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Local biochronology of Middle and Late Pleistocene mammals from the Caucasus

Gennady F. Baryshnikov

ABSTRACT. The seven faunal units (Akhalkalaki, Urup, Kudaro, Kvaisi, Binagady, Chasovali, Akhstyr) are recognized for the Caucasian Middle and Late Pleistocene mammals for the first time. These local groups correlate to the middle and late Galerian and Aurelian Mammal Ages in Western Europe. There are differences between species composition in the Transcaucasian localities, comprising warm-requiring and forest species and that in the Northern Caucasian localities, containing steppe and boreal species.

KEY-WORDS. Continental biochronology, Pleistocene, mammals, Caucasus.

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Локальная биохронология средне- и позднеплейстоценовых млекопитающих Кавказа

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РЕЗЮМЕ. Впервые выделены семь локальных фаунистических комплексов (Ахалкалакский, Урупский, Кударский, Квайсинский, Бинагадинский, Часовальский, Ахштырский) для млекопитающих среднего и позднего плейстоцена Кавказа. Проведена их корреляция с одновозрастными группировками млекопитающих Западной Европы. На Кавказе в плейстоцене наблюдаются различия в видовом составе между териофауной Закавказья и Северного Кавказа; в западном Закавказье преобладали теплолюбивые горные и лесные виды, на Северном Кавказе были обычнее степные и бореальные виды.

КЛЮЧЕВЫЕ СЛОВА. Континентальная биохронология, плейстоцен, млекопитающие, Кавказ.

Introduction

In the Caucasus the Middle and Late Pleistocene mammals were found mainly at archaeological excavations in caves and open-air sites situated from foot hills to height more than 2000 m above sea level (a.s.l.). Several large mammal remains (especially proboscides) came from localities, which were formed without activity of ancient man (alluvial deposits and asphalt pits).

In the Pleistocene, the forest area of the Transcaucasia has been a refuge for some species, which survived there for a longer time than in Europe (Guérin & Barychnikov, 1987; Baryshnikov, 1989; Guérin *et al.,* 1992). This situation complicates biochronological correlation for the Pleistocene mammals in the Caucasus. Therefore, for these procedures, the additional information on geomorphology of the river terraces, archaeological facts, scarce radiometric and palaeomagnetic dating and palynology data are desirable. Recently Nesmeyanov (1999) summarized such information for the Paleolithic sites in the Western Caucasus.

The paper provides the preliminary attempt to create a detailed chronological scale, based mainly on the mammals from the Paleolithic multilayer cave sites. Here I used for the first time for the Caucasus the faunal units (F.U.), similar to that elaborated for the faunal successions in Italy (Azzaroli *et al.,* 1982).

Stratigraphic position of the most significant Caucasian localities is shown in the Table. Biochronological scale was associated with the available oxygen isotope stages (Shackleton & Opdyke, 1976; Shackleton, 1995). The boundary between the Early and Middle Pleistocene is placed close to isotopic stage 25, the boundary between the Middle and the Late Pleistocene is placed at isotopic stage 5e (Aguirre & Pasini, 1985; Gliozzi *et al.,* 1997).

The large and small mammal species lists are given for the type localities of the each faunal unit, and species not found at the type localities are additionally listed for both Transcaucasia and Northern Caucasus.

Large mammals

Galerian Mammal Age

Middle and late Galerian assemblage corresponds to the Tiraspolian and early Singilian middle Pleistocene mammal complexes in Eastern Europe (Alexeeva, 1977). In the Caucasus, the first half Middle Pleistocene fauna is represented by the Akhalkalaki locality situated at height 1700 m a.s.l. near Akhalkalaki City in Georgia.

TABLE. CHRONOLOGICAL POSITION OF THE MAIN MIDDLE AND LOWER PLEISTOCENE LOCALITIES IN THE CAUCASUS.

