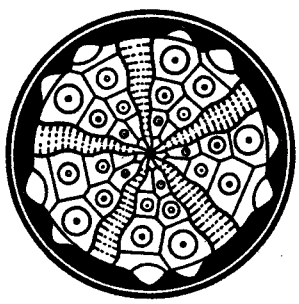
PALAEONTOGRAPHIA ITALICA

RACCOLTA DI MONOGRAFIE PALEONTOLOGICHE

FONDATA DA MARIO CANAVARI NELL'ANNO 1895

PUBBLICATA A CURA DELLA SOCIETÀ TOSCANA DI SCIENZE NATURALI

VOL. LXXIV - ANNO 1986



PISA
PACINI EDITORE
1987

Palaeontographia Italica	74	1986	63-96	tav. 12	Pisa, Giugno 1986

The Lower Pleistocene Mammalian Fauna of Akhalkalaki (Southern Georgia, USSR)

A. VEKUA (*)

KEY WORDS — Mammalia - Lower Pleistocene - Quaternary - Steppe - Semi-steppe - Transcaucasia - Asia.

ABSTRACT — The work is dedicated to study of bone remains of mammals of the locality of Akhalkalaki (Southern Georgia, USSR). The fauna of Akhalkalaki determined by the author as of Lower Pleistocene, has been founded in the lake deposits located at the foot of the dacitic hill Amiranis-mt.

In the locality of Akhalkalaki fossil remains occur in lense-like accumulations, containing bones and sometimes even the whole skeletons which obviously suggest their in situ deposition. In the faunal complex of Akhalkalaki 23 forms belong to six orders. The most pecular form of the fauna of Akhalkalaki is Equus hipparionoides *Vekua, being characterized by relatively small dimensions, well-proportioned limbs and presence of the exceptionally short protocone on the upper molar teeth, as well as of the parastylid, ectostylid and hypostylid on the lower constant ones.*

The presence within the fauna of Akhalkalaki of the big hippopotamus is of a great interest. It differs from certain fossil and recent forms with original specialization of the limbs testifying, apparently, to adaptation to drought.

Most specimens of the fauna of Akhalkalaki appear to be inhabitants of opened and semi-opened spaces. In the Early Quaternary the steppe and semi-steppe conditions seemingly predominated in the region of Akhalkalaki.

Asiatic element plays the leading part in the fauna of Akhalkalaki. In particular, the presence of Hippopotamus, Panthera, Crocuta *and many other forms apparently point out to the closest relationships between Transcaucasia and the anterior Asia in the Lower Pleistocene.*

RIASSUNTO — Il lavoro è dedicato allo studio di resti ossei di mammiferi della località di Akhalkalaki (Georgia meridionale, URSS). La fauna di Akhalkalaki, ritenuta dall'autore di età pleistocenica inferiore, è stata raccolta nei depositi lacustri situati ai piedi della collina dacitica di Monte Amiranis.

Nella località di Akhalkalaki i resti fossili si trovano in accumuli lentiformi che contengono ossa e talora anche interi scheletri, la qual cosa suggerisce una loro deposizione in situ. Nel complesso faunistico di Akhalkalaki compaiono 23 forme appartenenti a 6 ordini.

*La forma più peculiare della fauna di Akhalkalaki è l'*Equus hipparionoides *Vekua, che è caratterizzato da relativamente piccole dimensioni, con arti ben proporzionati, e dalla presenza di un protocono eccezionalmente corto sui denti molari superiori come pure dal parastilo, ectostilo ed ipostilo su quelli inferiori permanenti.*

La presenza nella fauna di Akhalkalaki di un grande ippopotamo è di notevole interesse. Esso differisce da altre forme fossili e recenti per la particolare specializzazione degli arti, che testimonia apparentemente un adattamento alla siccità.

La maggior parte degli esemplari di Akhalkalaki appaiono essere abitatori di spazi aperti e semi-aperti. Nel Quaternario basale condizioni di steppa e di semi-steppa verosimilmente predominavano nella regione di Akhalkalaki.

Gli elementi asiatici dominano nella fauna di Akhalkalaki. In particolare la presenza di Hippopotamus, Panthera, Crocuta *e di molte altre forme indica apparentemente strette relazioni tra la Transcaucasia e l'Asia anteriore durante il Pleistocene inferiore.*

(*) Institute of Palaeobiology. Academy of Sciences of Georgia, Tblisi Gruzia, SSR.

INTRODUCTION

The present work is a summary of a monographic study (Vekua, 1962) of an extensive collection of fossil Lower Pleistocene mammals unearthed near Akhalkalaki, a town in southern Georgia, the USSR. Volcanic formations marked by an almost complete nonoccurrence of organic remains are abundant in southern Georgia. It is only in lacustrine-diluvial and alluvial deposits buried in lavas that bones of terrestrial vertebrates occur. This record acquires supreme significance when stratigraphic position of both bone-bearing layers and volcanic rock mass as a whole is to be determined. Hence, particular interest is shown by researchers in the Akhalkalaki find which comprises a rich fauna of mammals.

Quite a few years have passed since the monographic study of the Akhalkalaki fauna was published in Georgia. Extensive material on the Pleistocene vertebrates has been collected in Eurasia throughout this time, quite a number of works on Quaternary geology have appeared, special attention being given to the problem of the

lower boundary and the time span of the Pleistocene. However, there is still little consensus among the workers with respect to the above mentioned problems.

Quaternary geologists show an increasing trend to rejuvenate Upper Pliocene deposits, the lower boundary of the Quaternary Period being accordingly pushed back. At the present stage the following boundaries falling under three categories are in the focus of the research: 1. The Akčagylian-Kujalnikian subface (the Ponto-Caspian region)/the Lower Villafranchian (Western Europe) boundary;

2. The Apsheronian-Gurian subface (the Ponto-Caspian region)/the Middle Villafranchian (Western Europe) boundary;

3. The Bakinski-Chaudy subface (the Ponto-Caspian region)/the Upper Villafranchian (Western Europe) upper boundary.

We are rather inclined to accept the view according to which the border is drawn above the beds containing the Lower Villafranchian and the Kvabebi mammalian faunas. It corresponds to the Akčagylian/the Apsheronian in the Caspian basin and the Kujalnikian/the Gurian in the Black Sea basin.

Taking account of the fact, however, that the geologists of Transcaucasia strictly adhere to the classical stratigraphic scheme according to which the lower boundary of the Pleistocene is drawn across the upper limit of the Apsheronian and Gurian beds in the Ponto-Caspian region, we, in our work, refer the Akhalkalaki fauna and its analogues to the Lower Pleistocene, believing it to be a faunal and chronological equivalent of the Epivillafranchian fauna in Western Europe.

The work opens with the geology of the Akhalkalaki bonebearing rocks to be followed by a brief review of the Akhalkalaki fauna, the ecologic features of this fauna and its correlation with Pleistocene faunas in Eurasia.

The monograph being of a considerably larger volume than the present work, naturally quite a few questions dealing with the history of formation in the Akhalkalaki fauna are missing in an abridged account, tables of measurements (with few exceptions) and the description of bone remains have not been included, etc.

Nevertheless, we believe that the work may prove useful to the workers concerned with the study of the Quaternary Period.

THE GEOLOGY OF THE AKHALKALAKI FAUNAL DEPOSITS

The fauna of Akhalkalaki has been found in the lacustrine deposits at the foot of Amiranis-Mt., a dacitic hill in southern Georgia. A brief review of the geology in the Akhalkalaki locality will be helpful to determine the age and origin of the Amiranis-Mt. bone-bearing lake deposits.

Within the Javakheti lava upland the Akhalkalaki and Tsalka sequences represented by a complex alternance of effusive and continental formations are quite frequent. Effusive formations are marked by a prevalence of dolerites, basalts and andesite-basalts, andesites occurring more rarely. Continental formations in the region are represented by lacustrine deposits as well as by alluvial-diluvial ones. Continental deposits and effusives are deformed into folds throughout the junction zone of the lava upland and the Trialeti Mountains.

Views vary as to the geologic age of the Akhalkalaki effusive lavas. Some researchers date them to the Oligocene, others refer them to the Pliocene. The majority of workers, however, determine the age of these dolerites by the Pleistocene. The lack of consensus is aggravated by the fact that no finds of fossil remains have been recorded in clays buried in the lava.

