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Quaternary fauna and flora of the Southern Urals region (Bashkortostan Republic)

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A B S T R A C T

From the 1960s a considerable amount of data on mammals, molluscs, and vegetation from Quaternary deposits of the Southern Urals region has been produced. The age of key stratigraphic localities was established by using different geological and palaeontological evidence, palaeomagnetic and absolute dating. The flora and fauna history is summarized for the southern part of the Urals. The result is that the history of fossil organic forms and plant associations could be traced, characteristic complexes could be recognized and a curve with changes in the vegetation could be constructed. Results of biostratigraphical investigations are given in the review.

1. Introduction

The described region is located in the eastern part of the Eastern European Plain and the Southern Urals (Russian Federation) (Fig. 1).

From the 1960s a considerable amount of data on mammals, molluscs, and floras from Quaternary deposits of key stratigraphic localities of the Southern Urals region has been produced. The age of key stratigraphic localities was established by using different geological and palaeontological evidence, as well as palaeomagnetic and absolute dating.

The principal aim of the manuscript is to give an overview of the main results of many years of investigations of the Quaternary fauna and flora in the region.

The result is that the history of fossil organic forms and plant associations could be traced, characteristic complexes could be recognized and a curve with changes in the vegetation could be constructed.

The regional stratigraphic scheme by Yakhimovich et al. (1987) has been used in this paper. Its correlation with the scheme of the East-European Platform can be found in Shik et al. (2002).

Fauna and flora remains have been investigated from more than 28 Late Pliocene/Eopleistocene and 210 Quaternary localities. The authors of this paper have investigated and described more than half of all sites and critically revised the other data (Yakhimovich et al., 1965, 1972, 1977, 1981, 1983, 1985, 1987, 1992, 1998, 2000; Yakovlev, 1985, 1988, 1996; Khabibullina, 1986; Danukalova and Yakovlev, 1988; Danukalova and Yakovlev, (2001); Danukalova, 1996; Danukalova et al., 1997, 2000a,b, 2001, 2002 and others).

2. Floras

2.1. Akchagyl

Late Kinel floras existed during sedimentation of the deposits of the Karlaman and Kumurly suites (Fig. 2). During this time the total number of species decreased, and at the end of this time many Pliocene species had disappeared. Coniferous forests with an admixture of broad-leaved trees spread southward. *Pinus* sect. *Cembrae* and *Picea* dominated in the taiga forests and the number of broad-leaved trees decreased in the northern part (Yakhimovich et al., 1983, 2000).

Floras of Akchagyl type existed during the Middle Akchagyl in the Zilim-Vasiljevo and Akkulaevo suites. These floras are characterized by a low variety of main forest tree species and by predominance of modern species. During the first part of the Zilim-Vasiljevo, steppes with a small *Betula* and broad-leaved forests were widespread. Coniferous *Picea–Tsuga* and *Picea–Abies* forests dominated in the second part of the Zilim-Vasiljevo. The percentage of deciduous trees decreased (Yakhimovich et al., 1977, 2000).

Similar coniferous woods were preserved in the beginning of the Akkulaevo suite, but the percentage of deciduous trees and *Tsuga* decreased in the composition. Later these woods were

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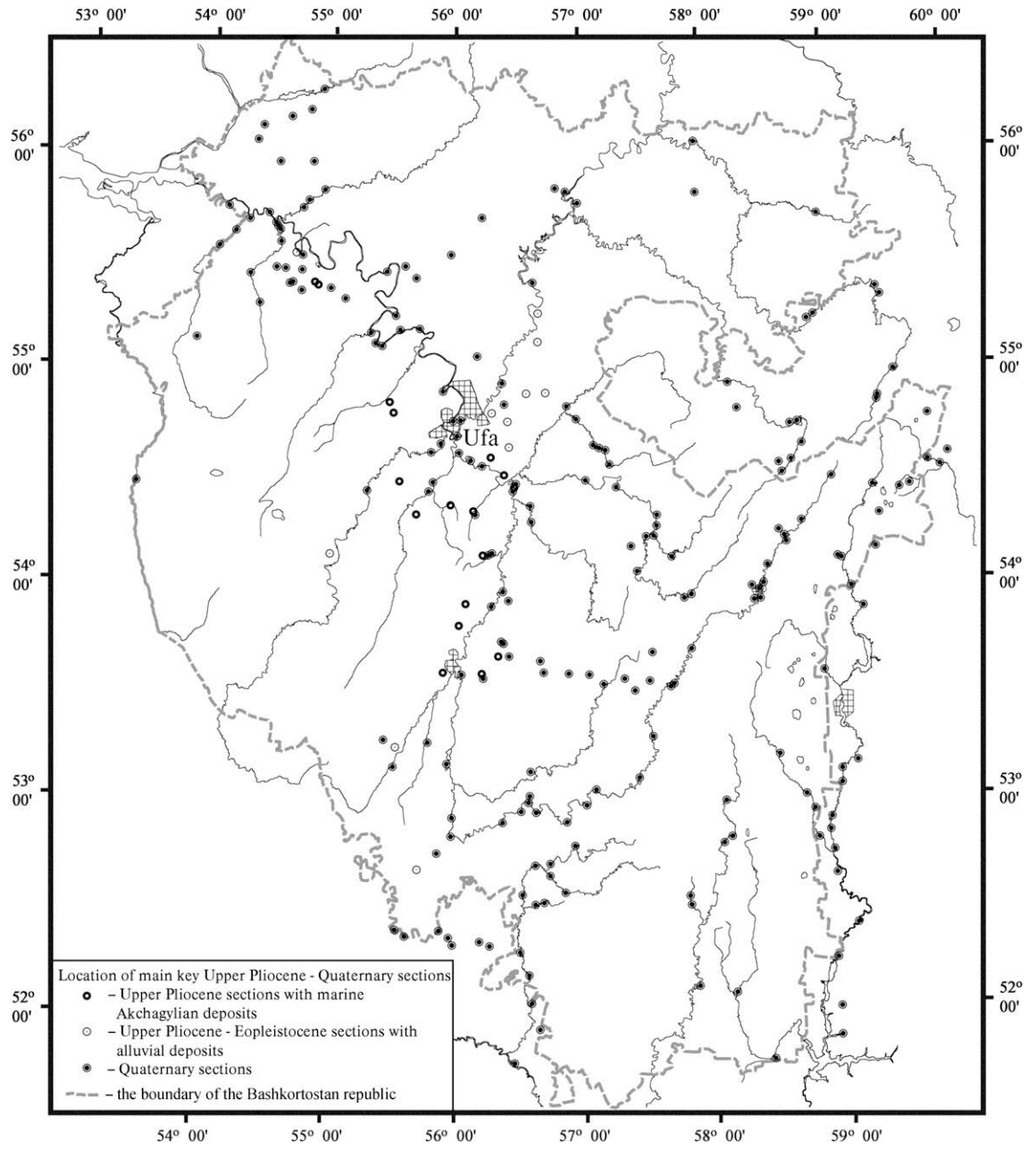

