

Dynamics of the Pleistocene bat fauna from the Matuzka Paleolithic site (Northern Caucasus, Russia) (Chiroptera)

Dynamika netopýří fauny paleolitického stanoviště Matuzka (severní Kavkaz, Rusko) (Chiroptera)

Valentina V. ROSSINA¹, Gennadiy F. BARYSHNIKOV² & Bronislaw W. WOLOSZYN³

¹ Paleontological Institute, Russian Academy of Sciences, Moskva, Russia; ros@paleo.ru

² Zoological Institute, Russian Academy of Sciences, 199 034 Sankt Petersburg, Russia

³ Institute of Systematics and Evolution of Animals PAS, Slawkowska 17, PL–31-016 Kraków, Poland

received on 31 May 2006

Abstract. The upper Pleistocene sedimentary series in Matuzka cave (northern Caucasus) covering a period from MIS6 to MIS2 provided remains of 18 species of bats. The bat record is particularly rich in the layers corresponding to Eemian and early Vistulian. It is characterized with appearance of thermophilous elements *Rhinolophus ferrumequinum* and *Miniopterus schreibersii* and a broad spectrum of taxa including dendrophilous and demanding elements such as *Plecotus auritus*, *Myotis brandtii*, *M. emarginatus*, *M. nattereri* and *M. blythii*. The lithophilous forms *Eptesicus serotinus*, *Vespertilio murinus* and *Nyctalus noctula* appear continuously in all layers and represent a dominant component of the assemblage. In Eemian layers they are supplemented also with *Hypsugo savii* and *Pipistrellus cf. kuhlii* which absent from the upper layers while *Pipistrellus pipistrellus* appear as late as in the Early Holocene.

INTRODUCTION

During the last decades, many Paleolithic sites have been discovered on the northwestern Caucasus. The rich bone material from these sites includes numerous records of bats.

The Caucasus is a unique region particularly in respect to its climatic specificities and biogeographical role. The Caucasian mammal fauna is characterized by considerable species richness and high degree of endemism. This holds true also for bats: the northern Caucasus is presently inhabited by one of the richest bat fauna of Russia. Unfortunately, until now almost no information was available on the history of the Caucasian bat fauna except for rather episodic and isolated records (comp. VEREŠČAGIN 1959). To gain a better understanding of the development of bat faunas, the study of new paleontological data on this group is required.

The present paper describes the material of Late Pleistocene bats collected by G. F. BARYSHNIKOV during archeological excavations of the Matuzka Paleolithic site. This study provides insight into the major stages of the formation of Caucasian bat communities during the essential part of the last glacial cycle, Eemian and Vistulian.

MATERIAL AND METHODS

The cave site Matuzka (42° 26' N, 39° 45' E) is located at 720 m above sea level, at the northern margin of the Lagonakskoe Plateau on the right bank of the Matuzka River, a right tributary of the Pshekha River, 27 km south-southeast of Apsheronk (Fig. 1). The cave cavity is in Upper Jurassic limestones, has a dome-shaped roof and karstic niches in the walls and roof. The cave is up to 35 m wide and about 40 m deep, the entrance faces southwest and is 20 m high.

According to geomorphologic analysis performed by NESMEYANOV (1999), the primary cave cavity, which is most likely of karstic-erosive origin, was formed about 150–130 thousand years ago. The analysis of limestone pack deformation has shown that the cave initially had two, or possibly, three layers.

The three-floor primary cavity of Matuzka cave, with the total height up to 30–35 m, suggests a long time of the cavity formation, with the participation of lateral river erosion. This process apparently resulted in the large final size of Matuzka cave (NESMEYANOV 1999). The cave is presently a large grotto.

The site was excavated from 1985 to 1988. The 6-m-deep sequence of Pleistocene-Holocene deposits was exposed in the site. The section of excavation comprises 8 major lithologic beds (Table 1; BARYSHNIKOV & GOLOVANOVA 1989).

The sequence is subdivided by lithologic features into four units. Three lower units (beds 7–3a) contain a Pleistocene mammal fauna and Mousterian artifacts (GOLOVANOVA et al. 1995).

The first lower unit is 0.6 m thick (beds 8a–7b) includes the deluvial deposits composed of slightly inclined laminated loam with insertion of gruss. Apparently, it was formed under conditions of low-activity washout.

The second and third units (beds 7a–3a) are composed of rubbly-clumpy material with varying content of loamy-gruss-rubbly filler. The second unit (beds 7a–5) is 3 m thick, of land-rockslide genesis, composed of yellow loam. The third unit (beds 4d–3a) is formed by gray loam. Bed 4b is 0.1 m thick, contains charcoals of fire spots (NESMEYANOV 1999), with the absolute date 34200 ± 1410 BP (GOLOVANOVA 1996).