Skhirtladze (1958) suggests the following sequence of volcanic layers in the locality of Akhalkalaki:

1. The Goderdzi suite, represented by bright dacites (Upper Miocene-Lower Pliocene);

2. The Akhalkalaki suite, represented by doleritic lavas with alternating layers of clay lacustrine deposits three meters thick (Upper Pliocene-Lower Pleistocene);

3. Black andesite-dacites overlapping the dolerites of the Akhalkalaki Plateau (Upper Pleistocene-Holocene). According to Skhirtladze (1958) and Adamia (1960), a relatively analogous sequence is observed throughout southern and southeastern Georgia, with the Akhalkalaki sequence and its analogues overlying unconformably with angular discordance the dislocated Goderdzi suite placed by geologists in the Upper Miocene-Lower Pliocene.

There is little controversy as to the lower margin of the Akhalkalaki suite. Indeed, it positively cannot be older than the Lower Pliocene as it unconformably overlies the Goderdzi suite. This also agrees with paleontological data.

In 1948 Zaridze and Tatrishvili found bits of animal teeth in the western part of the Bedenski range (the locality of Tsalka), referred by Burchak - Abramovich (1951) to *Archidiskodon* aff. *planifrons* and *Equus* cf. *stenonis*. The dating of the Tsalka lava complex by the Upper Pliocene was based on this record.

Recently we have undertaken some additional

PLATE 1

1. *Marmota* sp. Fragment of the cranium; 2. *Marmota* sp. Mandibula (sin.)
3. *Lepus* sp. First phalanx
4. *Vormela peregusna* Güld. Mandibula (sin.)
5. *Lutra* cf. *lutra* L. Fragment of the cranium
6. *Meles* cf. *meles* L. Cranium; 7. *Meles* cf. *meles* L. Mandibula (dex.); 8. *Meles* cf. *meles* L. Humerus (sin.); 9. *Meles* cf. *meles* L. Ulna (sin.)

excavation work in Tsalka which provided convincing evidence to be employed for stratigraphy of deposits in this region. To date, the Tsalka fauna includes *Archidiskodon meridionalis, Equus stenonis, Eucladoceros* sp., *Dama* aff. *nestii, Leptobos* sp., *Cervus* sp., *Canis* aff. *etruscus* (Vekua *et al.*, 1985).

The fauna, notwithstanding the scarcity of forms, is probably contemporary with the Kotsakhuri fauna (eastern Georgia) placed in the Lower Apsheronian layers which we are inclined to correlate with the lower part of the Upper Villafranchian in western Mediterranean. The Kotsakhuri and Tsalka faunas, however, show great similarity with those of Yukari-Sögütöni (Anatolia) and Coupet (Western Europe).

Accordingly, the lower part of the Akhalkalaki dolerites and the interlaying lake deposits which are well correlated with the Tsalka dolerites may be assigned to the Lower Apsheronian. As to the maximum age margin of the Akhalkalaki suite it can now be estimated by the Akhalkalaki mammalian fauna with a great deal of precision.

Fig. 1 - Total view of the Akhalkalaki location.

To the east of Akhalkalaki, at the foot of Amiranis-Mt. lake deposits are well developed. They consist chiefly of volcanic ashes in their lower portion, the upper one being a composition of a mixture of volcanic ashes and sandy clays (fig. 1). The visible rock mass of these deposits does not exceed 3-4 meters. Throughout the beds fossil mammalian remains occur in the form of lense-like accumulations often containing a large amount of coprolites, joint bones, and even complete skeletons which convincingly evidence their deposition in situ. Fossil bones from various groups of mammals are found heaped up with no evident traces of selective deposition.

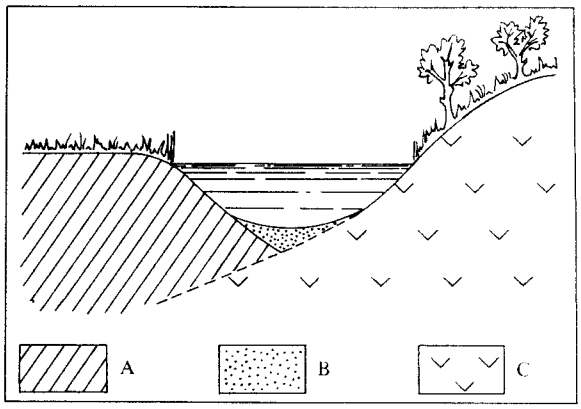


Fig. 2 - Attempt to restore the formations of location: a. dolerites; b. lake deposits; c. dacites.

The relation of bone-bearing deposits to doleritic lavas in Akhalkalaki is rather obscure. It seems to be a controversial point whether the lake deposits pass along the strike into the so called upper dolerites of the Akhalkalaki suite (fig. 2) or are underlain by them. The latter seems less probable, the petrographic analysis of lake deposits providing no evidence of dolerite in them.

In any case, the upper portion of the Akhalkalaki suite is dated to the Lower Pleistocene (The Bakinski layer) on the basis of evidence provided by the Akhalkalaki fauna. The Tsalka dolerites, accordingly, must obviously be referred to the Lower Pleistocene.

We will present some record of fossil mammals that throws light on the geologic age of effusives in the Dmanisi and Gomareti Plateaus. The occur-

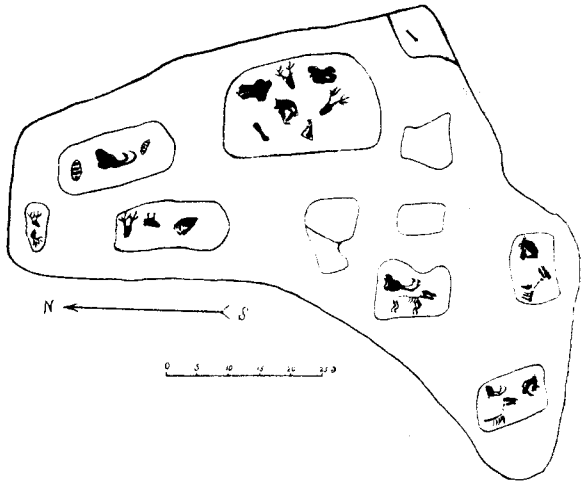


Fig. 3 - Plan of excavations of the Akhalkalaki location.

PLATE 2

1. *Canis tengisii* Vekua. Maxilla (dex.); 2.3. *Canis tengisii* Vekua. Mandibula; 4. *Canis tengisii* Vekua. Atlas; 5. *Canis tengisii* Vekua. Radius; 6. *Canis tengisii* Vekua. Metatarsalia

7. *Ursus* sp. M_3 (sin.); 8. *Ursus* sp. C; 9. *Ursus* sp. Mt II; 10. *Ursus* sp. Astragalus (sin.)

11. *Crocuta* cf. *sinensis* Zdan. Fragment of the P^4 (dex.); 12. *Crocuta* cf. *sinensis* Zdan. P^3 (dex.); 13. *Crocuta* cf. *sinensis* Zdan. Mandibula (sin.)

TABLE 1

The fauna of Akhalkalaki	Number of bones	Minimun number of individuals	% of bones
Erinaceus sp.	2	2	0,08
Lepus europaeus Pallas	7	2	0,28
Citellus aff. *citellus* L.	1	1	0,04
Marmota sp.	51	9	2,07
Canis tengisii Vekua	304	11	12,3
Crocuta cf. *sinensis* Zdan.	7	2	0,28
Ursus sp.	7	1	0,28
Vormela peregusna Güld.	1	1	0,04
Lutra cf. *lutra* L.	1	1	0,04
Meles meles L.	78	7	3,2
Panthera cf. *tigris* L.	5	1	0,2
Panthera sp.	1	1	0,04
Mammuthus aff. *trogontherii* Pohl.	27	9	1,1
Archidiskodon sp.	19	4	0,77
Equus süssenbornensis Wust	634	43	25,7
Equus hipparionoides Vekua	31	7	1,26
Dicerorhinus etruscus Falc.	6	2	0,24
Hippopotamus georgicus Vekua	19	1	0,77
Praemegaceros verticornis (Dawkins)	718	52	29,1
Sinoreas sp.	1	1	0,04
Capra sp.	24	8	0,97
Bos sp.	314	21	12,7
Bison sp.	211	12	8,5
	2469	199	100

rence of *Marmota* sp., *Panthera* f. *spelaea, Equus caballus* cf. *strictipes, Bos* cf. *primigenius, Cervus* cf. *elaphus, Megaloceros* sp., etc. has been traced in lake deposits interlaying the lavas of the Dmanisi Plateau (the locality of Upper Orozmani).

We maintain (Vekua, 1958) that the fauna in question provides sufficient evidence for dating the Dmanisi lake deposits and dolerites to the Middle or Upper Pleistocene.