Time, MA	Oxygen-Isotope Stage	Mammal Ages		Faunal Units	Localities	
		Western Europe	Eastern Europe		Transcaucasia	Northern Caucasus
0.025	2	Aurellian	Sungilian	Akhstyr	Akhstyrskaya Cave (layer 2), Kudaro 3 (layer 2), Gvardzhilas-Klde	Matuzka (layer 2), Gubs Shelter 1, Satanai
	3			Chasovali	Kudaro 3 (layer 3)	Mezmaiskaya Cave (layers 2–3)
0.073	4		Shkurlatian		Kudaro 3 (layers 4a–4e), Machagua, Akhstyrskaya Cave (layer 4), Bisonova, Erevan, Taglar	Ilskaya 2 (layers 5–6), Matuzka (layers 5–5b), Barakaevskaya Cave, Mezmaiskaya Cave (layers 2–3)
0.116	5a–5d					
0.128	5e			Binagady	Binagady, Kudaro 3 (layer 4f)	Girei, Matuzka (layer 6)
0.195	6		Khazarian	Kvaisi		Matuzka (layer 7)
0.251	7				Kudaro 3 (layer 5)	
	8					
0.367	9		Singillian	Kudaro	Kudaro 1 (layer 5b)	
	10				Kudaro 1 (layer 5c), Leninakan	Treugolnaya Cave (layers 5a–5b)
0.440	11					Treugolnaya Cave (layer 5c)
	12			Urup		
	13	Galerian			Azykh (layer 6)	Treugolnaya Cave (layers 6–7)
0.542	14					
0.592	15					
	16–18		Tiraspolian			
	18–20					
0.782	21			Akhal-kalaki	Akhalkalaki, Azykh (layers 7–10)	
	22					

Akhalkalaki F.U. (stratum type — Akhalkalaki): *Canis mosbachensis (= C. tengisii), Ursus deningeri, Lutra* cf. *lutra, Meles* cf. *meles, Vormela peregusna, Pachycrocuta brevirostris, Homotherium* sp., *Panthera gombaszogensis, Mammuthus meridionalis, Mammuthus trogontherii, Equus hipparionoides* (close to *E. altidens*), *Equus suessenbornensis, Stephanorhinus etruscus, Hippopotamus georgicus, Megaloceros solilhacus, Bos* sp., *Bison* sp., ?*Sinoreas* sp., *Capra* sp. (Vekua, 1962, 1987, 1995; Azzaroli, 1983; Dzhaparidze *et al.,* 1989; Baryshnikov & Vereshchagin, 1996; Guérin, 1996).

Vekua (1962, 1987, 1995) has attributed this fauna to the Tamanian mammals complex of the Early Pleistocene, however the presence of *Mammuthus trogontherii* as well as the genera *Bos* and *Capra* suggests a younger age for this fauna (Alexeeva, 1977).

In Italy, *Pachycrocuta brevirostris* reaches up to Slivia F.U., where both *Mammuthus trogontherii* and *Bos galerianus* were also recorded, while *Megaloceros solilhacus* was found for the first time only in Isernia F.U. (Petronio & Sardella, 1999). Mazza (1991) noted the similarity of *Hippopotamus georgicus* with *H. antiquus*, which existed in Europe up to Mosbach. These data allow us to place Akhalkalaki F.U. in the middle Galerian mammal assemblage. In the central Europe, Voigtstedt in Germany and Koneprusy in Czech Republic demonstrate the similar stratigraphic position (Koenigswald & Heinrich, 1999).

Urup F.U. (stratum type — Treugolnaya Cave, layers 6, 7a, and 7b): *Canis mosbachensis, Ursus deningeri, Meles hollitzeri, Mustela nivalis, Crocuta spelaea* (cf. *praespelaea*), *Panthera spelaea, Equus altidens, Stephanorhinus hundsheimensis, Capreolus* cf. *suessenbornensis, Cervus elaphus, Bison schoetensacki* (Baryshnikov, 1993, with additions).

I have earlier established the Urup local fauna for the lower layers of Treugolnaya Cave, which is located near Urup River in the Karachai-Cherkess Republic in the Northern Caucasus at height 1510 m a.s.l. (Baryshnikov, 1993). The layer 7a was dated by the electron-paramagnetic resonance technique (EPR) 583 000 ± 25 000 (Doronichev, 1991; Molodkov, 2001). The species association in the layers 6, 7a, and 7b indicates both the cold and warm climatic phases, which may be linked with isotopic stages 13–15. Paleomagnetic analysis indicates that these horizons were deposited during the Brunhes Normal Chron and postdate 780 000 years ago (Pospelova *et al*., 1996).

Other localities. Transcaucasia (Azykh Cave, layer 6): *Vulpes vulpes, Ursus* aff. *arctos, Panthera pardus, Lynx issidorensis, Stephanorhinus kirchbergensis, Equus*

cf. *suessenbornensis, Equus hydruntinus, Sus* sp., *Megaloceros giganteus, Dama* cf. *mesopotamica* (determined by D. Gadzhiev and A. Aliev; Suleimanov, 1982; Lioubine, 1998). Northern Caucasus: *Mammuthus trogontherii* (Girei quarry, lower level) (Vereshchagin, 1959).