There are no absolute dates for the others layers. However, based on rodent fauna (NADACHOWSKI & BARYSHNIKOV 1991) beds 7–6 are dated to terminal Middle Pleistocene, beds 5–3 are assigned to the time of the last glaciation, and beds 2–1 are dated Upper Pleistocene-Holocene boundary (ZAITSEV & OSIPOVA 2004). The fourth unit (beds 2–1) is 0.6 m thick, composed of lumpy-rubbly loam and contains of ceramics fragments and burnt bones of domestic animals (NESMEYANOV 1999).



Fig. 1. The region of investigation with a location of the Matuzka cave (asterisk).

Obr. 1. Oblast výzkumu s lokalisací jeskyně Matuzka (hvězdička).

In addition to the main sites, excavations were performed in further trench assigned as trench 3. Based on the mammal fauna and bone fossilization pattern, the layers of trench 3 were dated to Pleistocene-Holocene boundary, i.e. they correspond roughly to beds 3 and 1–2.

A total of 217 skull fragments and isolated teeth of bats were examined (Table 1). The material was examined by binocular microscope, identified and compared with the samples of Recent species. The parataxonomic categories were applied in few cases in which considerable fragmentation and poor preservation of specimens did not allow exact identification: “small-sized *Myotis*” means of the same size as *M. brandtii*, “medium-sized *Myotis*” means of the *M. emarginatus* size.

RESULTS

Structure of the oryctocoenoses

The complete list of species found in individual samples from the Late Quaternary beds of Matuzka cave is in Table 1. In total, 17 species were recorded: *Eptesicus serotinus* (Schreber, 1774), incl. cf. *E. serotinus*; *Vespertilio murinus* Linnaeus, 1758 (cf. *V. murinus*); *Nyctalus noctula* (Schreber, 1774) (incl. cf. *N. noctula*); *Nyctalus leisleri* (Kuhl, 1817); *Myotis blythii* (Tomes, 1857) (*M. cf. blythii*); *Barbastella barbastellus* (Schreber, 1774); *Plecotus auritus* (Linnaeus, 1758); *Rhinolophus ferrumequinum* (Schreber, 1774); *Miniopterus schreibersii* (Kuhl, 1817); *Pipistrellus pipistrellus* (Schreber, 1774); *P. nathusii* (Keyserling et Blasius, 1839); *P. cf. kuhlii* (Kuhl, 1817); *Hypsugo savii* (Bonaparte, 1837); *Myotis brandtii* (Eversmann, 1845) (*Myotis cf. brandtii*); *M. nattereri* (Kuhl, 1817) (*M. cf. nattereri*); *M. bechsteinii* (Kuhl, 1817) (*M. cf. bechsteinii*); *M. emarginatus* (Geoffroy, 1806) (*M. cf. emarginatus*). The particular remains were directly compared to the samples of Recent specimens and apparently fall in variation of the respective Recent species except for several Pleistocene items which appear to be somewhat larger than reported for the Recent Caucasian material.

The most abundant species of the oryctocoenosis were *E. serotinus* and *V. murinus* (30% and 26% of all remains, respectively). *N. noctula*, *Plecotus auritus* (both about 7%), *B. barbastellus* and *R. ferrumequinum* (about 5%) were recedent elements while *Myotis blythii* (with somewhat more than 2%) and all remaining species (with less than 1.9%) represent the subrecedent elements of the sample.

As concerns the structural characteristics of the oryctocoenoses the whole set clearly splits into two markedly different units: (I) The faunal association of the bed 7 (accumulated during the Mikulino Interglacial = Eemian in the Western Europe) that is characterized by considerable species richness and includes thermophilous elements such as *R. ferrumequinum*, *M. schreibersii*, *P. kuhlii*, *H. savii*. Its essential characteristics are partly retained in the overlaying bed 6, where *Miniopterus* or *H. savii* are absent, of course (Fig. 2). The distribution of these species in the section marks the boundary between the Mikulino Interglacial and the onset of the Valdai Glacial Period (= Würm). (II) Beds 5–3a (accumulated during the Valdai glaciation) yielded the bat fauna that is slightly poorer both in species richness and abundance. It also differs from (I) by presence of *M. nattereri*, *M. emarginatus* and *M. bechsteinii* and well-pronounced instability in the proportions of particular taxa (Fig. 2). It is dominated with the mesophilous elements, among other *Plecotus auritus* and *B. barbastellus*, and *Nyctalus noctula* which reaches peak of its abundance in the middle Valdai horizons.

As demonstrated in Fig. 3, there is a clear correlation between the contribution of bats to the total mammalian community of a layer and contributions of the rodents inhabiting either forest or open-ground habitats: a positive correlation exists with the proportion of rodents inhabiting mountain forest formations and negative correlation with the proportion of rodents living in