The effusive lavas of the Dmanisi and Gomareti Plateaus are readily correlated and, thus, are obviously syncronous. Their Pleistocene age is evidenced by mammalian fossil remains found near the village of Akha (*Elephas* sp., *Equus caballus, Bos* sp., *Hyaena* sp.) and that of Zemo - Karabulakhi (*Bison pirscus, E. caballus, Ovis ophion, Asinus* sp., *Cervus elaphus*).

To sum up, we have arrived at the conclusion that the Akhalkalaki and Tsalka dolerites are coeval. The lower margin of these sequences may be approximately correlated with the bottom of the Apsheronian, the upper margin being comparable with the top of the Bakinski layer.

Presumably, the Dmanisi and Gomareti effusives are earlier than the Akhalkalaki dolerites. They can probably to be referred to the Middle Pleistocene or even Upper Pleistocene. Apparently all the previously mentioned effusives (those of Akhalkalaki, Gomareti, Tsalka, and Dmanisi) are products of one Upper Pliocene-Pleistocene phase of volcanic activity.

A BRIEF ACCOUNT OF THE AKHALKALAKI FAUNA

Over 4,000 fossil bones belonging to 21 mammalian species have been found in the bone-bearing layer of the Akhalkalaki locality. The fauna includes representatives of Insectivora, Rodentia, Carnivora, Proboscidea, Perissodactyla and Artiodactyla, Carnivora and Artiodactyla being represented with relative diversity.

PLATE 3

1. *Panthera* cf. *tigris* L. Mandibula (dex.); 2. *Panthera* cf. *tigris* L. C, P_3, P_4, M_1 (sin.); 3. *Panthera* cf. *tigris* L. Radius (dex.) 4. *Mammuthus* aff. *trogontherii* Pohl. Scaphoideum (sin.); 5. *Mammuthus* aff. *trogontherii* Pohl. Lunatum (sin.); 6. *Mammuthus* aff. *trogontherii* Pohl. Pyramidale (sin.)

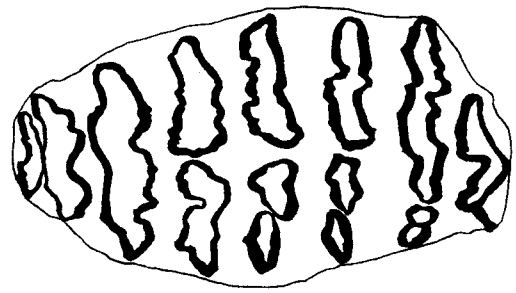


Fig. 6 - *Mammuthus* aff. *trogontherii* Pohl. DP.

Panthera sp.: the bone collection from the Akhalkalaki locality contains a superior half of a radius of a size undoubtedly larger than that of the radius of the Akhalkalaki tiger. Articular cavity wide, markedly concave, with a large incisura on the anterior surface; *epicondylus medialis* markedly thickened, with a downward bend; *tuberositas radii* forms an uneven platform; diaphysis of the bone flattened anterior-posteriously.

Proximal width - 44 mm;
proximal anterior-posterior - 28 mm;
width of diaphysis - 27 mm.

Definition of the status of this panther being hardly feasible on the basis of only a small fragment, it may have belonged to large cats of the Machairodontinae family, taking into consideration the size and the morphological characters of the proximal part of the radius.

PROBOSCIDEA. There has been no record of elephant teeth in Akhalkalaki (with the exception of DP^3), which makes it difficult to define the species. The DP^3 is slightly worn, and has eight plates (see fig. 6). The plate frequency (the number of plates for 10 cm) equals 9 to 10. The plane of wear is characteristic of *Archidiskodon*, though by the number and frequency of plates in DP^3, as well as by its size and the structure of limb bones the Akhalkalaki elephant may be related to *Mammuthus trogontherii*.

The faunal complex in Akhalkalaki also contains a series of manus bones (*pyramidale, lunatum, magnum, hamatum, metacarpalia* II, III, IV) found in anatomic articulation. Undoubtedly, it belongs to one individual. Garutt (1954) maintains that *Archidiskodon meridionalis* is characterized by a serial carpus while *M. trogontherii* and *M. primigenius* show an aserial carpus. The elephant manus from Akhalkalaki having a serial carpus, we tentatively related these remains to *Archidiskodon* sp.

PERISSODACTYLA. More than a half of the Akhalkalaki collection belongs to Perissodactyla. The presence of *Dicerorhinus etruscus, Equus süssenbornensis* and *E. hipparionoides* has been established here.

Dicerorhinus etruscus Falc. is represented but scarcely (DP^4, radius, ulna, Mc II, astragalus, Mt III), but the structure of the deciduous tooth and the metapodium shows that it can be with certainly identified with *D. etruscus* (fig. 7).

The record of *D. etruscus* in Transcaucasia is scarce, particularly in Quaternary beds. It is believed to have been a Tertiary relict in this region.

Equus süssenbornensis Wüst is represented abundantly by bones and teeth (see fig. 8, 9). The structure of molars and premolars (a relatively short protocome, a sharpened mesostyle, a double loop of stenonous type, etc.) as well as their large size are convincing evidence of their *Eq. süssenbornensis* relationship.

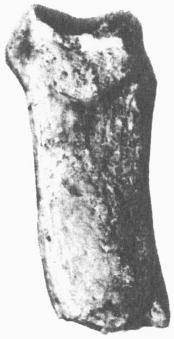
Eq. süssenbornensis of Akhalkalaki shows the following distinctive features: (1) a strongly pronunced parastylid and hypostylid on lower cheek milk teeth (fig. 8b); (2) a feebly pronounced parastylid on *dens permanens* and DP_1 on the mandible.

Equus hipparionoides Vekua is probably the most intersting form among the mammals of Akhalkalaki. The collected material (upper maxilla with P^4 - M^3, a complete row of lower cheek molars and premolars, metapodium, astragalus) affords a reliable ground for distinguishing a distinct species of *Equus* (fig. 10). Its most typical features are revealed in dental characters. The upper cheek molars and premolars are of medium size, enamel thin and strongly plicated, an exceptionally short protocone of peculiar shape, and a strikingly long calcar on p^4. There is a duble loop of *Eq. stenonis* type on lower cheek molars and premolars with symmetrical metoconid and metastylid and a deep lingual sinus.

PLATE 6

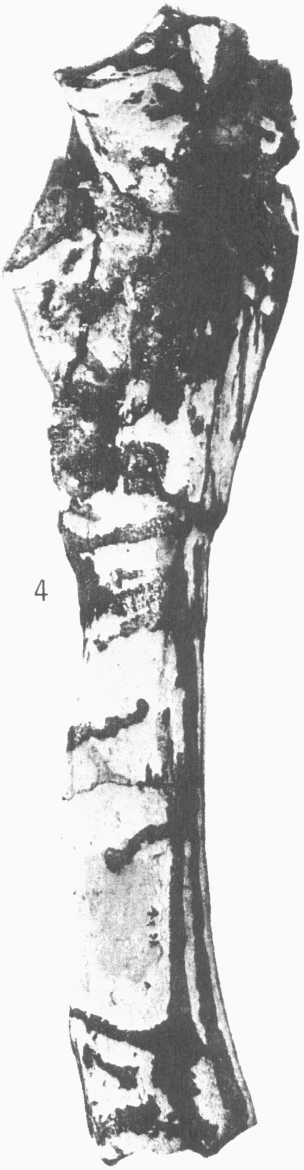
1. *Diserorhinus* cf. *etruscus* Falc. DP^3 or DP^4; 2. *Dicerorhinus* cf. *etruscus* Falc. Mc II (dex.); 3. *Dicerorhinus* cf. *etruscus* Falc. Mt III (sin.); 4. *Dicerorhinus* cf. *etruscus* Falc. Ulna (dex.); 5. *Dicerorhinus* cf. *etruscus* Falc. Humerus (sin.); 6. *Dicerorhinus* cf. *etruscus* Falc. Astragalus (sin.)

