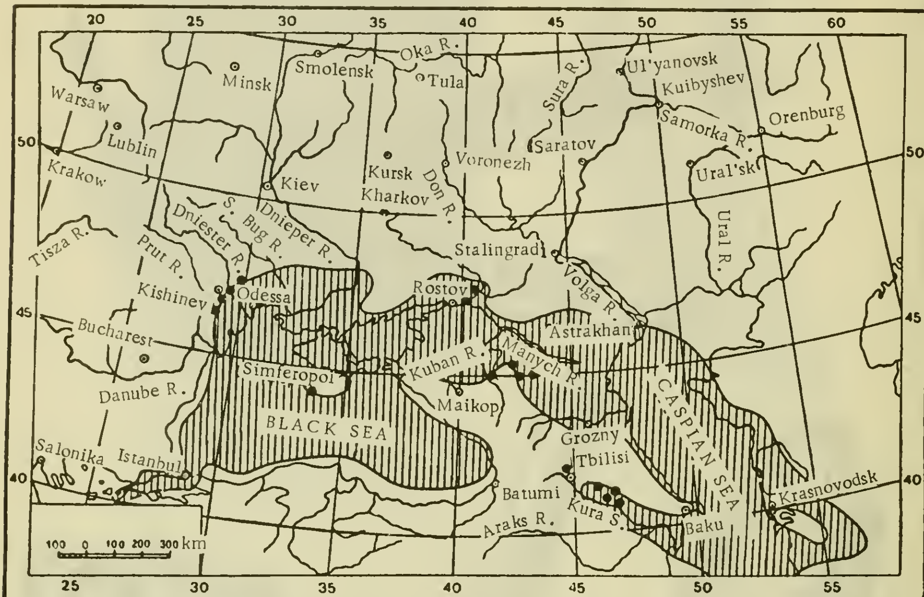


FIGURE 16. Land formations in the Upper Miocene (Upper Sarmatian)
(From Kolesnikov; see Zhizhchenko and others, 1940.)
Dots indicate main occurrences of land vertebrates

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 (C a r p i n u s), oak (Q u e r c u s), willow (S a l i x), maple (A c e r), chestnut (C a s t a n e a), zelkova (Z e l k o v a u n g e r i), and shrubs of Indian hemp (A p o c y n u m), bladder senna (C o l u t e a s a l t e r i) 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.