Table 1. Chronological position of Matuzka cave strata and numbers of Chiroptera records
 Tab. 1. Chronologická posice vrstev jeskyně Matuzka a počty v nich nalezených netopýrů

time MA	O-isotope stage	mammal age Eastern Europe	Caucasus	Matuzka cave layer	Chiroptera (217)
0.025	2	Sungilian	Akhtyr	1–2 + shaft 3	<i>P. pipistrellus</i> (3), <i>P. nathusii</i> (1) <i>E. serotinus</i> (13) <i>V. murinus</i> (4), <i>P. auritus</i> (1) <i>M. nattereri</i> (1) <i>M. bechsteinii</i> (2) <i>M. emarginatus</i> (1)
	3		Chasovali	3	<i>E. serotinus</i> (3), <i>N. leisleri</i> (1) <i>B. barbastellus</i> (2) <i>M. brandtii</i> (1) medium-sized <i>Myotis</i> (2)
0.073	4	Shkurlatian		4	<i>E. serotinus</i> (19) <i>V. murinus</i> (6), <i>P. auritus</i> (7) <i>B. barbastellus</i> (8) medium-sized <i>Myotis</i> (1) small-sized <i>Myotis</i> (1) <i>M. nattereri</i> (1) <i>M. bechsteinii</i> (2) <i>M. emarginatus</i> (2) <i>N. noctula</i> (12)
0.116	5a–5d			5–5b	<i>E. serotinus</i> (2) <i>V. murinus</i> (3), <i>P. auritus</i> (1) <i>M. nattereri</i> (1) <i>M. emarginatus</i> (1) <i>M. blythii</i> (1), <i>N. noctula</i> (1)
0.128	5e		Binagady	6	<i>P. cf. kuhlii</i> (1), <i>N. leisleri</i> (1) <i>E. serotinus</i> (13) <i>V. murinus</i> (21), <i>P. auritus</i> (1) <i>M. nattereri</i> (3), <i>M. blythii</i> (1) <i>M. emarginatus</i> (1) <i>R. ferrumequinum</i> (1)
0.195	6	Khazarian	Kvaisi	7	<i>P. cf. kuhlii</i> (1), <i>H. savii</i> (1) <i>E. serotinus</i> (20) <i>V. murinus</i> (23), <i>P. auritus</i> (4) <i>B. barbastellus</i> (2) <i>M. brandtii</i> (2), <i>M. blythii</i> (3) <i>R. ferrumequinum</i> (10) <i>N. noctula</i> (2) <i>M. schreibersii</i> (2)

open landscapes, such as mountain-steppe and shrub-and-grassland habitats. This suggests considerable retreat of bat populations in periods of the most pronounced glacial conditions (indicated by percentage of open-ground elements).

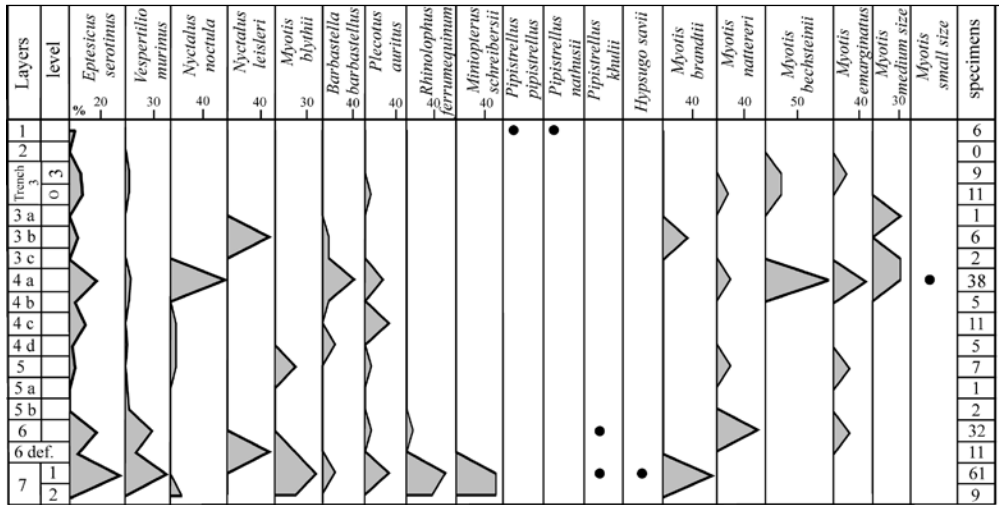


Fig. 2. Percentual distribution of a total number of individuals of particular bats species in sequence of layers of the Matuzka cave.

Obr. 2. Procentuální rozložení celkového počtu jedinců jednotlivých druhů netopýřů ve sledu vrstev jeskyně Matuzka.