Fig. 1. Map of the studied area and main Late Pliocene–Quaternary sections.

replaced by xerophytic steppe and small *Betula* and broad-leaved forests, and the prevalent type of vegetation again became woods of coniferous trees. Forest-steppe landscapes predominated at the end of the Akkulaevo (Yakhimovich et al., 1981).

In the Late Akchagyl (Voevodskoye) *Artemisia*–Chenopodiaceae and herbs–Poaceae steppes were widespread.

2.2. Eopleistocene

Before the Eopleistocene, the climate became colder and moisture increased. Taiga forest with *Pinus*, *Abies* and *Tsuga* spread to the south.

Modern flora existed in the Southern Fore-Urals from the beginning of the Eopleistocene. The main types of vegetation changed during the Early Eopleistocene: from warm forest-steppe to cold steppe (Dema), then to warm forest-steppe and again to cold steppe (Davlekanovo). During the Karmasan (Late Eopleistocene), the herbs–*Artemisia* steppe changed to coniferous – broad-leaved forests and later to *Betula*–*Pinus* forests. The percentage of broad-leaved trees decreased and the species variety of grasses reduced (Yakhimovich et al., 1981, 1992).

In the Oktober suite, taiga forest with small quantities of *Betula*, *Tilia* and *Fraxinus* covered the main part of the territory.

2.3. Neopleistocene

In the Early Neopleistocene, in the beginning of the Minzityarovo suite, the climate was warm and became colder towards the end of the interval. In this period *Artemisia*–Chenopodiaceae–herbs associations were widespread. The percentage of *Pinus* decreased and broad-leaved trees disappeared. In the Early Chui-Atasevo suite, herbs–*Artemisia* steppe and *Betula* forests with *Tilia*, *Quercus*