1

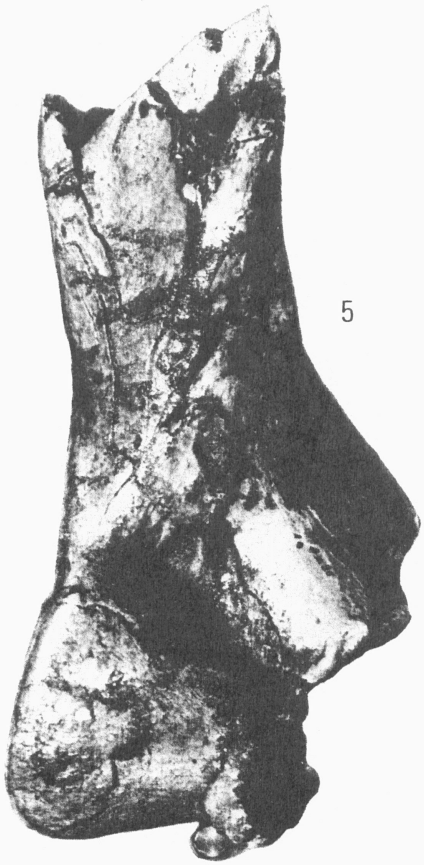


2

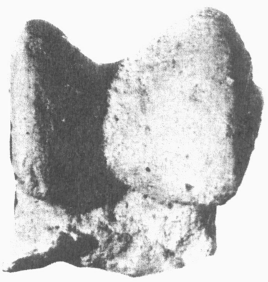
3



4



5



6

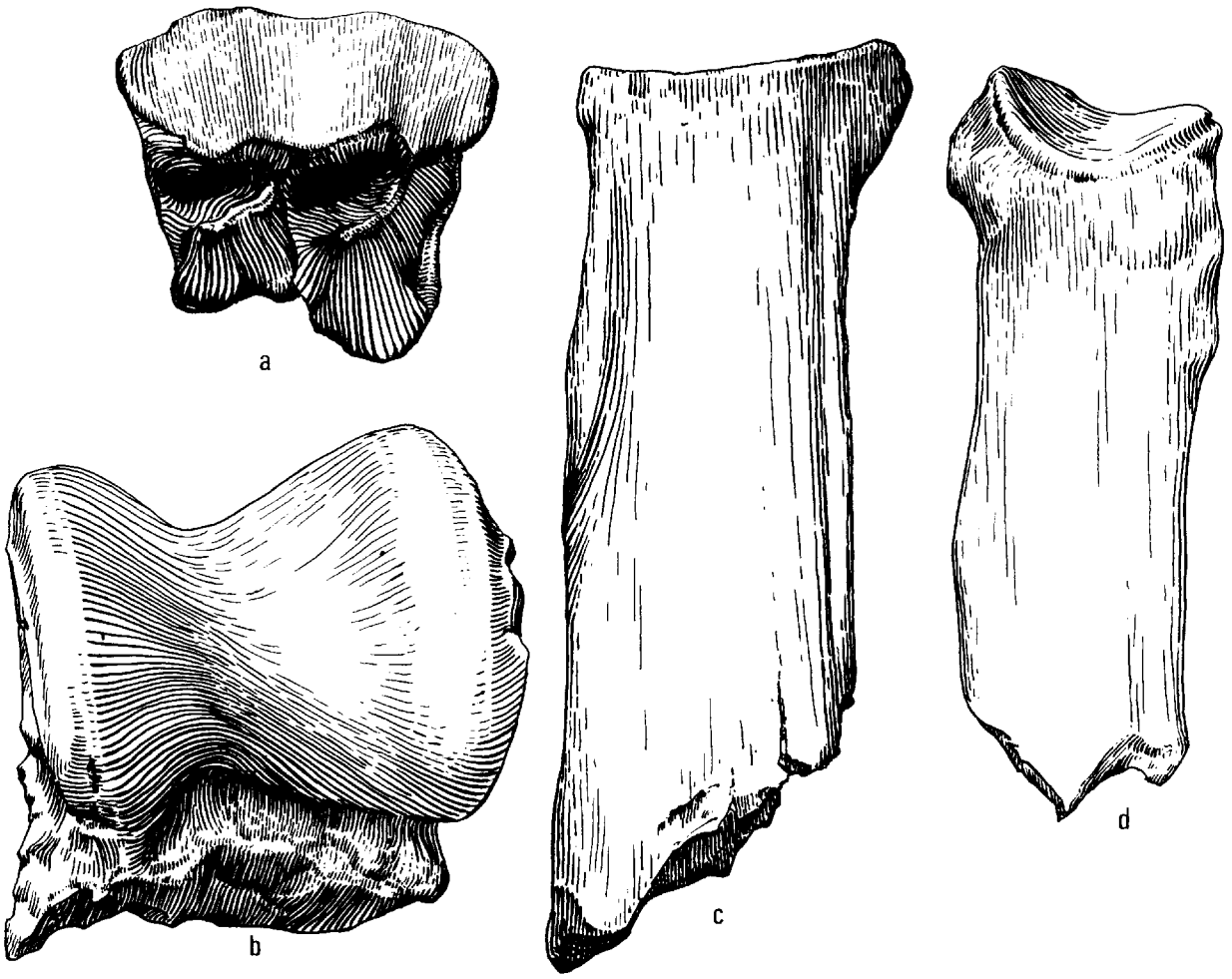


Fig. 7 - *Dicerorhinus* cf. *etruscus* Falc.: a. DP^4; b. Astragalus; c. Mt III; d. Mc II.

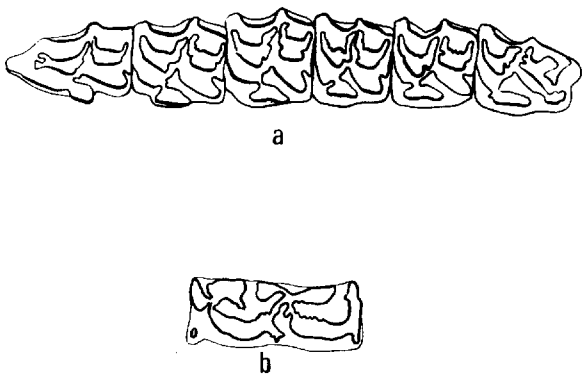


Fig. 8 - *Equus süssenbornensis* Wüst.: a. P^2 - M^3; b. DP_3.

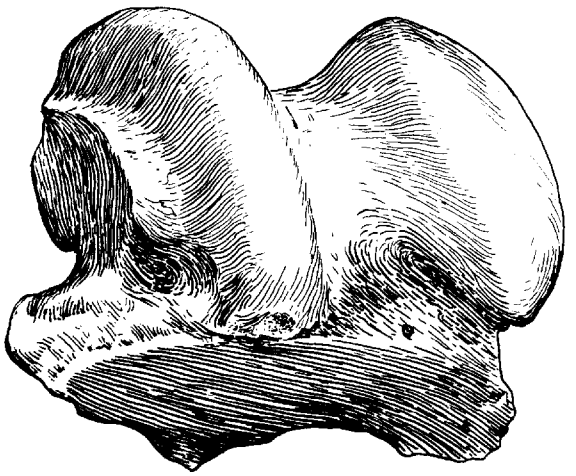


Fig. 9 - *Equus süssenbornensis* Wüst.: Astragalus.

SOME ECOLOGIC CHARACTERISTICS OF THE AKHALKALAKI FAUNA

Rodents in the Akhalkalaki fauna are represented chiefly by the inhabitants of xerophytic landscapes (gropher, marmot), thus evidencing dry and warm climate in the region.

Carnivores in Akhalkalaki are represented by thermophilic forms, characteristic of steppe and semi-steppe landscapes. In particular, the record of *Vormela* cf. *peregusna, Panthera* cf. *tigris, Canis tengisii,* a.o. testifies rather in favour of the prevalence of xerophytic conditions.

In making an attempt to reconstruct the habitat of the Akhalkalaki fauna, it is only natural that we should devote special consideration to perissodactyls which show the widest representation in the faunal complex we are describing. Bone and tooth remains of perissodactyls account for 34% (horse bones and teeth amounting to 33%) of the total number of fossil remains in Akhalkalaki.

It is common knowledge that horses, being the inhabitants of open spaces, show good adaptation to steppe conditions. The same holds true of *Equus süssenbornensis* whose record is most frequently found in complexes with a steppe habit. The other form *Equus hipparionoides,* apparently, was even better adapted to fast trot and coarse fare, this being testified by the slenderness of limbs and possibly, the pattern of tooth folding.

Dicerorhinus etruscus, another representative of perissodactyls in the Akhalkalaki fauna, is quite frequent in upper Pliocene and Lower Pleistocene steppe faunas, due to which fact it is often named «steppe rhinoceros».

Neither do the characteristics of artiodactyls found in Akhalkalaki contradict the hypothesis of the steppe character of the Akhalkalaki fauna.

The question of habitat of the Akhalkalaki hippopotamus needs to be considered separately. The clear evidence of the hippopotamus in Akhalkalaki might seem to indicate humid climatic conditions at the time when the burial of the faunal remains under consideration took place. It must be noted, however, that such assumptions do not always agree with the overall paleontological data on faunal complexes.