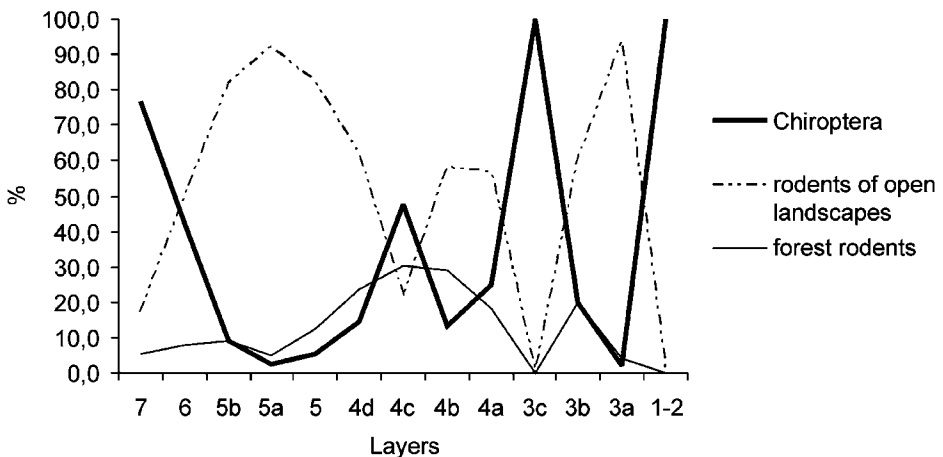


Fig. 3. Percentages of the bats in the total mammalian samples of particular layers (bold line) compared to those of forest and open-ground rodents.

Obr. 3. Procentuální zastoupení netopýřů v celkovém vzorku savců (silná čára) ve srovnání se zastoupením lesních druhů hlodavců a hlodavců otevřené krajiny.

T a p h o n o m y

Holocene bones from bed 1 have natural white colour. Most of the Pleistocene bone specimens are light brown, some are colored with manganese. Some bones (mostly teeth) were damaged by the digestive juice (enzymes): bed 4b (*N. noctula*), trench 3 (bed 3, *V. murinus*), bed 6 (3 specimens of *E. serotinus* (2) and *P. auritus* (1)), bed 7 (10 specimens; 4 *V. murinus*, 5 *E. serotinus* and 1 *M. cf. brandtii*). This suggests that a significant part of bat sample may represent a taphocenosis. The predominating representation of the lithophilous elements in the samples (*Eptesicus serotinus*, *Vespertilio murinus*, *Nyctalus* spp. *Pipistrellus* spp., *Hypsugo savii*) suggests at the same time that a considerable part of the material may originated from autochthonous sources, supposedly winter colonies of the respective species roosting in the ceiling fissures in the cave entrance and/or in the rocky walls surrounding the cave.

DISCUSSION

Out of 23 bat species presently inhabiting the northern Caucasus, 17 have been recorded in the fossil assemblages under study. The species: *Rhinolophus hipposideros*, *R. euryale*, *Myotis daubentonii*, *M. aurascens*, *M. mystacinus* and *Nyctalus lasiopterus* are absent from the Matuzka orictocenosis. It is very important to recognize the reasons for their absence for analysis of the species diversity in the Pleistocene bat community.

At present, *Rhinolophus hipposideros* is a common bat species in Caucasia which range is restricted to the forest zone (GAZARYAN 2002). Though it frequently occurs in cave roosts it does not form large colonies but prefers smaller caverns for roosting which would indicate its possible incidence in Matuzka cave. In respect to the positive prediction on its appearance in fossil record, its absence may suggest that the pattern of abundance and geographical range of this species differed from those in the present time.

In the case of *R. euryale*, a strict cave-dweller, extremely rare in the area under study (only one record by BOBRINSKOJ et al. 1965), its incidence in the site under study seems to be quite improbable, similarly as in the case of the migratory bat *Nyctalus lasiopterus*, a tree-dweller closely associated with forest vegetation. Also the remaining species of the Recent list which absents in the site are not too probable to appear there.

The group of small-sized *Myotis* (*M. brandtii*, *M. daubentonii*, *M. aurascens* and *M. mystacinus*) is scarce in the orictocenosis, it is represented by ten specimens only. It is noteworthy that all the listed species are considered abundant in the Recent of Caucasia (GAZARYAN 2002, 2003). The total abundance of *Myotis daubentonii*, extent of its range and degree of synanthropy substantially increased during past decades (GAZARYAN 2003). The natural habitats of this species are confined to the foothills and river valleys. This species seems to avoid the altitudes above 1000 m above sea level (GAZARYAN 2003). The sibling species *M. aurascens* and *M. mystacinus* were only recently distinguished as the separate species based on detailed morphological analysis (BENDA & TSYTSULINA 2000). At present, *M. aurascens* inhabits lowlands and plains of Western Caucasus; it has not been recorded higher than 400 m above sea level (GAZARYAN 2002). *M. mystacinus* and *M. brandtii* are very similar ecologically, both inhabiting mountain forests near water bodies. They coexist in the region under study (GAZARYAN 2002). In case of all these species, their habitat preferences and abundances do not suggest particularly high probability of their incidence in Matuzka cave – therefore, their absence in the fossil sample need not be of a serious indication value.