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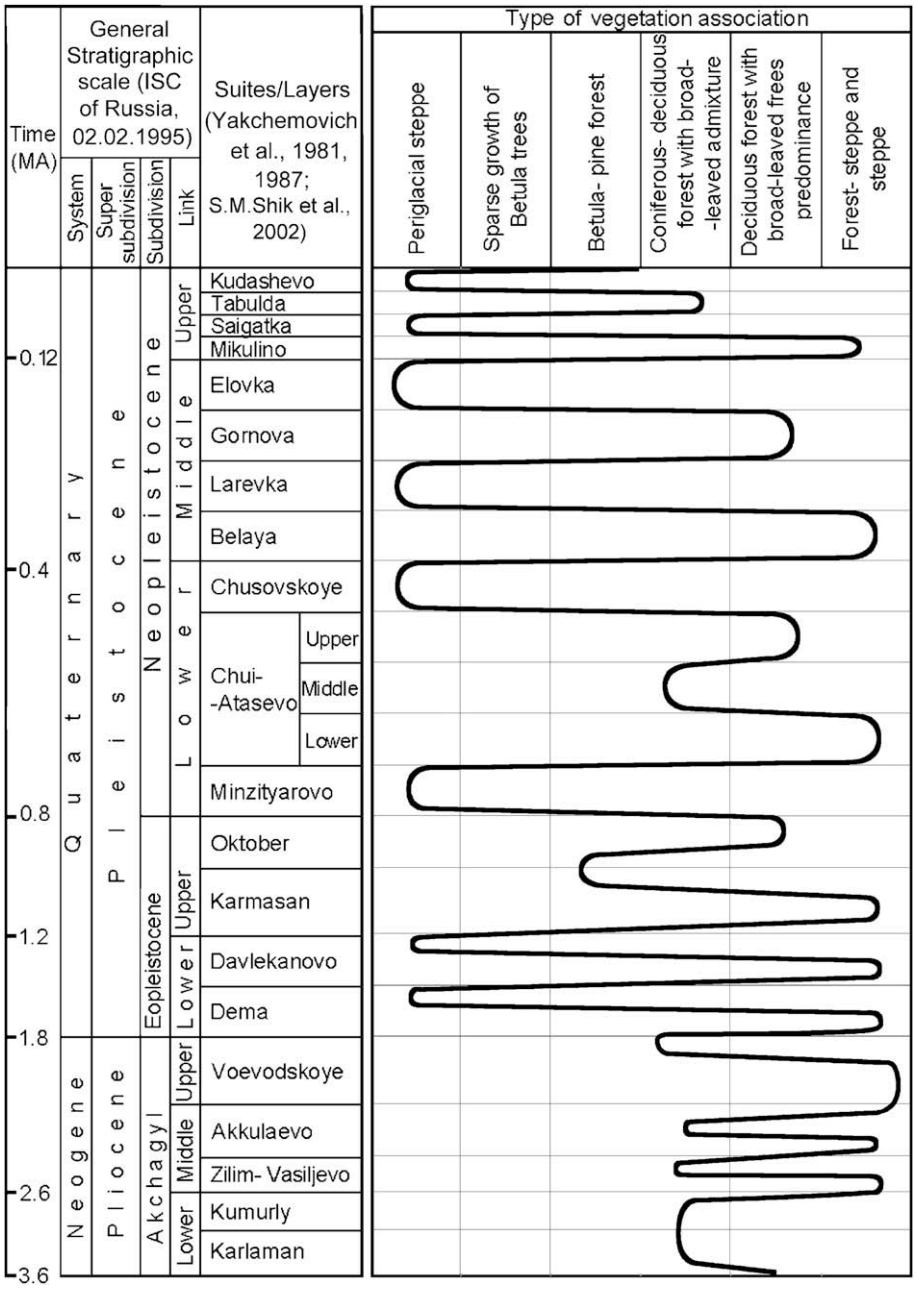

Fig. 2. Reconstruction of the main stages of flora development in the Pliocene and Pleistocene, Southern Fore-Urals (Yakhimovich et al., 1981 and authors' interpretation).

and *Fraxinus* existed. In the Middle Chui-Atasevo, the climate became colder and moisture increased. In this interval taiga forests dominated. In the Late Chui-Atasevo broad-leaved-*Betula* forests and meadow-steppes increased. Periglacial landscapes dominated during the Oka glaciation (Yakhimovich et al., 1981, 1987).

In the Middle Neopleistocene of the Southern Fore-Urals, two warm (Belaya and Gornova) and two cold (Larevka and Elovka) intervals are recognized (Yakhimovich et al., 1981, 1987, 1992). Herbs–steppe communities predominated in the beginning of the Belaya interval, while in the second part of this period the role of taiga forests increased. In the beginning of the Larevka, cold steppe conditions dominated and the role of *Picea* taiga forests increased. In the beginning of the Gornova interglacial, the role of *Pinus–Betula* forests with broad-leaved trees increased. *Picea* forests spread in the northern part of the territory. Herbs–*Artemisia* steppe with rare coniferous forests prevailed in the Elovka.

The Late Neopleistocene can be subdivided into two warm and two cold phases. Forest–steppe and steppe (southern parts of the region) and *Betula–Pinus* forests with *Ulmus*, *Quercus* and *Tilia* (northern parts of the region) dominated during the Mikulino. In the beginning of the Saigatka (Kalinin[1]), broad-leaved trees disappeared from the forest biocoenosis, the percentage of coniferous trees and Chenopodiaceae increased, and *Ephedra* appeared. *Abies–Picea–Pinus* forests with small quantities of broad-leaved trees prevailed in the Tabulda (Leningrad). In the Kudashevo (Ostashkovo), a cold climate dominated and herb–*Artemisia*–Chenopodiaceae meadow–steppe associations dominated in the southern part of the territory and at the latitude

[1] Many researchers consider Kalinin, Leningrad, and Ostashkov as separate units of the Late Pleistocene Valdai glacial interval.

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of Ufa town. In the northern parts of the region *Picea–Pinus* forests with *Betula* admixture predominated.

Data on the vegetation of the Late Glacial are not numerous (Fig. 3), and the Early Dryas was not well determined (Yakhimovich et al., 1992).

The Bølling was described near Karmaskaly district centre (the Chatra creek) and in cave deposits. Single *Tilia*, *Betula* and *Pinus* sect. *Cembrae* were found in *Picea* forests of that time. In the Early-Middle Dryas, open woodlands with Cyperaceae, Poaceae, *Artemisia* and Chenopodiaceae predominated in the Southern Fore-Urals. Rare *Betula–Pinus* forests covered small areas. During the Allerød, *Pinus* forests with *Picea*, *Tilia* and *Betula* were widespread. Meadow–steppe associations with sparse growth of coniferous-*Betula* trees existed in the Late Dryas (Nemkova, 1978).

Evidence of five phases in changes of vegetation was found in the Holocene in the Fore-Urals. *Betula* forests with a small admixture of coniferous and broad-leaved trees characterized the Preboreal; herb–*Artemisia* steppe dominated in the forest-steppe zone.