Fossil hippopotami are rather frequent in associations of forms more characteristic of steppe landscapes. In particular, hippopotamus remains were recorded in some localities in Italy (Sala, 1977), Germany (Adam, 1954; Kalke, 1954), the steppe element being obviously prevalent in these faunal complexes.

Abundant record of hippopotamus bones is known from Palestine, where it was found amidst the kitchen waste in artifact-bearing beds of the Paleolithic. Bate (1937), who studied this paleontological material, arrived at the conclusion that the climate must have been warm and dry there in the Paleolithic.

Hence, it is assumed that some representatives of fossil Hippopotamidae could live in relatively arid climatic conditions as well. We maintain that the Akhalkalaki hippopotamus, like the living *Choeropsis liberiensis,* was to a certain extent a land animal, evolving in this direction even farther than the Liberian specimen.

The fruit record of xerophytic plants (*Lithospermum arvense* L., *Celtis glabrata* Stev.) in the Akhalkalaki bone-bearing lacustrine beds provides good evidence of the presence of a xerophytic landscape in the area of the burial of the Akhalkalaki fauna in the lower Pleistocene.

Finally, the occurrence of shells from xerophile, thermophilic terrestrial molluscs [*Iaminia pupoides* Kryn, and *Helicella (Xeropicta) derbentina* Kryn.], which inhabit the contemporaneous steppe and semidesert in anterior Asia and Transcaucasia, should be noted in the Akhalkalaki lacustrine beds.

In the whole, the data obtained provide convincing evidence of steppe landscapes with dry and warm climate in the south of Georgia in the lower Pleistocene, conducive to the formation of biocoenoses, whose representatives are found in the Akhalkalaki complex.

Apparently, the xerophytic landscape was not quite frequent throughout Transcaucasia, as well as in the adjoining areas of Asia in the early Pleistocene. The conditions of this landscape in the

above mentioned period of time are assumed to predominate in the Armenian highland (Vereshchagin, 1959), Iran (Coon, 1951), Palestine (Bate, 1937), Turkey (Fyüron, 1955), etc.

Some environmental changes are observed in the Middle Pleistocene period that, apparently, manifested themselves in a relative temperature fall and in increased humidity of the climate. Orogenetic processes and frequent volcanic eruptions occurring in eastern Georgia and neighbouring regions early in the Anthropogen were probably also conducive to the changing of paleogeographical situation. The presence in the Dmanisi fauna (Middle Pleistocene) of a fallow-deer, a stag, a primitive bull, etc. bears convincing evidence of the afforestation in the Middle Pleistocene of that region in Georgia which in the Lower Pleistocene was inhabited by the representatives of the Akhalkalaki complex.

The relative fall in temperature could have been but a weak echo of plan glaciation. However, it does not seem to have been as significant as to cause the replacement of a thermophile fauna by a cold-enduring one.

Georgia was inhabited by monkeys at that time (Vereshchagin, 1959), and Paleolithic men lived in mountain caves 2,000 m above the sea level (South Ossetia) throughout Acheulian-Mousterian and later, which would hardly be possible under low temperature conditions.

ON THE GEOLOGIC AGE OF THE AKHALKALAKI FAUNA

Precise age determination of the Akhalkalaki fauna is very important not only for the dating of the bone-bearing lacustrine deposits and younger effusives that are widely developed in southern Georgia, but also for the elucidation of some key phases in the history of the development of Quaternary mammals in Transcaucasia. It is with this aim in view that we undertook a biostratigraphical correlational analysis of the Akhalkalaki mammalian fauna and the recorded Pleistocene faunal complexes in Europe and Asia.

The list of the Akhalkalaki fauna previously presented shows that both its representatives such as *M. trogontherii, E. süssenbernensis, D. etruscus, Hippopotamus georgicus* and the faunal complex in general rather testify in favour of its lower Pleistocene age and, accordingly, allow us to assess the age of the Akhalkalaki lacustrine beds containing the faunal remains to the Lower Pleistocene.

The dating of the Akhalkalaki lacustrine deposits to the early Pleistocene provides an opportunity to attempt a tentative age estimate of the upper doleritic sheet of the Akhalkalaki suite which possibly underlies the bone bearing beds. The doleritic sheet is either relatively older than the Lower Pleistocene lacustrine beds or, more likely, they are coeval, as the presence of a Lower Quaternary lake in the Akhalkalaki locality is most probably connected with the last eruption of volcanic lava in the region under discussion.

In contrast with the Pleistocene faunas in Eurasia that supply good material for correlation, the Akhalkalaki fauna, containing several identical species occurring in all the faunas under analysis, shows at the same time peculiar forms that complicate stratigraphic correlation. However, the presence of some basic parallel features in the Akhalkalaki fauna and some European Lower Pleistocene complexes convincingly supports our hypothesis concerning its Lower Pleistocene age.

Of all recorded Pleistocene faunas in the European part of the Soviet Union the Taman faunal complex reveals closest similarity to the Akhalkalaki. Identical forms, occurring in both faunas, are characteristic representatives of the early Pleistocene - *M. trogontherii, E. süssenbornensis, D. etruscus*. The similarity of these two faunas becomes even more obvious if the presence in both these complexes of gigantic deer and a peculiar type of small dog is mentioned.

Some differences that are observed in the process of correlation may be accounted for by environmental peculiarities in the habitat of their representatives. Thus, the evidence of a camel in the Taman fauna is justly qualified by Vereshchagin (1957) as an indication of proximity to desert or semidesert landscapes. At the same time, steppe and semi-steppe conditions were likely to prevail in the South of Georgia, as indicated by the character of the Akhalkalaki fauna.

We will not hold to the conventional view that the Taman fauna should be dated to the Pliocene on the basis of its correlation with the faunas of Valdarno and Khapry. Suffice it to say, that the abundance in the Valdarno locality of remains related to *Mastodon, Archidiskodon meridionalis, Machairodus, Tapir* and *Equus stenonis* provides incontrovertible evidence that the fauna belongs to an older period. The occurrence in Khapry of *Mastodon, Machairodus, Hipparion, Equus stenonis* and *Protelephas planifrons*, we believe, likewise makes it impossible to correlate the Khapry and Taman faunas. The latter has no record of *Mastodon*, the role of *Archidiskodon meridionalis* is reduced by the appearance of *Mammuthus trogontherii. Equus stenonis* is succeded by the vicarian and more progressive *Equus süssenbornensis*; invariable members of Pleistocene complexes such as gigantic deer and elks emerge. Thus, we fully agree with the scholars who stratigraphically place the Taman fauna higher than the faunas of Khapry and Psekups, referring it to the Lower Pleistocene.

The Tiraspol fauna also shows some affinity to the Akhalkalaki one, though it is seemingly younger than the Akhalkalaki and Taman faunas.

We will also mention the similarity that the Akhalkalaki fauna bears to that of Koshkurgan (the Kazakh SSR), though some of the representatives of the latter are characteristic of a later period.

Unfortunately, it is impossible to compare the Akhalkalaki fauna with the Leninakan fauna of Armenia (Avakyan, 1959), territorially proximal to

the former, as it contains forms that are obviously not coeval.

No other Lower Pleistocene faunas have been recorded in the Soviet Union, though some independent evidence witnesses a prominent development of the Taman type fauna, at least in the Caucasus.

The identity of forms characteristic of the early Pleistocene should be viewed as a major specific feature of faunas we are describing, the differences being chiefly connected with the presence of endemic forms in some of the Pleistocene complexes. The latter feature is particularly observable in the Akhalkalaki fauna, which is evidently due to a relative zoogeographical isolation of Transcaucasia in the earliest Anthropogen that caused some environmental conservatism.

A number of characteristics representatives in the Akhalkalaki fauna, with no doubt, testify its affinity to the recorded early Pleistocene faunas of Western Europe. They are the faunas of Forest Bed, Norfolk, partly Norwich Crag (Great Britain), Tegelen (Holland), Abbeville and Somme (France), Süssenborn, Mosbach and Iockgrim (Germany), Ponte Galeria (Italy), etc.

All the above listed faunas have the following identical forms; *Mammuthus trogontherii, E. süssenbornensis* or allied species, *Dicerorhinus etruscus, Praemegaceros verticornis,* some Carnivora and, possibly, *Trogontherium* sp.