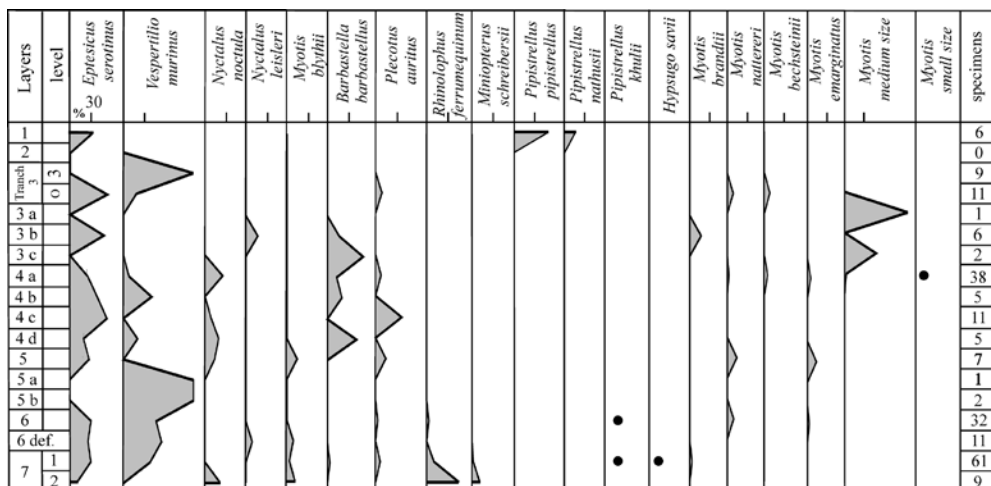


Fig. 4. Percentual contributions of particular bat species to a community structure of individual layers of the Matuzka cave.

Obr. 4. Procentuální zastoupení jednotlivých druhů netopýřů ve sledu vrstev jeskyně Matuzka.

Single records of *P. pipistrellus* and *P. nathusii* in the early Holocene sediments of Matuzka cave are of the particular significance. They suggest the spread of these species in that period (especially in comparison to their absence in the earlier strata) which corresponds well to the scenario presented for their spread in central and Western Europe by HORÁČEK & JAHELKOVÁ (2005).

There are more factors which supposedly might considerably influenced structure of the record and actual dynamics of bat communities recorded in Matuzka cave. Here we will discuss briefly three of them: (1) activity of the Paleolithic man; (2) aspects of bone accumulation; and (3) the climatic and environmental dynamics of the period under study.

(1) The reconstruction of bat fauna history in the northwestern Altai region from the Pleistocene to the present time demonstrated that the historical development of cave-dwelling bat community was considerably affected by cave-dwelling effort of the Paleolithic humans (AGADJANIAN & ROSSINA 2001, ROSSINA 2004). Occupation of caves by the humans apparently reduced the population of the majority of bat species because of the smoke produced by human fires. Thus, humans were a limitative factor for the cave-dwelling bat community since the Pleistocene (ROSSINA 2005).

The Mousterian man did not produce tools in Matuzka cave, but brought there artifacts ready for use (NESMEYANOV 1999). However, Paleolithic humans regularly visited Matuzka cave for many ten thousand years, which is evident from the regular distribution of tools in beds 7–3 (GOLOVANOV et al. 1995). The analysis of large mammal fauna leads to the same conclusion; the Mousterian man used Matuzka cave as a short-term shelter for humans during hunting (BARYSHNIKOV & GOLOVANOV 1989). Thus, in the case under consideration, human activity exerted a little effect on the bat community.

(2) It is commonly accepted that the main source of fossil bats in cave deposits is dying bats from seasonal cave-dwelling colonies (OVODOV 1974, TIUNOV 1997, FILIPPOV & TIUNOV

1999). But it is doubtful in the case under consideration. During the past 120 thousand years, Matuzka cave was a large grotto (POTAPOVA 1992, NESMEYANOV 1999). Thus it seems largely improbable that it may serve a roost for large winter colonies of cave-dwelling bat species, such as *Myotis emarginatus* or *Miniopterus schreibersii*, though occasional appearance of these bats during vegetation period (which used the cave e.g. as a night roost) or in transient period cannot be excluded, of course. On contrary, the regular appearance of the species inhabiting rocky fissures is here quite a probable, and their considerable representation in the sample fits to that possibility quite a well.

The considerable fragmentation of all specimens and signs of treatment by the digestive juice indicate that pellets of birds of prey may were possibly a significant source of fossil material from Matuzka cave. Such a possibility would be indirectly supported also by the conclusion resulting of the study of fossil birds from Matuzka cave which demonstrated that a degree and character of damage of birds bones as well as the species composition of the sample indicate that fossils come from owl pellets (POTAPOVA 1992). In these connection, the specificities of the two most abundant bat species, *E. serotinus* and *V. murinus* are worth mentioning. At present, they are synanthropic species which roost preferably in human buildings while the records from their natural roosts are generally rare. Correspondingly, only few winter records of *E. serotinus* and *V. murinus* are known from the western Caucasus (KUZJAKIN 1950, GAZARYAN 2002). *V. murinus* similarly like *Nyctalus noctula* and *N. leisleri* are seasonal migrants. Particularly worth of attention is that the large seasonal colonies of these bats may become a hunting objects of owls and the frequency of these species in owl diet may thus locally grow quite a high (SCHMIDT & TOPAL 1971, RUPRECHT 1990, 2005, OBUCH 1989, original data). It should be mentioned that also in several teeth of *P. auritus* and *M. cf. brandtii* the enamel shows clear signs of corrosion by the digestive juice. Note that *Plecotus* along with *E. serotinus* and *N. noctula* is the most favorite object of owls hunting (KOWALSKI 1995).