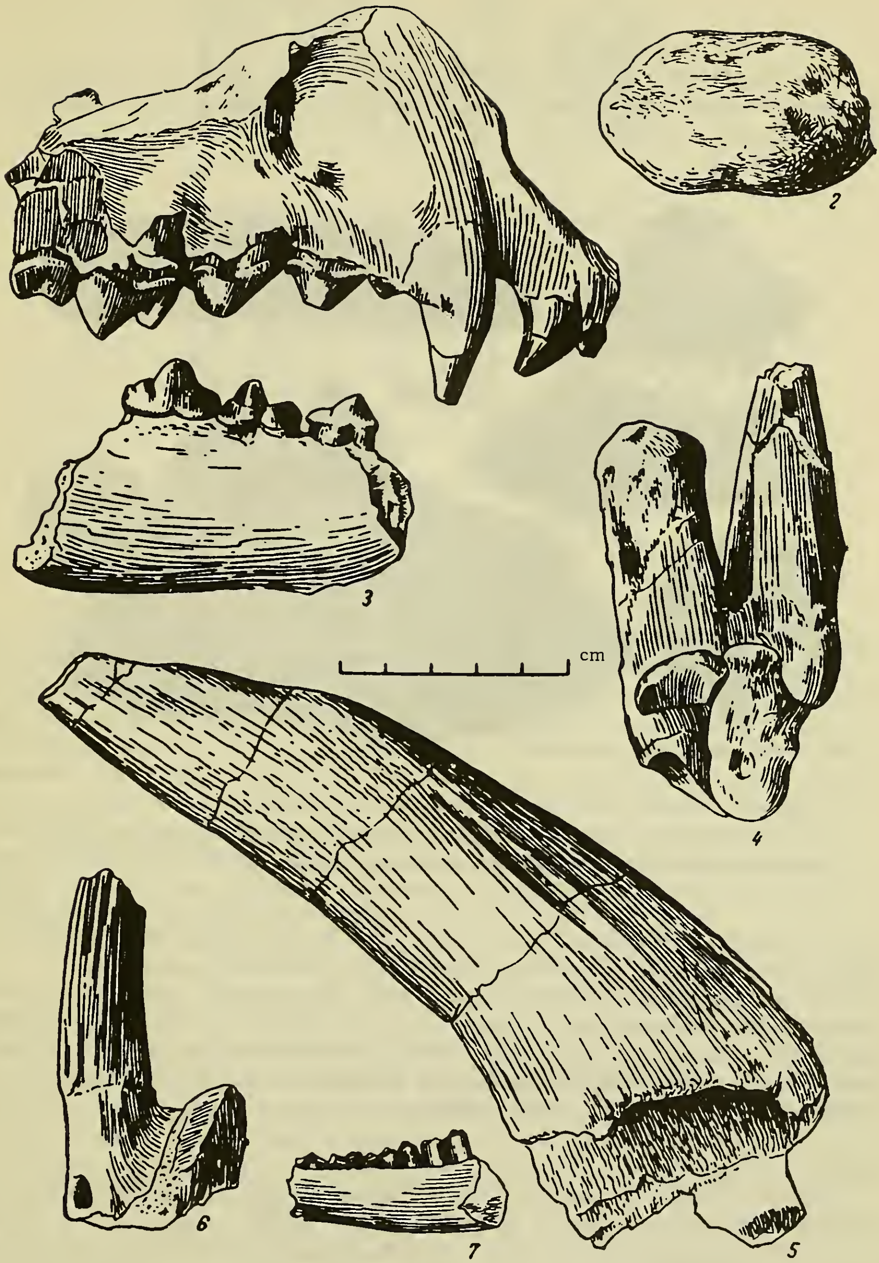


FIGURE 17. Remains of carnivores and hoofed mammals from El'dar

1, 3 — skull of H y a e n a sp.; 2 — coprolite of hyena; 4, 5 — tarsal joint and horn axis of T r a g o c e r u s sp.; 6, 7 — horn axis and jaw of G a z e l l a 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.

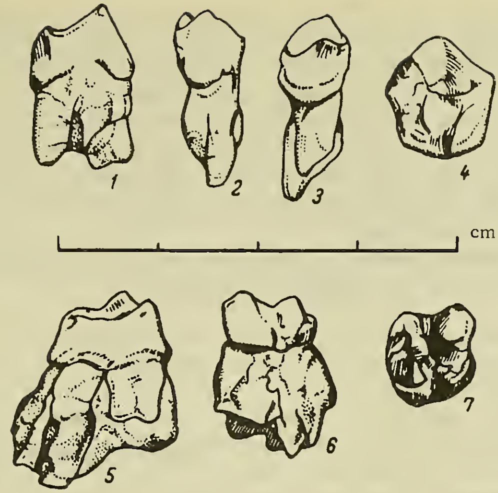


FIGURE 19. Teeth of *Udabnopithecus garedziensis*

1-4 — Pm^2: anterior, outer, inner surfaces ($\times 1\frac{1}{2}$), upper surface ($\times 2\frac{1}{4}$); 5-7 — M^1 ($\times 1\frac{1}{2}$) anterior, outer and upper surfaces (from Burchak-Abramovich and Gabashvili, 1950)

12 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:

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 F i c u s , A r a u c a r i a and palms.