Forests with coniferous (*Pinus*) trees existed during the Boreal. The role of *Picea* and broad-leaved trees increased in forests during the Atlantic. *Pinus* were usual in forests of the northern territories, *Tilia* and *Betula* dominated in the forests in southern parts during the Subboreal. The type of vegetation during the Subatlantic was close to the modern type: *Picea–Pinus* forests in the northern part of

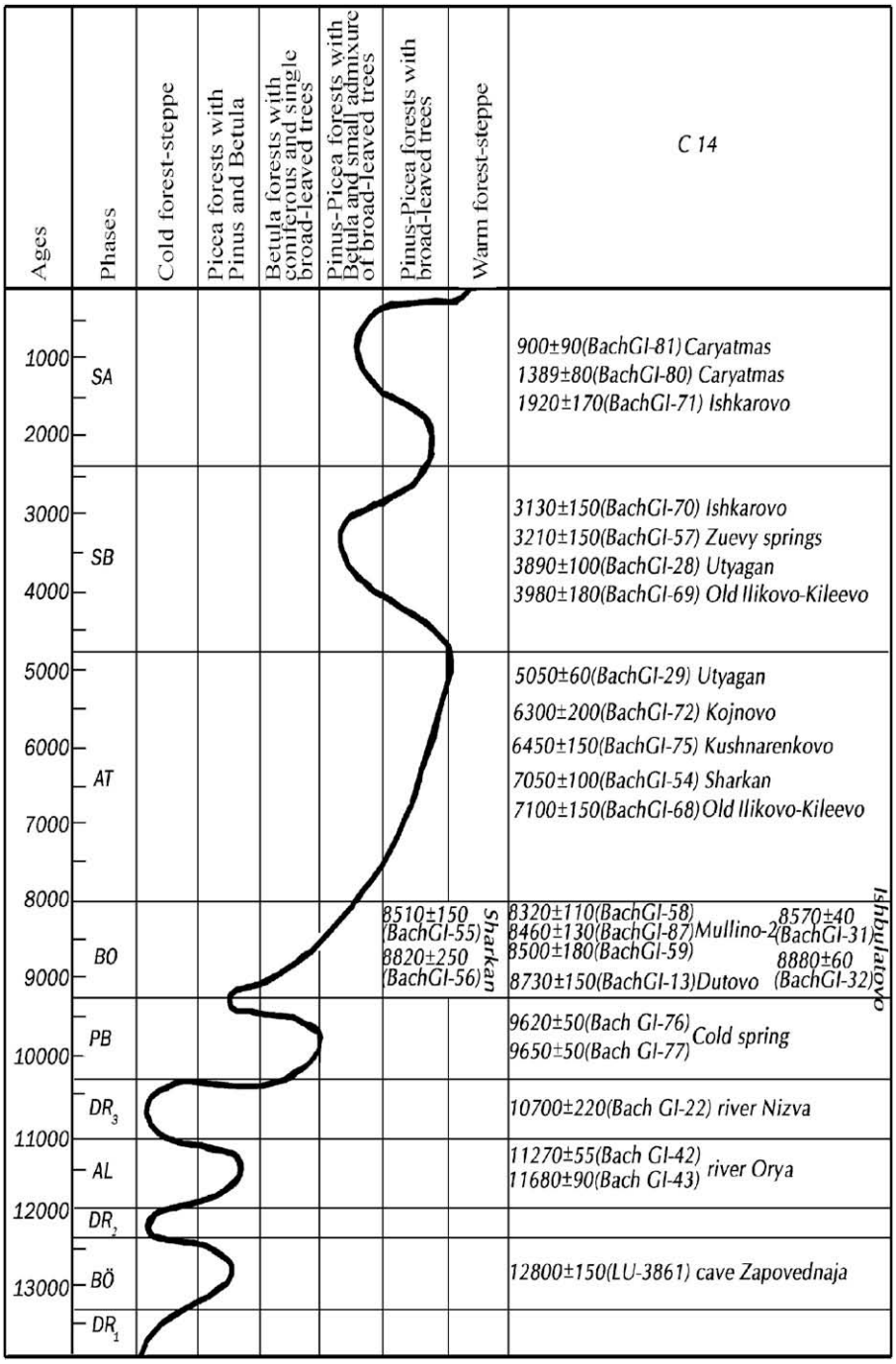

Fig. 3. Reconstruction of the main stages of flora development in the Holocene, Southern Fore-Urals (Nemkova, 1978 and authors' interpretation).

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the Southern Fore-Urals, and with an admixture of *Quercus* and *Ulmus* in the southern part. The percentage of open woodlands increased towards the end of that time.

3. Mega mammals of the Southern Urals in the Late Pliocene–Holocene

Bone remains of mega mammals were found in alluvium, lakes, and cave sites and at ancient human settlements. All the Pliocene, Eopleistocene, and Early Neopleistocene finds and most of the Middle Neopleistocene fauna finds are related to alluvium and lake sediments. Two Middle Neopleistocene sites, most of Late Neopleistocene sites and part of the Holocene fauna sites were found in caves. Most of the Holocene fauna localities are archaeological sites (Table 1).

Table 1
Species composition of South Ural Mega mammals during the Neopleistocene and Holocene.