Unfortunately, the material is too small to allow a detailed statistical analysis of possible taphonomic effects. In any case, it is clear that the fauna is to be considered a true oryctocenosis contributed both by taphocenoses and thanatocenoses. Despite the, of course, the stratigraphic setting of the site and the particular records prove that the records under study come from a well defined stratigraphical context and bear the respective stratigraphical and paleoecological information. The comparison of the absolute amount of bat records and percentages of habitat specialists in rodents (Fig. 3) is particularly significant in these connections. An increase of bat percentage in layers with increased frequency of woodland elements conforms well to a general expectations on the paleoclimatic significance of chiropteran record. The general dynamics of the bat fauna in study thus apparently reflects changes in landscape and climatic conditions in the source area. In this sense the analysis of the structure of fossil bat assemblages not only provides additional information on environmental changes, but, in some cases, it promises to regard some aspects not accessible from other evidence (thermal balance of rocky massif as a key factor for hibernation of fissure-dwelling bats etc.). In addition, the analysis of faunal structure of Pleistocene bats provides important stratigraphic results.

(3) The greatest proportion and taxonomic diversity of Chiroptera (about 30% of all specimens) is recorded in beds 7–5b. The absolute maximum of bats is in bed 7.1 (Figs. 2, 4). The oryctocenosis contains forest species of *Pipistrellus* and *Nyctalus* and the forest-steppe *Myotis blythii* (GAZARYAN 2002). Apparently, during the accumulation of beds 7–6, a vast area was occupied by forests. The small mammal fauna includes forest species of the genera *Pitymys* and *Dryomys*. However, the proportions of mountain-steppe and shrub-and-grass rodent species are

also high (BARYSHNIKOV & GOLOVANOVA 1989, BARYSHNIKOV et al. 1995). The climate was warm; this is evident from the highest diversity of the bat assemblage from these beds (14 bat species out of 17 are recorded) and the presence of migratory species of *Pipistrellus* and thermophilous species, such as *Rhinolophus ferrumequinum* and *Miniopterus schreibersii* (more than 40% of all bat specimens; Fig. 4).

At the boundary between beds 6 and 5b, the bat populations sharply decreased in number, with the absolute minimum in bed 5a (Figs. 2, 3). Apparently, at that time, the area of open landscapes increased and a more mosaic landscape structure was formed. This is supported by an increase in the number and proportion of mountain-steppe rodents (Fig. 3), such as *Spermophilus* cf. *musicus*, *Spalax microphthalmus* and *Cricetulus migratorius guamensis*. The climate became somewhat cooler (BARYSHNIKOV & GOLOVANOVA 1989).

During the accumulation of beds 5–4d–4c, the abundance and proportion of bats gradually increased (Figs. 2, 3). The proportion of forest rodent species increased, while rodents of open landscapes decreased in number (Fig. 3). This suggests an increase in the area of forest landscapes and, as follows from palynological data, the mountain pine forests spread, although they were more xerophilous than at the present time (BARYSHNIKOV et al. 1995).

Bed 4b shows a decrease in the proportion and abundance of bat remains, while the proportions of forest and steppe rodent species are approximately equal (Fig. 3). According to palynological data, the forest-steppe or steppe with mixed broad-leaved and pine forests were widespread at that time. However, grasslands dominated. The climate was relatively arid and temperate (BARYSHNIKOV & GOLOVANOVA 1989, BARYSHNIKOV et al. 1995). Against the background of a general increase in the proportion of rodents in bed 4a, the diversity and abundance of bats also increased (more than 16% of all specimens) (Figs. 2, 3). Apparently, the landscapes showed a mosaic pattern of distribution, so that mountain forests alternated with steppes and grasslands. The pollen spectra suggest the presence of mixed pine-birch forests with alder-tree and grass meadows (BARYSHNIKOV et al. 1995).

Bed 3c yielded only *Barbastella barbastellus* and medium-sized *Myotis* (Fig. 2). In bed 3b, the proportion of bat remains is equal to that of forest rodents (Fig. 3). At that time, the proportion of *Chionomys* increased and steppe rodent taxa predominated (BARYSHNIKOV & GOLOVANOVA 1989). Palynological data suggest that the subalpine grasslands and mesophilic motley grasses dominated (BARYSHNIKOV et al. 1995). The finds of bats and forest rodents are sporadic in bed 3a but steppe rodents predominate here as well (more than 90%; Fig. 3). Apparently, open landscapes dominated at that time. Floral samples contain underdeveloped pollen of trees and traces of turf-uncovered slopes, and *Woodsia alpina*. This suggests that at that time the cave was in the Alpine belt, close to the upper boundary of forests (BARYSHNIKOV et al. 1995).

As demonstrated above, the bat assemblage from Matuzka cave is divisible into two faunal associations, which describe different climatic periods of the terminal Pleistocene.