In the Western Europe, the similar species combination is typical of the late Galerian fauna — Fontana Raniccio F.U. in Italy (Gliozzi *et al.,* 1997), Miesenheim 1, Mosbach 2, Mauer, and Erpfingen 1 in Germany and Hundsheim in Austria (Koenigswald & Heinrich, 1999).

Aurelian Mammal Age

In the Eastern Europe, this faunal assemblage is associated with the late Singilian, Khazarian, Shkurlatian and the Upper Paleolithic (Mammoth) mammal complexes (Alexeeva, 1977, 1990).

Kudaro F.U. (stratum type — Kudaro 1 Cave, layer 5c): *Macaca* sp., *Homo* sp., *Vulpes vulpes*, *Cuon alpinus* (?), *Canis* sp. (cf. *C. latrans*), *Canis mosbachensis*, *Ursus thibetanus mediterraneus*, *Ursus deningeri praekudarensis*, *Meles meles*, *Martes foina*, *Vormela peregusna*, *Mustela nivalis*, *Panthera pardus*, *Panthera gombaszoegensis*, *Lynx lynx*, *Felis silvestris, Stephanorhinus hundsheimensis, Cervus elaphus*, *Capreolus capreolus*, *Alces alces* (?), *Megaloceros* sp., *Bison* sp., *Soergelia* sp., *Rupicapra rupicapra*, *Capra caucasica*, *Ovis* cf. *ammon* (determined by the author).

This faunal unit has been recognized for the lower Acheulean layer 5c in Kudaro 1 Cave, situating in the Dzhodzhori River valley near Kvaisi town in the northern Georgia at height 1600 m a.s.l. (Baryshnikov, 1993). This layer was dated by radiothermoluminescence method as 360 000 ± 90 000 (RTL-379) (Lioubine, 1998). For the overlaying layer 5b, the obtained date was 350 000 ± 70 000 (RTL-373).

Other localities. Transcaucasia — Azykh Cave (layer 5): *Homo* sp. (cf. *H. heidelbergensis*), *Canis aureus* (?), *Felis chaus, Stephanorhinus kirchbergensis, Equus* cf. *mosbachensis, Equus hydruntinus, Sus scrofa, Megaloceros* sp., *Dama mesopotamica, Saiga* sp., *Capra aegagrus* (determined by D. Gadzhiev and A. Aliev; Suleimanov, 1982; Lioubine, 1998); Leninakan and Engidzha: *Palaeoloxodon antiquus, Mammuthus trogontherii, Camelus knoblochi, Bos trochoceros* (Alexeeva, 1977). Northern Caucasus — Treugolnaya Cave (layers 5a–5c, with EPR-data of 393 000 ± 27 000; Doronichev, 1991): *Bison schoetensacki*; Girei quarry (middle level): *Mammuthus trogontherii* (Vereshchagin, 1959).

In the Western Europe, the same age faunal complexes appear to be those from Torre in Pietra F.U. in Italy (Gliozzi *et al.,* 1997) and Heppenloch, Steinheim and Bilzingsleben 2 in Germany (Koenigswald & Heinrich, 1999).

Kvaisi F.U. (stratum type — Kudaro 3 Cave, layer 5): *Canis lupus, Vulpes vulpes, Ursus thibetanus, Ursus deningeri* (transitional form between *U. d. praekudarensis* and *U. d. kudarensis*), *Meles meles, Panthera spelaea*, *Panthera pardus, Capreolus capreolus, Cervus elaphus, Bison* sp. (determined by the author).

Kudaro 3 Cave is situated adjacent to the Kudaro 1 Cave of the Chasovali Mountain. For the unclear contact of the Acheulean layer 5 and lower level of the Mousterian deposits in Kudaro 3 Cave, the two RTL-dates: 252 000 ± 51 000 and 245 000 ± 49 000 are available (Lioubine, 1998). According to these dates and presence of the warm-requiring species Kvaisa F.U. may be correlated to the isotope stage 7.

In the Western Europe, Vitinia F.U. in Italy and Hunas and Weimar-Ehringsdorf in Germany are analogous in age with Kvaisa F.U. (Gliozzi *et al.,* 1997, Koenigswald & Heinrich, 1999).