Species	Chronological periods						
	Q^2_{II}	Q^{2-3}_{III}	Q^3_{III}	DR-3	AT	SB	SA
Lepus tanaiticus		+	+	+	+	–	
Lepus timidus						+	+
Lepus europaeus							+
Lepus sp.	+						
Marmota bobac		+	+	+	+	+	
Marmota sp.	+						
Castor fiber	+	+		+	+	+	+
Canis lupus	+	+	+	+	+	+	+
Canis cf. *lupus*	+						
Alopex lagopus	+	+	+	+			
Vulpes vulpes	+	+	+		+	+	+
Vulpes corsac		+	+				
Ursus arctos			+		+	+	+
Ursus spelaeus	+	+	+	–	–	–	–
Ursus rossicus	+	+	–	–	–	–	–
Martes sp.	+	+	+		+	+	+
Gulo gulo		+	+		+	+	+
G. gulo	+						
Mustela sp.	+	+	+	+	+	+	+
Putorius sp.	+	+	+		+	+	+
Meles meles					+	+	+
Lutra lutra	+				+	+	+
Crocuta spelaea		+	–	–	–	–	–
Panthera spelaea		+	+	–	–	–	–
Lynx lynx						+	+
Mammuthus primigenius		+	+	–	–	–	–
Equus (E.) cf. *latipes*		+	+	–	–	–	–
Equus (E.) sp.	+						
Coelodonta antiquitatis	+	+	+	–	–	–	–
Sus scrofa					+	+	
Cervus elaphus	+	+			+	+	
Capreolus pygargus				+	+	+	+
Megaloceros giganteus		+		+	–	–	–
Alces alces			+		+	+	+
Rangifer tarandus	+	+	+	+	+	+	+
Bos primigenius					+	+	–
Bison priscus	+	+	+	+	–	–	–
Saiga tatarica		+	+	+			
Ovis ammon		+					
Equus caballus						+	+
Bos taurus						+	+
Ovis aries et *Capra hireus*						+	+
Sus scrofa f. *domestica*						+	+
Canis familaris					+	+	+

(+) – Significant bone finds; (–) – extinct species; Q^2_{II} – second half of the Middle Neopleistocene; Q^{2-3}_{III} – Mega interstadial of the Late Neopleistocene; Q^3_{III} – Late Glacial; DR-3 – Late Dryas; AT, SB, SA – Atlantic, Subboreal, and Subatlantic periods of the Holocene.

Fauna complexes of the Late Pliocene are represented by solitary bone finds of *Mastodon borsoni* Hays, 1834 and *Tragelaphini* gen. (Beliaeva, 1948; Yakhimovich et al., 1965).

Eopleistocene faunas are represented by scarce finds of *Mammuthus meridionalis* Nesti, 1825 and *Equus stenonis* Cocchi, 1867 (Beliaeva, 1948).

Early Neopleistocene faunas are represented by finds of *Mammuthus trogotherii* Pohlid, 1885, *Dicerorhinus kirchbergensis* Jager, 1839, *Elasmotherium sibiricum* Fischer, 1808, *Cervalces latifions* Johnson, 1834 and *Bison* cf. *schoetensacki* Freudenberg, 1910 (Yakhimovich et al., 1965, 1985).

Middle Neopleistocene faunas are represented by finds of early forms of *Mammuthus primigenius* Blumenbach, 1799, *E. sibiricum* Fischer, 1808, *Megaloceros giganteus* Blumenbach, 1803.

Richer fauna complexes are known from caves. The earlier fauna is dated to the second half of the Middle Neopleistocene, and corresponds to the Gorkinsky or Moscow periods of Eastern Europe (Shik et al., 2002). This fauna is found in two caves: Ignatievskaia (Test pit V, layer 9) and Serpievsky I (layer 3). A special feature of the fauna is the presence in its composition of small wolverine (*Gulo gulo*) forms and wolf (*Canis* cf. *lupus*). The fauna is synchronous with the Khazar fauna complex of Eastern Europe.

The next period of the fauna complex, according to radiocarbon data, belongs to the middle of the Late Neopleistocene and corresponds to the Middle Valdai mega interstadial of Eastern Europe or to the Middle Würm of Western Europe. The theriofauna of this period is characterized by the presence of *Ovis ammon* and *Castor fiber* remains, and relatively large numbers of *Cervus elaphus* remains. The Late Glacial fauna is represented by localities which have uncalibrated radiocarbon data from 17,000 to 13,000 BP. The theriofauna of that period is characterized by an absence of *C. elaphus*, *O. ammon*, *Crocuta spelea* and a presence of *Ursus arctos* and *Alces alces*. Two localities were referred to the Late Dryas (DR-3) on the basis of radiocarbon data. Specific for this period is the presence of *Megaloceros giganteus*. Bones of this species are dated by AMS to 10775 ± 75 (OxA-10704) and 10260 ± 55 (OxA-10676) BP. In this period *Capreolus pygargus* first appeared.

Holocene faunas are dated both by radiocarbon method and by archaeological material. A speciality of the theriofauna composition of the Early and beginning of the Middle Holocene (Preboreal-Atlantic) is the presence of *Bos primigenius* and *Lepus tanaiticus*. The Middle Holocene fauna (Subboreal) is characterized by the presence of *Marmota bobac* and *Lepus timidus*, and the Late Holocene fauna (Subatlantic) is characterized by the appearance of *Lepus europaeus*. During the Late and Middle Holocene wild horse – tarpan (*Equus gmelini*) was part of the fauna composition and was replaced by the domestic horse during the Late Holocene. During the second half of the Middle Holocene domestic animals appeared.