Particular elements of the bat fauna can be used as biostratigraphic markers of time boundaries in Late Quaternary sediments of the Caucasus.

CONCLUSIONS

(1) Out of 23 bat species presently inhabiting the western Caucasus, 17 have been found in the fossil record. Absence of some species in Matuzka oryctocenosis (*Rhinolophus hipposideros*, *R. euryale*, *Myotis daubentonii*, *M. auraszensis*, *M. mystacinus* and *Nyctalus lasiopterus*) is most likely caused by taphonomic factors. Thus, by the end of the Middle Pleistocene, the

general appearance of the bat fauna had already been formed and remained almost constant to the present time.

(2) Considerable part of the fauna is formed by lithophilous forms *Eptesicus serotinus*, *Vespertilio murinus*, *Nyctalus noctula*, supposedly inhabiting rocky fissures in the site. At least part of the sample apparently represents a taphocenosis coming from bird pellets.

(3) The general dynamics of the number and structure of Pleistocene bat communities from Matuzka cave are in accordance with those of rodents inhabiting different landscapes and, hence, indirectly reflect environmental changes in the area of Matuzka cave. The bat fauna apparently decreased in time of spread of open-ground habitats.

(4) In the Eemian Interglacial, the fauna of bats was the richest and included thermophilic *R. ferrumequium* and *Miniopterus schreibersii*, besides of the records of *Hypsugo savii* and *Pipistrellus kuhlii*, which demonstrate in the Eemian the ranges corresponding to their Recent distribution.

(5) The Valdai glaciation (the time of beds 6–3a accumulation) is characterized by a slightly poorer and less numerous bat fauna, which includes *Myotis nattereri*, *M. emarginatus* and *M. bechsteini*, and is distinguished by well-pronounced fluctuations of the proportions of taxa. The proportion of psychrophilic faunal elements, such as *Plecotus auritus* and *B. barbastellus*, noticeably increased.

SOUHRN

Svrchnopleistocenní sled vrstev sedimentů jeskyně Matuzka, která se nachází na severním Kavkaze (Rusko), postihuje období od MIS6 po MIS2. V těchto vrstvách byly nalezeny zbytky nejméně 217 jedinců 18 druhů netopýřů. Faunový nález netopýřů je nebyvale bohatý ve vrstvách odpovídajících Eemu a spodnímu Vistulianu. Ten je typický přítomností termofilních prvků (*Rhinolophus ferrumequium* a *Miniopterus schreibersii*) a širokým spektrem taxonů včetně dendrofilních a vzácných prvků (*Plecotus auritus*, *Myotis brandtii*, *M. emarginatus*, *M. nattereri* a *M. blythii*). Lithofilní formy (*Eptesicus serotinus*, *Vespertilio murinus* a *Nyctalus noctula*) se objevují nepřetržitě ve všech vrstvách a představují dominující složku společenstva. V eemských vrstvách jsou ale navíc druhy *Hypsugo savii* a *Pipistrellus* cf. *kuhlii*, které chybějí ve svrchních vrstvách, zatímco *Pipistrellus pipistrellus* se objevuje nejdříve až ve spodním holocénu.

ACKNOWLEDGMENTS

We are heartily grateful to Professor A. K. AGADJANIAN (PIN RAS) for an all-round support in our research. We would also like to thank G. S. RAUTIAN (PIN RAS) for valuable comments on the manuscript. This study was supported by the Presidium of the Russian Academy of Sciences (Program no. 25, “Biosphere Origin and Evolution”) and “Historical Dynamics of Bioresources As a Prerequisite for Their Conservation and Harmonious Exploitation,” the Russian Foundation for Basic Research (project nos. 04-05-64805 and 05-04-48493), and the Russian State Program for Support of Leading Scientific Schools (project no. NSh-6228.2006.4).