Binagady F.U. (stratum type — Binagady): *Canis lupus, Vulpes corsac, Vulpes vulpes, Ursus arctos binagadensis, Meles meles, Vormela peregusna, Crocuta spelaea, Panthera spelaea, Acinonyx jubatus, Felis lybica, Equus* cf. *hydruntinus, Equus hemionus binagadensis, Equus ferus, Stephanorhinus hemitoechus, Sus apscheronicus, Cervus elaphus, Megaloceros giganteus, Bos mastanzadei, Bos primigenius, Saiga tatarica binagadensis, Ovis* cf. *ammon* (Vereshchagin, 1959; Guérin & Barychnikov, 1987; Eisenmann & Mashkour, 1999).

Binagady locality is situated in environs of Baku in Azerbaijan and represents an asphalt trap, in which the large and small mammal bones were accumulated. The locality age is not determined exactly, however it is usually associated with the age of the Shkurlatian mammal complex in the Eastern Europe correlated to the latest Interglacial (= Eem in the Western Europe) (Alexeeva, 1990).

Other localities. Transcaucasia (Kudaro 3, layer 4f): *Ursus thibetanus, Ursus deningeri kudarensis, Capreolus capreolus, Cervus elaphus, Bison* sp., *Capra caucasica* (determined by the author). Northern Caucasus (Girei quarry, upper level, Ilskaya 2, layer 7, Krasnodar, Matuzka Cave, layer 6): *Ursus rossicus, Mustela nivalis, Palaeoloxodon antiquus, Mammuthus primigenius* (early form), *Stephanorhinus* sp., *Coelodonta antiquitatis* (Borissiak, 1932; Vereshchagin, 1959; Baryshnikov & Golovanova, 1989; Alexeeva, 1990).

In Germany, Burgtonna and Taubach localities have the similar age (Koenigswald & Heinrich, 1999).

Chasovali F.U. (stratum type — Kudaro 3 Cave, layer 3): *Vulpes vulpes, Cuon alpinus caucasicus, Canis lupus, Ursus arctos, Ursus deningeri kudarensis* (earlier form), *Meles meles, Martes foina, Martes martes, Vormela peregusna, Mustela nivalis, Panthera pardus, Panthera spelaea, Lynx lynx, Felis silvestris, Capreolus capreolus, Cervus elaphus, Rupicapra rupicapra, Capra caucasica* (determined by the author). *Hemitragus* sp. found in Kudaro 1 Cave may be added to this complex (determined by E. Crégut).

The composition of this faunal unit is well known by collections from numerous Mousterian sites situated on the northern and southern slopes of the Greater Cauca-

sus. The layer 3a of Kudaro 1 Cave has radiocarbon date 44 100 ± 2 400.1 850 (Gr-6079) (Lioubine, 1989).

Other localities. Transcaucasia: *Homo neanderthalensis, Crocuta spelaea, Equus ferus, Equus hydruntinus, Stephanorhinus hundsheimensis*(Erevan),*Sus scrofa, Megaloceros giganteus, Alces alces, Bison priscus, Gazella subgutturosa, Capra aegagrus, Ovis ammon* (Vekua, 1978; Dzhafarov, 1983; Lioubine, 1989; Guérin *et al.,* 1992). Vekua (1978) cited provisionally for Verkhnyaya Cave in Georgia also *Canis aureus.* Northern Caucasus: *Ursus spelaeus* (Ilskaya 1), *Mammuthus primigenius, Equus hydruntinus, Equus ferus taubachensis*(Ilskaya 2, layer 5),*Rangifer tarandus* (Mezmaiskaya Cave), *Saiga tatarica, Ovis orientalis* (Baryshnikov & Hoffecker, 1994) and possibly *Coelodonta antiquitatis* (Vereshchagin, 1959).

Faunal lists of Transcaucasian sites generally contain cave bear assigned to *Ursus spelaeus*. However, the study of the cave bear remains from Mousterian levels in Kudaro 1 and 3 caves and Akhstyrskaya Cave revealed its archaic dentition, resembling that of *Ursus deningeri* from Europe (Baryshnikov, 1998). It is quite possible that finds from Transcaucasia belong to *U. deningeri kudarensis*, while *U. spelaeus* occurred in the Northern Caucasus only.