4. Late Pliocene small mammals

In Bashkortostan, two Pliocene localities containing abundant small mammals, Akkulaevo-1 and Simbugino, were described by Yakhimovich et al. (1972) and Sukhov (1970). The stratigraphic position and correlation of these faunas are shown in Fig. 4.

The Akkulaevo locality is in the Dema River basin, a left tributary of the Belaya River near the town of Davlekanovo. The base of the section is composed of coastal-marine deposits changing to river mouth deposits. These deposits contain a rich fauna of brackish water molluscs of the Middle Akchagyl and bones of small mammals. A revision of the material collected by Sukhov resulted in the following faunal list for Akkulaevo-1: Insectivora:? *Crocidurosorex* sp., *Sorex* sp., and *Talpa* sp.; Lagomorpha: *Ochotona* sp. and *Pliolagus* cf. *brachygnatus*; Rodentia: *Trogontherium* sp., *Apodemus* cf. *sylvaticus*, *Cricetus nanus*, *Cricetulus* sp., *Prosiphneus* ex gr. *praetingi*, *Villanyia* ex gr. *exilis*, *Borsodia* sp., *Promimomys*

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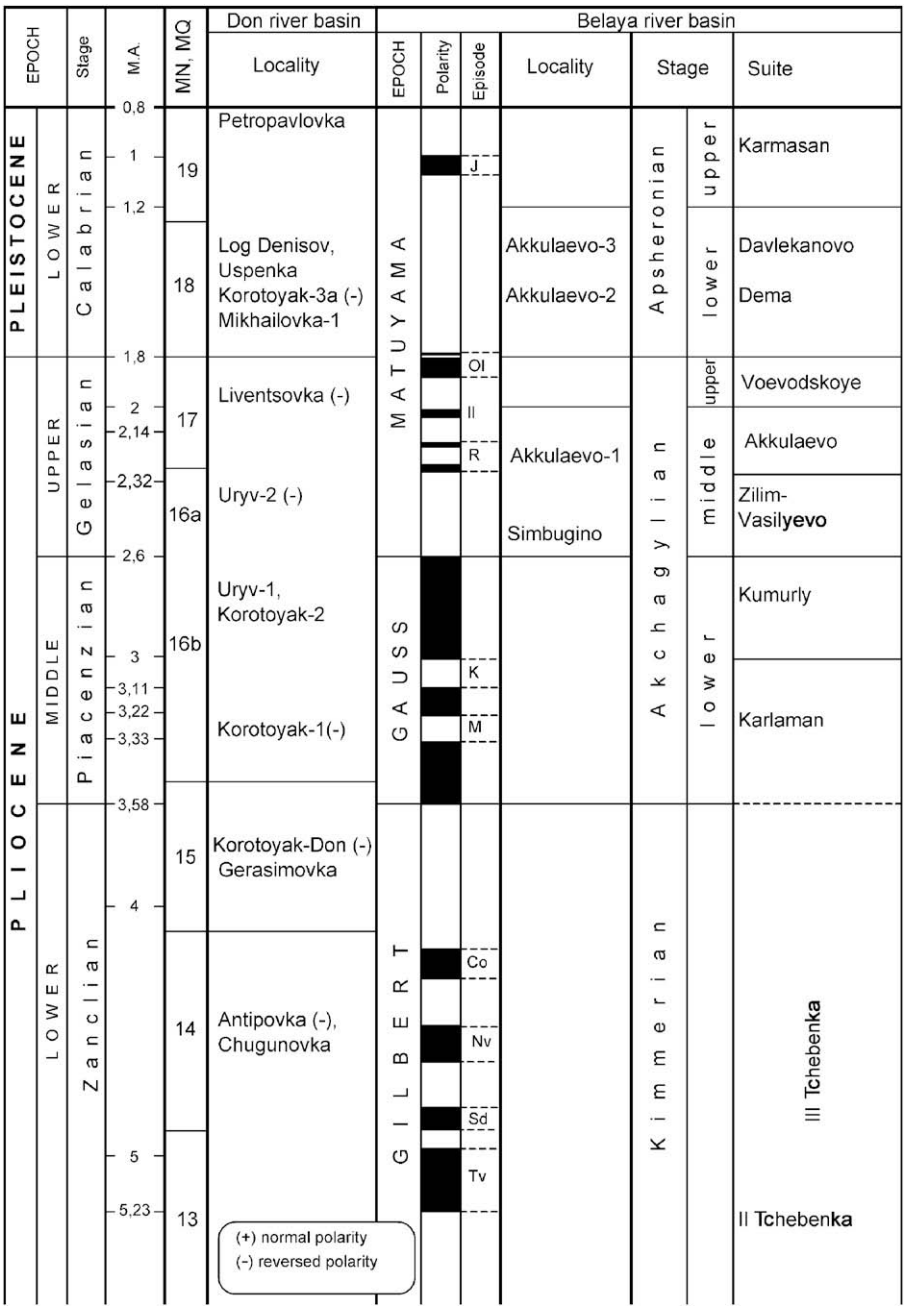

Fig. 4. Stratigraphic position of the Pliocene small mammal faunas from the Southern Fore-Urals.

gracilis akkulaewae, *Promimomys baschkirica*, and *Mimomys polonicus*. Lagomorphs represent about 1% of the taphocoenosis. Voles of the genera *Villanyia*, *Promimomys*, and *Mimomys* appear highly specialized. Their molars have well-developed dentine tracks, and teeth of *Mimomys* have external cement. The features mentioned above allow a correlation of the small mammals from the Akkulaevo Formation to faunas of the second half of the Middle Pliocene, such as the Uryv-2 (Don River) and Rebelice Krolewski (Poland) faunas.