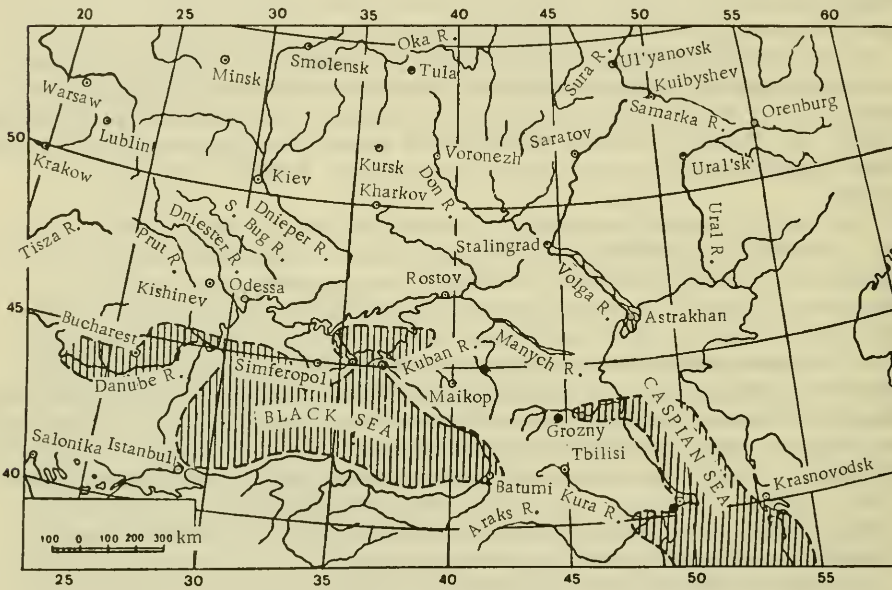


FIGURE 20. Cimmerian and Balakhany basins (from Kolesnikov; see Zhizhchenko and others, 1940) Dots indicate main localities of land vertebrates

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).

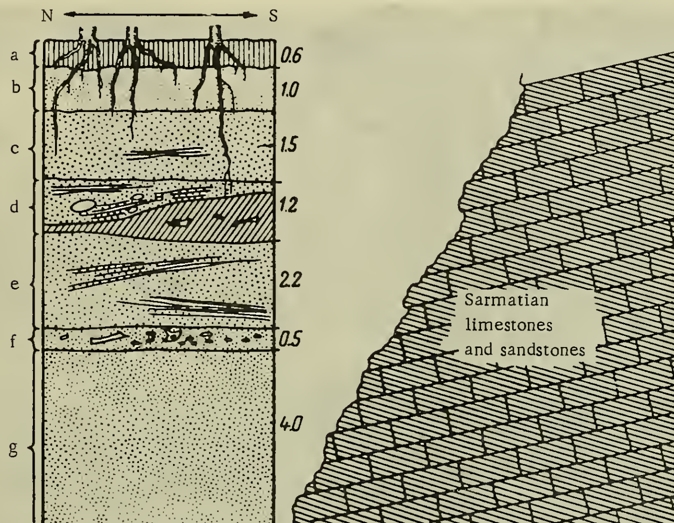


FIGURE 21. Stratigraphic section in the Kosyakin quarry

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

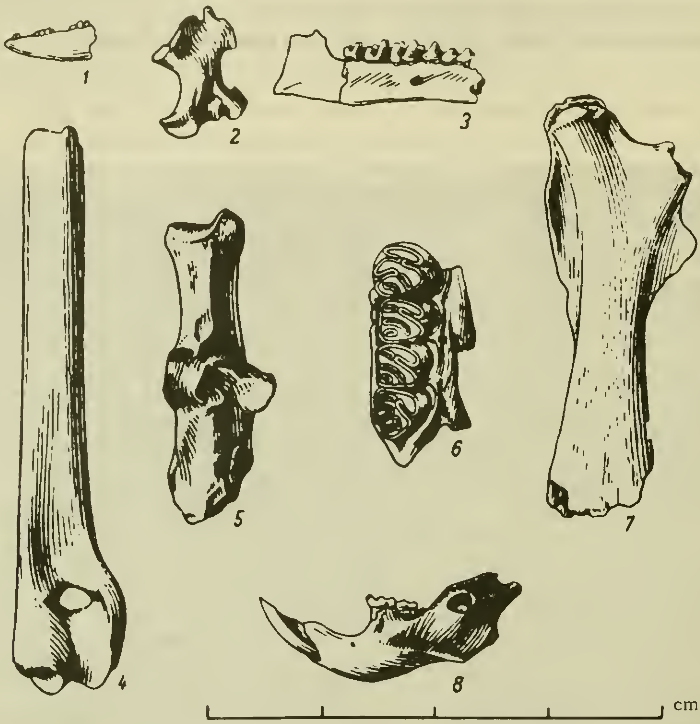


FIGURE 23. Bones of smaller vertebrates from the Kosyakin quarry

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 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.