The Akhalkalaki fauna also shows relative similarity with the Asiatic Lower Pleistocene complexes, such as the most commonly known faunas of Choukoutien (China), Boulder Conglomerates of Siwalik (India) and Narbada (Burma), that contain several forms characteristic of the Lower Pliocene (*Equus namadicus, Hippopotamus sivalensis, Palaeoloxodon namadicus,* etc.).

Unfortunately, no sufficient record of a Lower Pleistocene fauna in anterior Asia has been known up to now. We maintain, however, that it is from this region that some Asiatic forms, particularly the hippopotamus, are most likely to have penetrated into Transcaucasia.

With some degree of tentativeness the Akhalkalaki fauna could be compared with that of Kamisli (Anatolia), which contains *Canis etruscus, Panthera* sp., *Hyaena* sp., *Hystrix* sp., *Eucladoceros* sp., *Spiroceros* sp., *Bison* sp., *Equus stenonis* sp. (Sickenberg & Tobien, 1971).

The evidence of *Eq. stenonis* in this fauna rather disagrees with its general character, and it may be that some additional data will testify its relation to a more progressive grade of evolution of Equinae.

Apparently, an Asiatic element plays a dominant role in the early Pleistocene mammalian fauna of Transcaucasia, this being evidenced by the fact that in the Akhalkalaki fauna *Hippopotamus, Crocuta, Panthera, Vormela,* etc. are quite abundant. The picture is, evidently, different in the Middle Pleistocene. Asiatic forms either

TABLE 3

Canis tengisii Vekua

Maxilla	
Length prosthion - M^2	107,3
Length C - M^1	86
» P^1 - M^2	72,3
» P^1 - P^4	56
» M^1 - M^2	21
» P^4	22
Mandibula	
Height on the level M_1	23,0
Length C - M_3	93
» P_1 - M_3	80
» P_1 - P_4	42,1
» M_1 - M_3	38
» M_3	5
Humerus	
Distal width	31,9
Distal antero—posterior	24,3
Radius	
Distal width	23,9
Distal antero—posterior	14
Tibia	
Proximal width	30
Distal width	20,1
Distal antero—posterior	15,2
Astragalus	
Total length	24-27,4
Width	16,5-18
Calcaneus	
Length	43,5
Width	15,5
Metacarpale	
Length Mc II	61,5
» Mc III	65
» Mc IV	65
» Mc V	56,4
Metatarsale	
Total width	22,3
Length Mt II	67,1
» Mt III	74,3
» Mt IV	75,8
» Mt V	69,8

TABLE 4

	Meles cf. *meles* Akhalkalaki	*Meles meles* recent n-7
Cranium		
Total length	125	117-128
Width on the level bulla tympani	59	57-61
Height on the level bulla tympani	47	45-49
Length C - M^1	41	37-40,5
Length P^4	8,3	7-9
Width P^4	7,5	7,5-9
Length M^1	14	12-15,2
Width M^1	12	10-12
Mandibula		
Height on the level M_1	14-15,2	13-16,1
Length P_2 - M_2	38-39,2	37-41,5
Length M_1	14,9-15,9	16,1-18,3
Width M_1	6,2-6,9	7,1-8,3

TABLE 5

Upper teeth		1	2	3
Length P^2 - M^3		195-200	—	—
Length P^2 - P^4		104-110	—	—
Length M^1 - M^3		90-94	81,9	—
P^2	length	42-49	—	45
	length	32-38	—	35; 36
P^3	length protocone	12-14	—	13-14
	index protocone	35,1-37,5	—	37,1; 38,9
	length	31-33,5	29,1	32-36
P^4	length protocone	12,3-13,6	6,8	11,5-15
	index protocone	38,4-45	23,4	35,9-42,5
	length	26-32	25,8	30-32
M^1	length protocone	11-13,3	6,0	11-12
	index protocone	37,5-42,9	23,3	34,4-39,3
	length	29-33	27,1	31
M^2	length protocone	13-14,6	7,5	13
	index protocone	40-48,2	27,7	41,9
	length	35,5-38	28,3	29-32
M^3	length protocone	15-18	9,5	14,5; 14
	index protocone	40,6-44,4	36,5	50; 43,8
Molar-premolar index		86,5-87	—	—

1. *Equus süssenbornensis* (Akhalkalaki); 2. *Equus hipparionoides* (Akhalkalaki); 3. *Equus süssenbornensis* (Süssenborn, Gromova, 1949).

gradually retreat to the south to be replaced by those from Western Europe or become extinct (*Hippopotamus*). Evidence of this is found in the composition of faunas in Georgia and throughout Transcaucasia, that obviously date to later time.

ON THE CAUSES OF DEATH OF THE AKHALKALAKI MAMMALS

The question concerning the causes of what obviously must be qualified as a mass death of the

TABLE 6

Lower teeth	1	2	3	4	5
Length P_2 - M_3	204-212	193	—	—	—
Length P_2 - P_4	103-112	98,5	—	—	—
Length M_1 - M_3	96,1-101	95	—	—	—
Length					
P_2	39-43	35,7	30-44	43	32,5
P_3	33-36	32	30-35	35	31
P_4	30-36	30,2	27-35	35	—
M_1	28-32	29,5	26-32	32	30
M_2	30-34	28,8	30-33	32	32
M_3	38-44	37	—	35,5	—
Molar-premolar index	86,5-91,6	95,8	—	—	—

1. *Equus süssenbornensis* (Akhalkalaki); 2. *Equus hipparionoides* (Akhalkalaki); 3. *Eq.* aff. *süssenbornensis* (Tiraspol, Gromova and Dubrovo, 1971); 4. *Eq.* aff. *süssenbornensis* (Süssenborn, Gromova, 1949); 5. *Eq.* cf. *süssenbornensis* (Taman, Vereshchagin, 1957).

TABLE 7

	1	2	3	4
Mc				
Total length	260-286	239	233	242,5-258,5
Proximal width	63-69	53; 58	—	51,5-59
Proximal antero-posterior	41-47	53; 36	—	36,2-39?
Distal width (tubercula)	58-62	47; 46	—	50?-55,5
Distal width (articulation)	57-61	46; 47	—	39-40,7
Shaft width	41-46	32; 33	33,4	39-40,7
Mt				
Total length	303-323	293	—	290-307
Proximal width	57-62	47	—	51,3-60
Proximal antero-posterior	50-55	46	—	48
Distal width (tubercula)	58-63	42; 48	—	51,5-56
Distal width (articulation)	58-62	43; 48	—	49-58,9
Shaft width	39-42	30	33,5	36,4-44

1. *Equus süssenbornensis* (Akhalkalaki); 2. *Eq. hipparionoides* (Akhalkalaki); 3. *Eq.* cf. *süssenbornensis* (Taman, Vereshchagin, 1957); 4. *Eq.* aff. *süssenbornensis* (Tiraspol, Gromova and Dubrovo, 1971).

Pleistocene animals buried near Akhalkalaki is rather obscure.

The extreme scarcity of complete skeletons in the locality as well as the conglomeration of separate bones heaped up with no visible order definitely indicates the absence of any catastrophal causes that brought about the death of the Akhalkalaki mammals (fig. 3). It is assumed that one of the most probable causes of animal death there was frequent eruption of volcanic lava that covered almost all southern and south-eastern Georgia in Late Pliocene and Early Pleistocene times. A prominent development of lava sheet evidently brought about rapid diminishment of grassland and reduction of reservoirs containing potable water. It is only natural that under such environmental conditions the animals accumulated in the areas not yet affected by volcanic activity; hence, a far wider than usual spread of epidemic, famine and the extermination of animals by carnivores.

Our view of the history of the Akhalkalaki locality is as follows. Obviously, the animals with few exceptions died on the foreshore and were then carried away to the lake by torrential streams. The carcasses were seemingly transported after maceration, the assumption being supported specifically by the fact that the bone-bearing lenses contain for the most part limb bones which are known to separate from the dead body earlier than other parts of the skeleton. The evidence of teeth belonging to carnivores and rodents on the bones may also be helpful in supporting our hypothesis.