The Akkulaevo section contains two bone-bearing horizons with Eopleistocene small mammals, including *Allophaiomys*.

The Simbugino locality is in the Blagovarsky District in the Karmasan River basin. The bone-bearing layer is composed of sands and shingles of the Kumurly Formation. The revised faunal list of small mammals includes Insectivora: *Sorex* cf. *runtonensis*, *Sorex* cf. *minutus*, *Petenyia* sp., *Beremendia* sp., *Blarinoides mariae*, *Allosorex* sp., *Talpa* sp., *Desmana* sp., and *Erinaceus* sp.; Lagomorpha: *Ochotona* sp. and *Pliolagus brachygnatus*, Rodentia: *Tamias orlovi*, *Spermophilus* sp., *Trogontherium minus*, *Castor* sp., *Sinocastor zdanskyi*, *Apodemus* sp., *Cricetus* sp., *Cricetulus* sp., *Prosiphneus* ex gr. *praetingi*, *Germanomys trilobodon*, *Synaptomys (Plioctomys) mimomiformis*, *Villanyia* ex gr. *exilis*, *Borsodia* sp., *Promimomys gracilis akkulaewae*, *Promimomys baschkirica*, and *Mimomys polonicus*. The proportion of lagomorphs in the Simbugino taphocoenosis is 10%. Insectivores and rodents are relatively diverse. However, the evolutionary level of voles is similar to that of voles from the Akkulaevo Formation. Their molars also have high tracks, and teeth of *Mimomys* have external cement. This shows that small mammals from Simbugino are comparable to the faunas from the second half of the

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Middle Pliocene, such as the Akkulaevo, Uryv-2, and Rebelice Krolewski faunas. However, it is not very probable that they are synchronous. The Simbugino fauna occurred in different, more favourable, palaeogeographical conditions and probably belonged to an earlier phase of the Middle Pliocene.

5. Quaternary small mammals

Sukhov (1972, 1976, 1978), Smirnov et al. (1990) and Yakovlev (Danukalova et al., 2002) studied the Neopleistocene and Holocene small mammals faunas of the region.

Microtus (Stenocranius) gregaloides, *Mimomys pusillus*, *Mimomys intermedius*, *Lagurus transiens*, *Myospalax* sp. (Table 2) and the appearance of *Arvicola mosbachensis* (Chui-Atasevo, section II) characterized the Early Neopleistocene faunas (Chui-Atasevo, sections I, II). The species composition reflects the forest-steppe conditions. In the Middle Neopleistocene small mammal associations were formed by steppe species – *Lagurus lagurus*, *Microtus gregalis*, *Eolagurus luteus*, and *Marmota* aff. *bobac*, *Alactagulus* sp. and others. *Arvicola* cf. *chosaricus* (Krasnyi Yar) was discovered in the fauna dating to the Larevka. Species which are characteristic of forest biotopes appeared in the second part of the Middle Neopleistocene: *Clethrionomys* cf. *glareolus*, *Microtus* ex gr. *arvalis-agrestis* (Klimovka, Gruzdevka).

The forest species *Apodemus flavicollis*, *Clethrionomys rufocanus*, *Microtus agrestis* and others (Krasnyi Bor) characterized the fauna of the beginning of the Late Pleistocene (Mikulino Interglacial). During the Saigatka cold time, *Microtus gregalis* and *Lagurus lagurus*, *Clethrionomys rufocanus*, *Clethrionomys* ex gr. *rutilus* (Gornova) are numerous in the forest-steppe faunas.

During Neopleistocene times, the Southern Fore-Urals were the European forest-steppe refugia where during the glacial interval steppe and forest species survived. After the glacial period the forest–steppe associations dispersed to the West as well as to the

Table 2
Small mammal faunas for some periods of the Neopleistocene (the Southern Urals region).