REFERENCES

- AGADJANIAN A. K. & ROSSINA V. V., 2001: [Bats from Pleistocene deposits of the Denisova cave]. *The Problems of Archeology, Ethnography, Anthropology of Siberia and Contiguous Territories* (Novosibirsk), **7**: 33–36 (in Russian, with a summary in English).
- BARYSHNIKOV G. F. & GOLOVANOVA L. V., 1989: [Mammals of the Mousterian site Matuzka in the Kuban Caucasus]. *Proc. Zool. Inst. AS USSR*, **189**: 3–55 (in Russian, with a summary in English).
- BENDA P. & TSYTSULINA K. A., 2000: Taxonomic revision of *Myotis mystacinus* group (Mammalia: Chiroptera) in Western Palearctic. *Acta Soc. Zool. Bohem.*, **64**: 331–398.
- BOBRINSKIJ N. A., KUZNECOV B. A. & KUZJAKIN A. P., 1965: [*Key to Identification of Mammals of the USSR*] Prosvjaščenie, Moskva, 384 pp (in Russian).
- FILIPPOV A. G. & TIUNOV M. P., 1999: [Bat remains in caves of Irkutsk region]. *Plecotus et al.*, **2**: 100–108 (in Russian, with a summary in English).
- GAZARYAN S. V., 2002: [*The Ecological and Faunal Analyses of the Bat Populations of the Western Caucasus*]. Unpublished PhD Thesis, Moskva, 216 pp (in Russian).
- GAZARYAN S. V., 2003: [Current faunal status of the Daubenton's bat *Myotis daubentonii* (Chiroptera, Vespertilionidae) in the Caucasus]. *Plecotus et al.*, **6**: 37–48 (in Russian, with a summary in English).
- GOLOVANOVA L., 1996: Paleolithic of the Northern Caucasus. Pp.: 260–261. In: *The Workshops and the Posters of the XIII International Congress of Prehistoric and Prohistoric Sciences*. Forli (Italy), 8–14 September 1996.
- GOLOVANOVA L. V., BARYSHNIKOV G. F., LEVKOVSKAYA G. M. & NESMEYANOV S. A., 1995: [Multilayer Mousterian site Matuzka in the Northern Caucasus (results of research 1985–1989)]. *Russian Archeology*, **3**: 105–118; **4**: 77–86 (in Russian, with summaries in English).
- HORÁČEK I. & JAHELKOVÁ H., 2005: History of the *Pipistrellus pipistrellus* group in Central Europe in light of its fossil record. *Acta Chiropterol.*, **7**: 189–204.
- KOWALSKI K., 1995: Taphonomy of bats (Chiroptera). *Geobios, M. S.*, **18**: 251–256
- KUZJAKIN A. P., 1950: [*Bats*]. Sovetskaja Nauka, Moskva, 443 pp (in Russian).
- NADACHOWSKI A. & BARYSHNIKOV G., 1991: Pleistocene snow voles (*Chionomys* Miller, 1908) (Rodentia, Mammalia) from Northern Caucasus (USSR). *Acta Zool. Cracov.*, **34**: 437–451.
- NESMEYANOV S. A., 1999: [*Geomorphological Aspects of Paleolithic Palaeoecology of the Western Caucasus*]. Scientific World, Moskva, 392 pp (in Russian, with a summary in English).
- OBUCH J., 1989: Chiropteran thanatocenoses in rocky fissures. P.: 453. In: Hanák V., HORÁČEK I. & GAILSER J. (eds): *European Bat Research 1987*. Charles University Press, Praha, 718 pp.
- OVIDOV N. D., 1974: [The subfossil bat records in the caves of Siberia and the Far East]. Pp.: 84–90. In: KUZJAKIN A. P. & STRELKOV P. P. (eds.): [*First All-Union Conference on Bats*]. Zoological Institute AN USSR, Leningrad (in Russian).
- POTAPOVA O. R., 1992: [Birds from the Mousterian site Matuzka in the North-Western Caucasus]. *Proc. Zool. Inst. RAS*, **246**: 141–159 (in Russian, with a summary in English).
- ROSSINA V. V., 2002: [Odontological diversity of mouse-eared bats (*Myotis*) from Palaeartic]. *Plecotus et al.*, Pars Spec.: 27–29 (in Russian, with a summary in English).
- ROSSINA V. V., 2004: [The dynamics of bat fauna (Chiroptera, Mammalia) of Northwest Altay in Pleistocene and Holocene]. Pp.: 208–218. In: [*Ecological Mechanisms of Dynamics and Stability of Biota*]. Institute of Plants and Animals Ecology UrO RAS, Ekaterinburg (in Russian).
- ROSSINA V. V., 2005: [The influence of the anthropogenous factor on bats community in Pleistocene of Altai]. Pp.: 78–80. In: [*Problems of Paleontology and Archeology of the South of Russia and Neighbouring Territories. Materials of International Conference, Azov, May 18–20, 2005*]. Rostov-na-Don (in Russian).
- RUPRECHT A. L., 1990: [Bats (Chiroptera) in the food of owls in the Nadnotecka Forest]. *Przegl. Zool.*, **34**: 349–358 (in Polish, with a summary in English).
- RUPRECHT A. L., 2005: [Some aspects of my research on bats (Chiroptera) of Poland in 1964–1990]. *Leśne Prace Badawcze*, **2005**(2): 107–119.

- SCHMIDT E. & TOPAL G., 1971: Fledermäuse in Eulengewöllen aus Ungarn. *Vertebrata Hungar.*, **12**: 93–102. (in Hungarian, with a summary in German).
- TIUNOV M. P., 1997: [*The Bats of the Far East of Russia*]. Dal'nauka, Vladivostok, 134 pp (in Russian, with a summary in English).
- VEREŠČAGIN H. K., 1959: [*Mammals of the Caucasus. History of the Fauna Forming*]. Zoological Institute AN USSR, Moskva and Leningrad, 704 pp (in Russian).
- ZAITSEV M. V. & OSIPOVA V. A., 2004: [Insectivorous mammals (Insectivora) of the Late Pleistocene in the Northern Caucasus]. *Zool. Žurnal*, **83**: 851–868 (in Russian, with a summary in English).