As it was previously mentioned, the Akalkalaki collection does not contain even one complete skull of a larger mammal. This may be partly due to

TABLE 8

	1	2	3	4	5	6	7	8
Mc II								
Length	139	—	130	—	145	—	—	60
Proximal width	48	—	35; 38	—	29	—	—	17
Proximal antero-posterior	50	—	43-46	—	43	—	—	17
Shaft width	43	—	36-39	—	31	—	—	17
Shaft antero-posterior	32	—	24-28	—	25	—	—	11
Distal width	52	—	38-41	—	38	—	—	20
Distal antero-posterior	49	—	37-41	—	37	—	—	18
Mc III								
Length	170,4	160	163	170	—	—	—	—
Proximal width	63,2	59	45-64	65	—	—	—	—
Distal width	56,1	47-48	40-50	60	—	—	—	—
Length Mc III correlated length Mc IV	120,8	113,4	115,8	120	—	—	—	—
Mc IV								
Length	141	141	142	141	—	—	—	—
Proximal width	61	55	47-59	70	—	—	—	—
Shaft width	50	46	39-48	53	—	—	—	—
Distal width	46,2	—	35,5	51	33	—	—	—
Mc IV								
Length	110	106	110	101	—	—	—	—
Proximal width	50	43	36; 41	37	—	—	—	—
Distal width	54	39	49	48	—	—	—	—
I phalanx of the third finger								
Length	69	60	59-69	—	62	—	—	43
Proximal width	58	48	44-54	—	40	35	—	27
Proximal antero-posterior	43	—	33-44	—	30	—	—	19
Distal width	51	42	37-46	—	33	—	—	23
Distal antero-posterior	22,9	—	21-36	—	21	—	—	14
Shaft width	42	—	32-43	—	31	—	—	21
Astragalus								
Medial height	99,6	95	81-86	—	—	75	114	—
Lateral height	110,8	—	84-90	138	75-85	90	—	53
Sagittal height	105,2	—	82-86	—	69-82	78	—	50
Proximal width	100,8	97-101	81-85	108-123	—	65	120	—
Distal width	70	83-93	77-79	103-116	64	66	115	40

1. *Hippopotamus georgicus* (Akhalkalaki, Vekua, 1962); 2. *H. antiquus* (Oberheim, Kuss, 1957); 3. *H. amphibius* (recent); 4. *H. major* (Val d'Arno, Faure, 1980); 5. *H. sivalensis* (Siwaliks, Hoojer, 1950); 6. *H. hipponensis* (Stromer, 1914); 7. *Hippopotamus* sp. (Issoire, Kuss, 1957); 8. *Choeropsis liberiensis* (recent, Hoojer, 1950).

the fact that the skulls of these mammals, being fairly heavy, remained for quite a long time at the place of the animal's death, were subjected to weathering and gradually decayed, thus reaching the place of the burial in fragmentary form.

It is possible that the skulls and bulky parts of skeletons belonging to larger mammals were buried elsewhere, i.e. nearer to the shore, whereas separate bones and teeth as well as other minor parts were carried farther into the lake. It is quite possible, too, that the main faunal locality in Akalkalaki has no been uncovered yet; in fact, it is still to be discovered.

The animal bones in the Akalkalaki locality are found in lenslike assemblages throughout the height of lacustrine beds. The remains are of milky colour, well fossilized. The bones are neither rounded, nor do they bear any traces of human agency, though the archeological material (Vekua & Gabunia, 1984) provided some evidence to the effect that the Akalkalaki plateau was widely populated by Paleolithic men. Bones bearing the traces of being gnawed by carnivores and rodents are fairly abundant. The horse phalanx (fig. 14) bears visible traces of the incisors belonging to a large rodent, most likely *Hystrix* or *Castor*.

TABLE 9

	1	2	3	4	5
M c					
Total length	352-355	342	—	—	—
Proximal width	54-60	71	68	—	—
Proximal antero-posterior	43-47	45	48	—	—
Shaft width	33-35	43	42	—	—
Shafth antero-posterior	35-40	43	41	—	—
Distal width	59-64	76	74	—	—
Distal antero-posterior	39-40	48	47	—	—
M t					
Total length	371-379	—	—	365	342
Proximal width	47-54	64	56	65	57
Proximal antero-posterior	51-63	58	59	66	57
Shaft width	28-33	39	37	40	36
Shaft antero-posterior	37-40	48	42	45	32
Distal width	56-65	74,5	68	72	66
Distal antero-posterior	36-42	47	42	47	42

1. *Praemegaceros verticornis* (Akhalkalaki, Vekua, 1962); 2. *Megaceros hibernicus* (Cherski, 1891); 3. *Megaloceros* sp. (East Georgia); 4. *Megaloceros giganteus* (West Georgia); 5. *Megaloceros giganteus* (Azerbajan).

The recorded of *Lutra* remains in the locality points out to the presence of a river, abundant in fish, early in the Pleistocene, fish being the major food for *Lutra*.

CONCLUSIONS

To sum up the Akalkalaki faunal evidence previously described, we would like to note that the faunal complex in general corresponds, without a doubt, to the initial grade of development of the Quaternary mammalian fauna in Eurasia and is dated to the Lower Pleistocene. Accordingly, the bone-bearing beds and the upper dolerites of Akalkalaki should likewise be placed in the Lower Pleistocene.

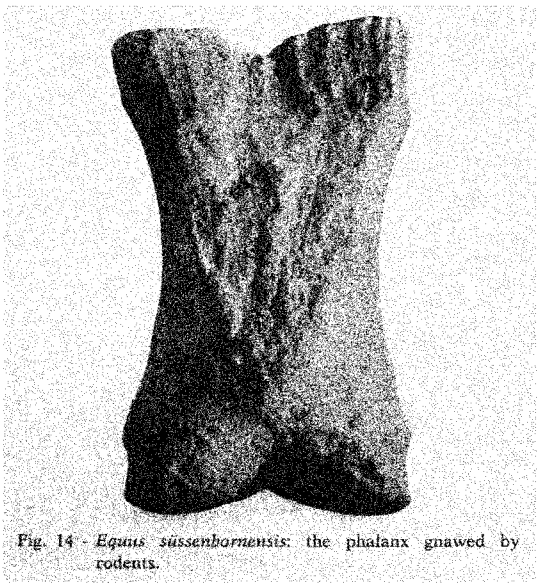


Fig. 14 - *Equus süssenbornensis*: the phalanx gnawed by rodents.

Faunal complexes bearing similarity with the Akalkalaki one in composition and age are recorded in Taman (Vereshschagin, 1954), Moldavia (David, 1969, Gromova *et al.*, 1971), Armenia (Avakyan, 1959), Kazakhstan (Kozhamkulova, 1974), etc.

In central and western Europe localities containing faunas of the Akalkalaki type are relatively frequent. These are the localities of Forest Bed, Norfolk, and, partly, Norwich Crag in Great Britain (Azzaroli, 1953; Zeuner, 1969), Abbeville and Somme in France (Zeuner, 1963), Süssenborn, Mosbach, Mauer, etc. in Germany (Adam, 1964; Kahlke, 1954, 1961), Ponte Galeria and possibly Slivia in Italy (Azzaroli & Ambrosetti 1972; Ambrosetti *et al.*, 1979).

In Asia the faunas bearing closest similarity to that of Akalkalaki are recorded from the localities of Choukoutien in China (Pei, 1936; Young, 1959), Kamisli in Turkey (Sickenberg, Tobien, 1972), etc.

The Akalkalaki faunal complex is chiefly represented by the steppe and semi-steppe dwellers which provide evidence of the predominance in southern Georgia of an open landscape with ephemeral impounded bodies at places abundant in coastal brushwood. The climate is most likely to have been moderately hot and dry.

Some environmental changes observable by the Middle Pleistocene obviously manifested themselves in a relative temperature fall and in-

creased humidity of the climate. The record of a fallow-deer, a stag, a primitive bull and other forestal forms undoubtedly testifies the afforestation of that region of Georgia, which in the Lower Pleistocene was inhabited by the representatives of the Akalkalaki fauna.

Later in the Pleistocene physicogeographical conditions changed again to the increasing aridity of the environment.

Analysis of the faunas from Zurtaketi, Tsopi and Dmanisi as well as the material provided by palinology testify to the conditions of a relatively dry and moderately warm climate in eastern Georgia late in the Pleistocene.