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.

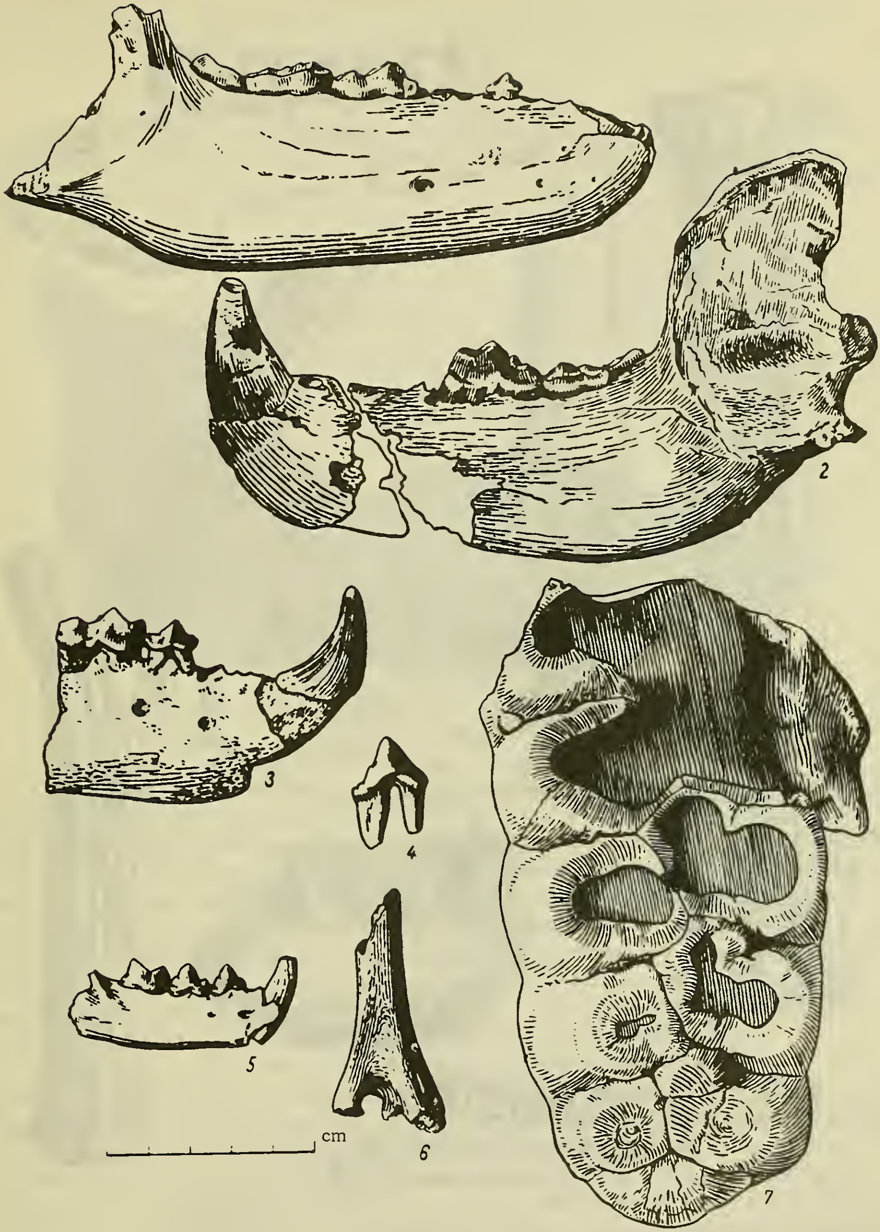


FIGURE 24. Remains of carnivores and proboscideans from the Kosyakin quarry

1, 3 — jaws of Ursus cf. arvernensis; 2 — jaw of Dinocyon cf. thenardi ($\times\frac{1}{2}$); 4 — premolar of Canidae gen. ($\times 2$); 5, 6 — jaw and shoulder of Felis cf. issiodorensis; 7 — M_4 Anancus arvernensis