Akhstyr F.U. (stratum type - Akhstyrskaya Cave, layer 2, lower part): *Homo sapiens, Vulpes vulpes, Ursus deningeri kudarensis* (later form)*, Sus scrofa, Alces alces, Capreolus capreolus, Cervus elaphus, Capra caucasica* (Gromova, 1948, with additions).

Akhstyrskaya Cave is situated near Sochi City and located at height 280 m a.s.l. For the middle part of the layer 2 the radiocarbon date 19 500 ± 500 has been obtained (Lioubine, 1989).

Other localities: *Canis lupus, Ursus arctos, Meles meles, Martes foina, Gulo gulo* (Gvardzhilas-Klde)*, Mustela erminea* (Matuzka), *Mustela nivalis, Panthera spelaea, Lynx lynx, Equus ferus strictipes, Equus hydruntinus* (Sakazhia), *Bos primigenius, Bison priscus, Bison bonasus, Rupicapra rupicapra, Ovis orientalis* (Vereshchagin, 1959; Burchak-Abramovich & Burchak, 1982; Baryshnikov & Golovanova, 1989; Lioubine, 1989).

This local fauna contains mainly the recent species with small addition of extinct species (*Ursus deningeri kudarensis, Panthera spelaea, Equus hydruntinus, Bison priscus*) which did not occur in the Holocene. In contrast with the Mousterian fauna, this species composition does not contain *Mammuthus primigenius, Coelodonta antiquitatis,* and *Megaloceros giganteus.*

Small mammals

The data on fossil small mammals from the Caucasus are rather scarce in comparison with that on large mammals, belonging mainly to rodents and lagomorphs. The records of bats are occasional. The insectivore examination being recently begun is still revealing the recent genera in the Pleistocene fauna (*Erinaceus, Talpa, Crocidura, Neomys, Sorex*).

Galerian Mammal Age

Akhalkalaki F.U.: *Erinaceus* sp., *Lepus* sp., *Spermophilus* aff.*citellus*, *Marmota longipes* (Vekua, 1987).

Other localities. Transcaucasia (Azykh Cave, layers 7–10, within those the boundary between Matuyama and Brunhes paleomagnetic zones has been found by Velichko *et al.,* 1980): *Allactaga* ex gr. *williamsi*, *Microtus* ex gr. *arvalis-socialis* (Markova, 1982).

Markova (1982) believed that the rodent fauna from the basic layers of Azykh Cave cannot be dated earlier than the Tiraspolian mammal complex in the Eastern Europe. In Italy *Microtus (Microtus)* aff. *arvalis* had appeared in the middle Galerian mammal assemblage (Slivia F.U.) (Gliozzi *et al.,* 1997).

The more precise dating of Akhalkalaki F.U. requires the additional micromammal fossil record.

Urup F.U.: *Drepanosorex* sp. (determined by M. Zaitsev), *Ochotona transcaucasica, Spalax* sp., *Apodemus* sp., *Ellobius* sp., *Mesocricetus* sp., *Clethrionomys* sp*., Lagurus transiens, Eolagurus luteus volgensis, Arvicola cantianus, Chionomys gud, Terricola* ex gr. *majori, Microtus* cf. *arvalis* (determined by the author).

The teeth of*Arvicola cantianus* are small, exhibiting a slight inversion of the enamel thickness. By the size, these teeth enter the zone of transgression between *A. cantianus* and *Mimomys savini*. In the Eastern Europe, the voles of this evolutionary level are poorly known, presumably being closely related with those from the early Singilian mammal complex of the Eastern Europe (Bolshaya Kamyshevakha) (Rekovets, 1990). In Germany, this level is represented by *A. cantianus* from Mosbach, Mauer, and Petersburch 1 (Koenigswald & Heinrich, 1999).

Other localities. Transcaucasia (Azykh, layer 6): *Mesocricetus* ex gr. *raddei, Ellobius* ex gr. *lutescens* (Markova, 1982).

Aurelian Mammal Age

Kudaro F.U.: *Erinaceus* sp., *Rhinolophus ferrumequinum*, *Rhinolophus mehelyi*, *Myotis blythi*, *Myotis nattereri*, *Vespertilio* cf.*murinus*, *Miniopterus schreibersi*, *Lepus europaeus gureevi, Castor fiber*, *Hystrix indica*, *Hystrix vinogradovi kudarensis*, *Apodemus* sp., *Cricetulus migratorius argyropuloi*, *Mesocricetus raddei planicola*, *Prometheomys schaposchnikovi palaeokudarensis*, *Clethrionomys* cf. *glareolus*, *Arvicola cantianus*, *Chionomys gud*, *Chionomys roberti*, *Terricola* ex gr.*majori, Terricola* cf. *arvalidens, Microtus arvalis* (Gadzhiev, 1980; Baryshnikov & Baranova, 1983; Averianov & Baryshnikov, 1992; with additions).