REFERENCES

1. Adam K.D. (1954): Die mittelpleistocänen Faunen von Steinheim an der Murr. *Quaternaria*, 1, 131-144.
2. Adamia Sh. (1960): The geology of the postneogen continental formations of the eastern part of South Georgia (in russian). *Works of the Institute of Geology*, 6, 24-68, Tbilisi.
3. Ambrosetti P., Bartolomei G., De Giuli C., Ficcarelli G., Torre D. (1979): La breccia ossifera di Slivia (Aurisina-Sistiana) nel Carso di Trieste. *Boll. Soc. Pal. It.*, 18 (2), 207-219, 4 figs.
4. Avakian L.A. (1959): The Quaternary fossil mammals of Armenia (in russian). 66 pp., 12 pls.. Erevan.
5. Azzaroli A. (1953): The Deer of the Weybourn Crag and Forest Bed of Norfolk. *Bull. British Museum, Natur. Hist., Geol.*, 2 (1), 1-96, 50 figs.
6. Azzaroli A., Ambrosetti P. (1972): Late Villafranchian and early Pleistocene faunas of Italy (in russian). In: The geology and fauna of lower and middle Pleistocene of Europe, 40-45, Moscow.
7. Bate D.M. (1973): The fossil fauna of the Wad-el-Mugahara Caves. In: The Stone Age of the Mount Carmel., 135-240.
8. Bazanov V.S. (1948): Contemporary distribution and history of the big suslik (in russian). *Bulletin of the Academy of Sciences of Kazakhstan SSR, Zool. Ser.*, 8, 113-117.
9. Birulya A. (1930): Note sur les metacarpiens et metatarsiens de l'ours des cavernes (in russian). *Proceedings of the Academy of Sciences of USSR*, 655-658.
10. Burchak-Abramocich I.N.Y. (1951): The ancient elephant (Elephas planifrons Falc.) and near forms in Transcaucasia (in russian). *Bulletin of the Academy of Sciences of the Azerbaijan SSR*, 75-81.
11. Cherski I.D. (1891): Description of the collection of the Late Tertiary mammals (in russian). *Notes of the Imperial Academy of Sciences*, 65, 1-706, 6 pls.
12. Coon C.S. (1951): Cave explorations in Iran. *Philad. Univ. Museum, Univ. of Pennsylvania*, 125 pp., Philadelphia.
13. Dal S.K. (1948): The vertebrates of the Pampak mountains ridge (in russian). *Zool. Articles, Academy of Sciences of Armenia SSR*, 5, 5-68.
14. David A. (1969): The mammals of the early anthropogen of Moldavia (in russian). *Bulletin of the Academy of Sciences of Moldavia SSR, Biol. Ser.*, 2, 18-41, 11 pls.
15. Faure M. (1980): Introduction a l'étude des Hippopotamidae (Mammalia, Arctiodactyla) Neogenes et Quaternaires d'Europe Occidental. 150 pp., Lyon.
16. Faure M. (1982): Les Hippopotames fossiles de la region d'Issoire. *Rev. Sc. Nat. d'Auvergne*, 48, 11-21, 3 pl.
17. Furon R. (1955): Introduction to geology and hydro-geology of Turkey (in russian). 142 pp., Edn. For. Lit., Moskow.
18. Garutt V.E. (1954): The South elephant Archidiskodon meridionalis (Nesti) from the Pliocene of the Northern coast of the Sea of Azov (in russian). *Works of the Committee on Investigations of the Quaternary Period*, 10 (2), 5-71, 33 figs.
19. Gromova V.I. (1948): The palaeontologic and archaeologic grounds of stratigraphy of the continental deposits of Quaternary Period in the territory of SSSR (in russian). *Works of the Institut of Geologic Sciences of the Academy of SSSR*, 64, 520 pp., Moscow.
20. Gromova V.I. (1949): The history of the hourses (gen. Equus) in the Old World, Part I (in russian). *Works of the Institute of Paleontology*, 17 (1), 3-373, 53 figs., 8 pls., Moscow.
21. Gromova V.I., Dubrovo I.A. (1971): Fam. Equidae (in russian). In: Pleistocene of Tiraspol, 108-124, fig. 43-50, Kichinev.
22. Hodjer D.A. (1950): The fossil Hippopotamidae of Asia, with notes on the recent species. *Zoologische Verhandelingen*, 8, 124 pp., 5 figs., 22 pls.
23. Kahlke H.D. (1954): Die Fauna der altpleistozänen Ilmkiese von Süssenborn bei Weimar. *Urania*, 17 (4), 141-146, Jena.
24. Kahlke H.D. (1961): Revision des Saugetierfaunen der klassischen deutschen Pleistozan. Fundstellen von Süssenborn, Mosbach und Taubach. *Geol. Jg.*, B, 10, 373-596, 7 pls., Berlin.
25. Kozamkulova B.S. (1974): The Koshkurgan fauna of Novoilemsk (in russian). *Collection of questions on the Geography of Kazakhstan*, 16, 31-41, Alma-Ata.
26. Krishnan M.S. (1954): The Geology of India and Burma (in russian). 105 pp., Moscow.
27. Kuss E. (1957): Altpleistozane Reste des Hippopotamus antiquus Desmarest vom Oberrein. *Jh. Geol. Landesamt Baden-Wurttenberg*, 1957 (2), 299-331, fig. 40-45, pl. 8-9.
28. Pei Wen Chung (1936): The mammalian remains from locality 3 at Choukoutien. *Pal. Sinica*, Ser. C, 7 (5).
29. Picard L. (1937): Inferences on the problem of the Pleistocene climate of Palestina and Syria drawn from flora, fauna and stratigraphy. *Proc. Prehist. Soc.*, 5 (3), 58-70.
30. Pidoplichko J.G. (1951): About the glacial period (in russian). 240 pp., Kiev.
31. Sickenberg O., Tobien H. (1971): New Neogene and Lower Quaternary vertebrate faunas in Turkey. *Newsl. Stratigr.*, 1 (3), 51-61, Leiden.
32. Skhirtladze N.I. (1958): Postpaleogenic effusive volcanism of the Georgia (in russian). *Institute of Geology of Academy of Sciences of USSR, Monograph.*, 8, 5-315, 70 figs.
33. Sokolov I.I. (1953): An attempt of natural classification of bovidae (in russian). *Works of the Institute of Zoology, Academy of Sciences of USSR*, 15, 5-284, 22 pls.
34. Sokolov I.I. (1955): The new species of antelope of the Tertiary fauna of the South of USSR (in russian). *Works of the Institute of Zoology, Academy of Sciences of USSR*, 17, 217-223.
35. Sokolov I.I., Vekua A.K. (1966): Sinoreas sp. from the Lower-Pleistocene deposits of Akhalkalaki (in russian). *Bulletin of the Academy of Sciences of the Georgian SSR*, 43 (1), 147-150, 1 fig.
36. Stromer E. (1914): Mitteilungen über Wirbeltierreste aus Mittelpliocän des Natrontales (Agypten). 3. Artiodactyla: A. Bunodontian Flusspferd. *Zeitschr. d. Deutsch. Geol. Ges.*, 66, 33 pp., 5 figs, 3 pls.

37. TEILHARD DE CHARDIN P., TRASSAERT M. (1938): Cavicornia of South-Eastern Shansi. *Pal. Sinica*, n.s. C, 6, 96 pp., 65 figs., 4 pls.

38. VEKUA A.K. (1958): About the new locations of the Quaternary mammals in the Eastern Georgia (in russian). *Bulletin of the Academy of Sciences of the Georgian SSR*, 20 (1), 47-49.

39. VEKUA A.K. (1962): The Lower Pleistocene Mammalian Fauna of Akhalkalaki (in georgian). 191 pp., 20 figs., 19 pls., Tbilisi.

40. VEKUA A.K., GABUNIA M.K. (1984): The Upper Palaeolithic man and its environment in Suthern Georgia (in georgian). *Bulletin of the Academy of the Georgian SSR*, 116 (1), 147-150, 1 fig.

41. VEKUA A.K., JIGAURI D., TOROZOV R. (1985): The new paleontologic findings in the environs of Tsalka (in russian). *Bulletin of the Academy of Sciences of the Georgian SSR*, 118 (2), 373-376.

42. VEKUA A.K. (1978): The fossil vertebrates of Tsutskvati Caves (in russian). In: Exploration of Caves in Cholchis, 94-115, fig. 24-51, Tbilisi.

43. VERESHCHAGIN N.K. (1957): The mammalian remains from the Lower Quaternary deposits of the peninsula of Thaman (in russian). *Works of the Institute of Zoology*, 22, 19-74, Moscow-Leningrad.

44. VERESHCHAGIN N.K. (1959): Mammals of the Caukasus. 693 pp., 218 figs., Moscow-Leningrad.

45. WOLF B. (1939): Fauna fossilis cavernarum. In: Fossilium Catalogus, 2, 97-208 (p. 89).

46. ZARIDZE G.M., TRATRISHVILI N.F. (1948): About the age of the lava complex of Akhalkalaki (Georgian SSR, South slope of the Adzara-Trialeti mountain ridge) (in russian). *Reports of the Academy of Sciences of SSSR*, 59 (1), 111-113.

47. ZEUNER F. (1963): Pleistocen (in russian). 1, 459 pp., Moscow.