(55)

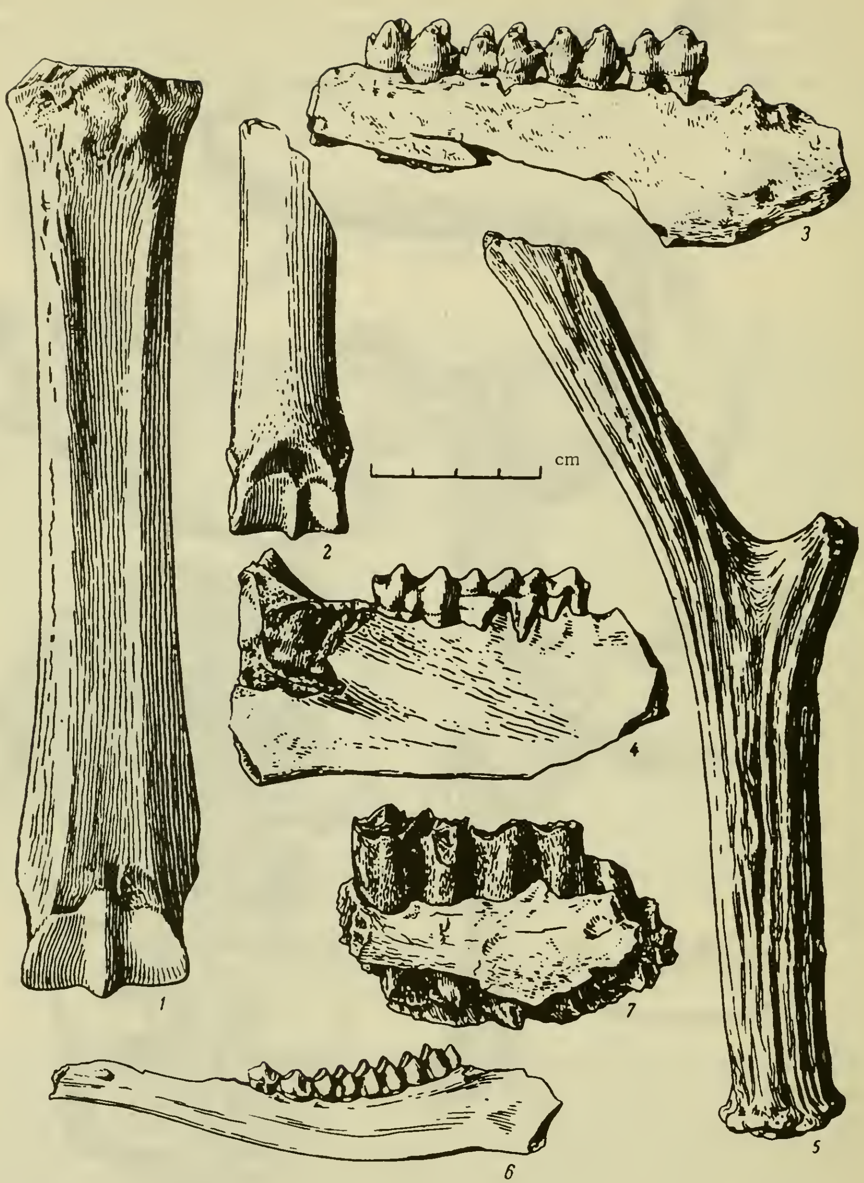


FIGURE 25. Remains of hoofed mammals from the Kosyakin quarry

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

FIGURE 26. Jaw of Dicerorhinus orientalis from the Kosyakin quarry

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.

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.