The teeth of *Arvicola cantianus* from the Kudaro F.U. are somewhat larger than those of specimens from the Urup F.U., the enamel differentiation being similar. The same features show the voles from Holstein (=Likhvin) faunas both of the Eastern Europe (Gunki, Chigirin, Pivikha) and the Western Europe (Petersburch 1, Bilzingsleben 2, Neede) (Rekovets, 1990; Markova, 1996).

Other localities. Transcaucasia: *Ochotona transcaucasica, Ochotona azerica, Marmota* sp., *Alactagulus acontion, Allactaga* sp., *Mus musculus*, *Apodemus sylvaticus, Meriones erythrourus, Ellobius* ex gr. *lutescens, Lagurus* sp., *Microtus* ex gr. *arvalis-socialis* (Markova, 1982; Vekua et al., 1987). Northern Caucasus (Treugolnaya Cave, layers 5a-5c): *Spermophilus* sp., *Spalax* sp., *Ellobius* sp., *Lagurus transiens, Eolagurus luteus volgensis* (determined by the author).

Kvaisi F.U.: *Lepus europaeus gureevi, Hystrix vinogradovi kudarensis, Apodemus uralensis, Cricetulus migratorius argyropuloi, Mesocricetus raddei planicola* (Baryshnikov & Baranova, 1983; Averianov & Baryshnikov, 1992). This group may also include *Marmota paleocaucasica, Chionomys* cf. *nivalis, Terricola daghestanicus* recorded in Kudaro 1 Cave (layer 5a) (determined by the author).

Other localities. Northern Caucasus (Treugolnaya Cave, layers 4b–4c; Matuzka Cave, layer 7): *Rhinolophus ferrumequinum*, *Dryomys nitedula, Cricetulus migratorius guamensis, Cricetus cricetus, Clethrionomys* cf. *glareolus, Arvicola terrestris chosaricus, Chionomys gud, Chionomys roberti, Terricola majori* (Baryshnikov & Golovanova, 1989; Nadachowski & Baryshnikov, 1991;with additions).

In the Eastern Europe, the same age rodent fauna is known from the Kamenka Interglacial (Priluki, Chernyi Yar, Rasskazovo) (Markova, 1990, 1996).

Binagady F.U.: *Lepus europaeus gureevi, Hystrix vinogradovi vinogradovi, Dryomys nitedula, Allactaga jaculus bogatschewi, Allactaga williamsi dzhafarovi, Allactaga elator, Mus musculus, Apodemus uralensis, Mesocricetus raddei planicola, Cricetulus migratorius argyropuloi, Meriones erythrourus intermedius, Ellobius* aff. *lutescens, Terricola apsheronicus, Microtus socialis, Microtus arvalis* (Gromov, 1952).

Other localities. Northern Caucasus (Matuzka Cave, layer 6): *Spermophilus* cf. *musicus, Spalax microphtalmus*, *Cricetulus migratorius guamensis, Cricetus cricetus, Arvicola terrestris chosaricus, Chionomys gud, Chionomys roberti, Terricola majori, Terricola daghestanicus* (Baryshnikov & Golovanova, 1989).

In the Western Europe the same age rodent fauna came from the Mikulino Interglacial (Ceremoshnik, Borisova Gora, Ulovka) (Markova, 1990).

Chasovali F.U.: *Myotis blythi, Myotis nattereri, Vespertilio* cf. *murinus, Miniopterus schreibersi, Lepus europaeus* (transitional form between *L. e. gureevi* and recent *L. e. cyrensis), Marmota paleocaucasica, Hystrix vinogradovi kudarensis, Dryomys nitedula*, *Allactaga euphratica, Apodemus uralensis, Cricetulus migratorius, Cricetus cricetus, Mesocricetus raddei planicola, Ellobius lutescens, Prometheomys schaposchnikovi palaeokudarensis, Arvicola terrestris chosaricus, Chionomys gud, Terricola majori fokanovi, Terricola daghestanicus, Microtus arvalis* (Gadzhiev, 1980; Baryshnikov & Baranova, 1983; Averianov & Baryshnikov, 1992).