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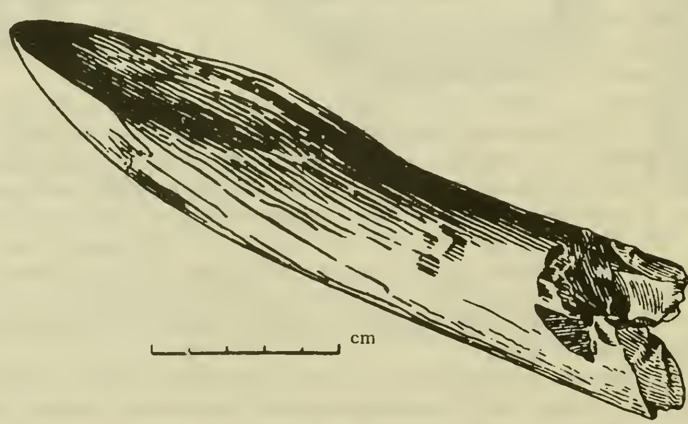

FIGURE 27. Canine (?) of Rhinocerotidae gen. from the Kosyakin quarry

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)

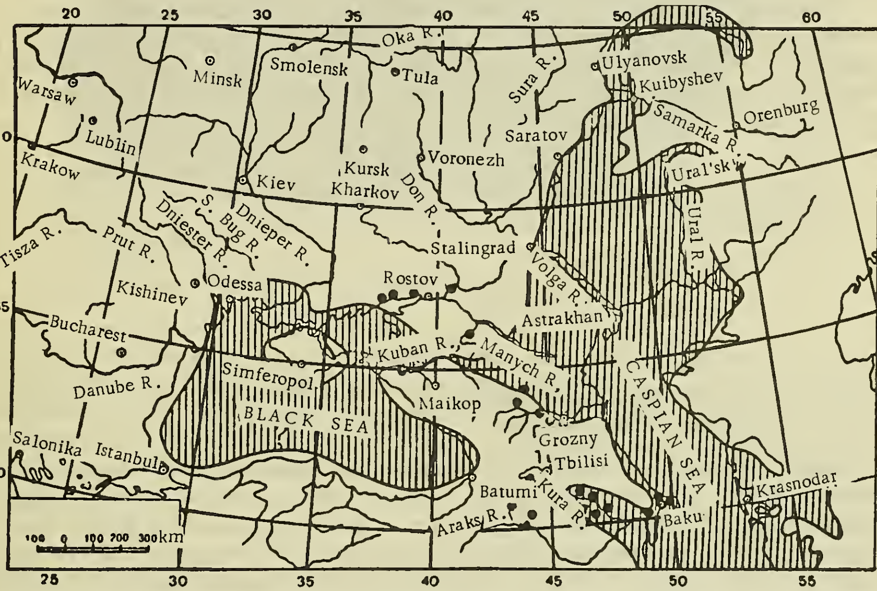

FIGURE 28. Kuyal'nitsk and Akchagyl basins (from Kolesnikov; see Zhizhchenko and others, 1940) Dots indicate main localities

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.).

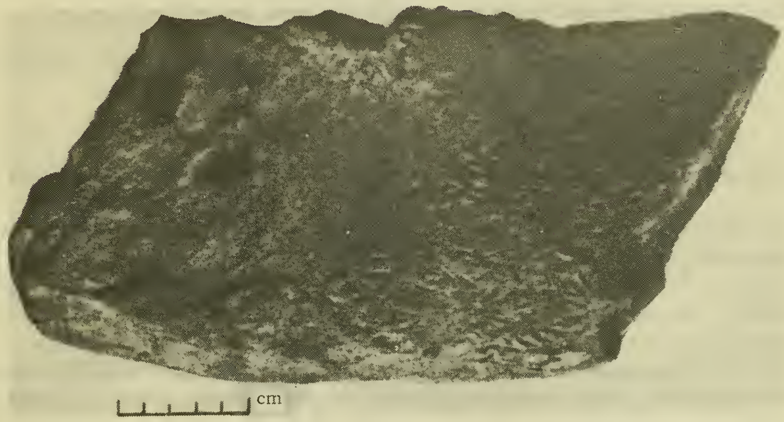

FIGURE 29. Jaw of Elephas meridionalis with borings caused by invertebrates From the Khapry sands on the right bank of the Don River (Orig.)

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.

* [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

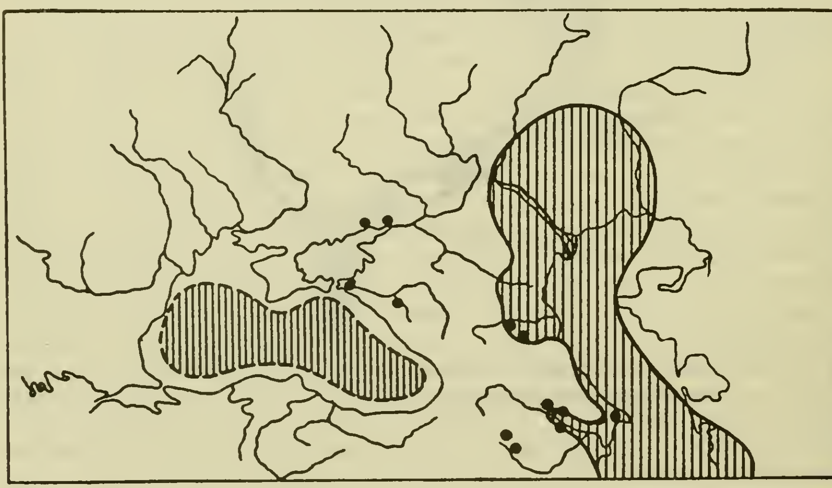

FIGURE 31. Chauda and Apsheron basins (from Kolesnikov; see Zhizhchenko and others, 1940) Dots indicate main localities

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.

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

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

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

* 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

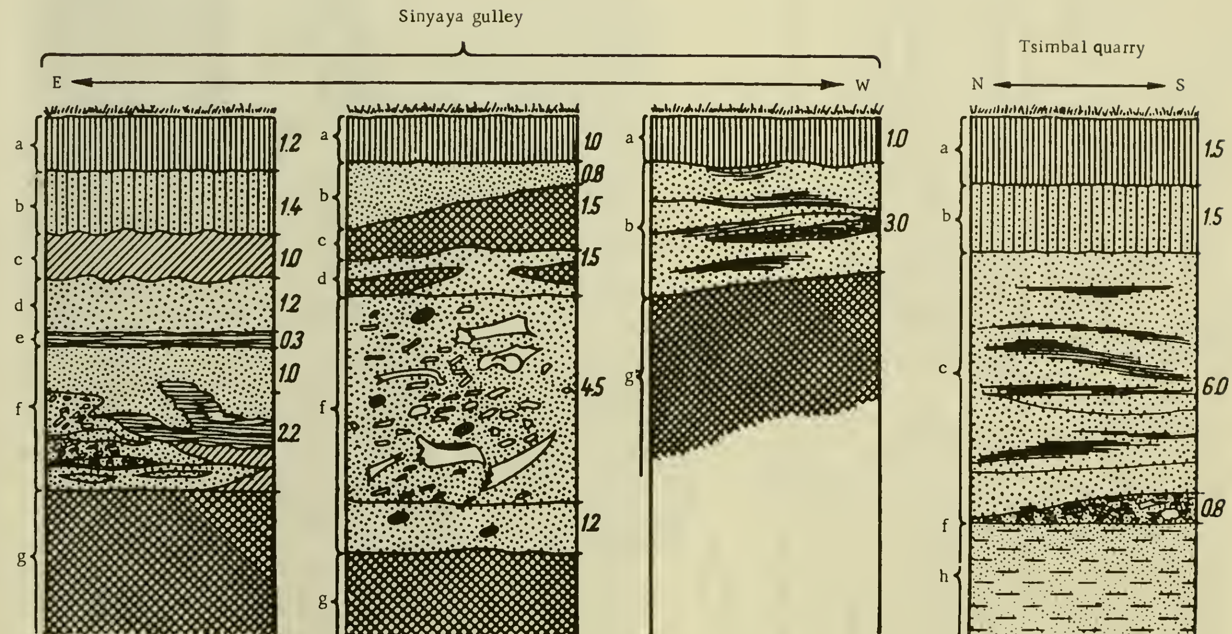

FIGURE 33. Stratigraphic sections at the Sinyaya gulley and Tsimbal quarry

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.