Other localities. Transcaucasia: *Myotis* sp., *Eptisicus* sp., *Ochotona transcaucasica, Spermophilus xanthoprymnus, Castor fiber, Meriones* sp. (Vekua, 1978; Lioubine, 1989). Northern Caucasus: *Ochotona pusilla liubine, Lepus capensis, Lepus europaeus, Spermophilus* cf. *musicus, Sicista* sp., *Spalax microphtalmus, Apodemus flavicollis, Cricetulus migratorius guamensis, Chionomys nivalis, Chionomys roberti* (Baryshnikov & Golovanova, 1989; Nadachowski & Baryshnikov, 1991; Averianov & Baryshnikov, 1992).

Akhstyr F.U.: *Sorex satunini, Sorex volnuchini, Apodemus* cf. *uralensis, Cricetus cricetus, Prometheomys schaposchnikovi, Arvicola terrestris, Chionomys roberti, Terricola majori, Microtus arvalis* (determined by the author and M. Zaitsev).

Other localities. Transcaucasia: *Marmota paleocaucasica, Castor fiber, Dryomys nitedula, Allactaga williamsi, Cricetulus migratorius, Mesocricetus raddei, Chionomys nivalis, Chionomys gud, Terricola majori, Terricola daghestanicus* (Baryshnikov & Baranova, 1983; Lioubine, 1989; Nadachowski & Baryshnikov, 1991). Northern Caucasus (Matuzka Cave): *Crocidura gueldenstaedti, Spermophilus musicus, Spalax microphtalmus, Chionomys nivalis* (Baryshnikov & Golovanova, 1989).

Conclusions

The four faunal units (Akhalkalaki, Urup, Kudaro, Kvaisi), characterizing the stages of the Caucasian mammal fauna development in the Middle Pleistocene, are well synchronized with those known for Italy (Isernia, Raniccio, Torre in Pietra, and Vitinia respectively). In the Caucasus, small mammals better indicate the stratigraphic limits for local complexes because some species of large mammals (*Ursus deningeri, Panthera gombaszoegensis, Stephanorhinus hundsheimensis*) survived in Transcaucasia longer than in Europe due to the more favorable environmental conditions. Chronosubspecies established by the data on evolutionary mammal dental changes allowed me to subdivide the Late Pleistocene Caucasian mammal complex in three faunal units (Binagady, Chasovali, Akhstyr) (see Table).

In the Caucasus, 34 species of large mammals and about 16 species of rodents have been recorded from the Middle Pleistocene. The better known Late Pleistocene fauna includes up to 50 species of large mammals as well as 40 species of rodents. An overwhelming majority of the Caucasian species has been also found in the Western Europe, only some of them being the Caucasian mountain endemics (*Ochotona transcaucasica, Prometheomys schaposchnikovi, Terricola majori, Terricola daghestanicus*) or came from Asian semi deserts (*Hystrix indica, Acinonyx jubatus, Equus hemionus, Camelus knoblochi, Gazella subgutturosa*).

There are noticeable zoogeographic differences between the Northern Caucasus and the Transcaucasia. The fauna of latter contained warm-requiring species (*Macaca* sp., *Hystrix indica, Ursus thibetanus, Hippopotamus georgicus*), which were not found in the Northern Caucasus. This area, in contrast, includes cold resis-

tant steppe species (*Ochotona pusilla, Cricetus cricetus, Spalax microphtalmus, Ursus rossicus*) and boreal species (*Mammuthus primigenius, Coelodonta antiquitatis, Rangifer tarandus*). At the same time, the typical Arctic mammals (*Dicrostonyx, Lemmus, Stenocranius, Alopex, Ovibos*) were not recorded there.

Certainly, the Greater Caucasian Ridge covered with strong glaciers during the Pleistocene has been an important barrier preventing the faunal interchange between the Northern Caucasus and Transcaucasia. Therefore, steppe and boreal mammals might occasionally come to the south along the Caspian Sea coast (*Saiga tatarica, Equus hydruntinus*) or through the lower mountain passes in the central part of the Caucasian Ridge (*Cricetus cricetus, Gulo gulo, Mammuthus primigenius*). The spatial differentiation of the Transcaucasian Pleistocene fauna has corresponded to the recent one; the forest species being predominated in the west, the semi desert mammals in the east.

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