Species	Neopleistocene					
	Lower		Middle		Upper	
	Chui-Atasevo 1[a]	Chui-Atasevo 2	Larevka	Klimovka–Elovka	Mikulino	Saigatka
Talpa sp.		++			++	
Sorex sp.		++			++	+
Lepus sp.		+			++	
Ochotona sp.	++	++	+	++		++
Spermophilus sp.	+	++	+	+		+
Marmota sp.				++		
Marmota aff. *Bobac*			+			
Gliridae gen.					++	
Sicista sp.	+			++		
Allactaga sp.		+	+			
Alactagulus sp.			+	+		
Apodemus ex gr. *uralensis-agrarius*					++	
Apodemus flavicollis					++	
Ellobius sp.				++		+
Allocricetulus eversmanni			+			+
Cricetulus sp.			+	+		
Cricetus cricetus					++	
Cricetus sp.		+				
Myospalax sp.	+	++				
Clethrionomys rufocanus					++	+
Clethrionomys glareolus				++		
Clethrionomys ex gr. *glareolus*	++	++		++		
Clethrionomys sp. (ex gr. *glareolus*)		++		+		
Prolagurus cf. *posterius*	+	++				
Lagurus transiens	++	++				
Lagurus lagurus			++++	++++		+++
Eolagurus luteus			++	++		++
Eolagurus luteus praeluteus		+				
Lemmus sp.		+				
Mimomys pusillus	+++	++				
Mimomys intermedius	++	++				
Arvicola mosbachensis		++				
Arvicola cf. *chosaricus*			+			
Arvicola terrestris					+++	+
Arvicola sp.				++		
Microtus (Stenocranius) hintoni	++	+++				
Microtus (Stenocranius) gregaloides	+	+++				
Microtus (Terricola) arvalidens		+				
Microtus (Stenocranius) gregalis	++	++	+++	++++		+++
Microtus oeconomus			++	++		+++
Microtus ex gr. *Oeconomus*	+++	++				
Microtus cf. *oeconomus*				++		
Microtus agrestis					++	
Microtus ex gr. *arvalis-agrestis*	+++	+++		++		
Microtus arvalis					++	
Microtus ex gr. *Arvalis*				++		
Microtus ex gr. *malei-hyperboreus*	++	++				
Microtus ex gr. *Malei*			+			

[a] Chui-Atasevo 1, Chui-Atasevo 2, Larevka and others are the names of the horizons.

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Table 3
Late Neopleistocene and Holocene small mammal faunas of the Southern Urals.

Species	Late Neopleistocene			Holocene			
	Mikulino	Tabulda	Kudashevo	Early	Middle	Late	
						Beginning	End
Talpa europaea				+	+	++	+++
Talpa sp.	+	+	+				
Sorex sp.	++	+	+	+	+	++	++
Neomys sp	+	+	+		+	+	++
Crocidura sp.	+					+	
Lepus sp.	+	+	+	+	++	+	++
Ochotona sp.	++	++	++	++	++	+	
Pteromys volans						+	+
Sciurus vulgaris				+		+	+
Tamias sibiricus							+
Spermophilus sp.	+	+	+	++	+	+	
Marmota sp.	+	+	+				
Eliomys quercinus						+	++
Sicista sp.	+		+	+	+	++	++
Allactaga sp.			+				
Allactaga major				+			
Alactagulus sp.			+				
Apodemus uralensis	+	+				++	++
Apodemus ex gr. *uralensis-agrarius*					+		++
Apodemus flavicollis	+	+		+		++	++
Micromys minutus						+	
Rattus sp.							+
Ellobius sp.				+	+	+	
Allocricetulus eversmanni	+		+	++			
Cricetulus migratorius	+	+	++	++		+	
Cricetus cricetus	+	+	+	+		+++	+++
Clethrionomys rufocanus	+	++	+	++		++	++
Clethrionomys glareolus	+	++				++	++
Clethrionomys ex gr. *glareolus-rutilus*				++	++		+++
Clethrionomys rutilus	++	+	+			+++	++
Lagurus lagurus	++	+	++	++	++	+	
Eolagurus luteus			+	+			
Dicrostonyx simplicior	++						
Dicrostonyx guilielmi		+	++				
Dicrostonyx sp.				+			
Lemmus sibiricus	++	++	+				
Myopus schisticolor	+						
Arvicola terrestris	++	++	+	++	++	+++	+++
Microtus gregalis	++++	++++	++++	+++	+++	+	
Microtus oeconomus	+++	++++	+++	+++	+++	++	++
Microtus agrestis	++	++	+	++	++	+++	+++
Microtus ex gr. *arvalis-agrestis*				+			++
Microtus arvalis	++		+	+	++	+++	++

+ – Rare and very rare (0.9%); ++ – common (1–9.9%); +++ – numerous (10–29.9%); ++++ – very numerous (more than 30%).

East, offering good correlations between Eastern European and Western Siberian faunas.

In the Southern Urals the development of the fauna differed from that of the Fore-Urals (Table 3). At the end of the Mikulino Interglacial (Serpievskaya fauna), *Dicrostonyx simplicior* and *Lemmus sibiricus* were common. Associations with *Dicrostonyx guilielmi*, *Lemmus sibiricus*, *Microtus gregalis* and others spread during the Late Neopleistocene (Aratskaya and Ignatievsky faunas).

In the Early Holocene fauna (Lemeza), species of the Late Neopleistocene have been preserved (*Dicrostonyx* sp., *Allactaga major*), *Microtus gregalis* was numerous, but the main part of this fauna consisting of *Ochotona* sp., *Lagurus lagurus*, *Clethrionomys rufocanus*, *Cl.* ex gr. *glareolus-rutilus*, *Microtus agrestis* was common (Nukatskaya, Lemeza III).

Species of steppe, forest and meadow biotopes (Lemeza II) characterized the Middle Holocene (Atysh fauna) – *Microtus gregalis*, *Lagurus lagurus*, *Clethrionomys* ex gr. *glareolus-rutilus*, *Cl. rufocanus*, and *Microtus agrestis*. In the Late Holocene (Sym fauna), the percentage of steppe species decreased: *Lagurus lagurus*, *Cricetulus migratorius* and *Spermophilus* sp. were rare.

Table 4
Late Pliocene land molluscs of the Southern Fore-Urals.

Species	Late Pliocene	
	Akchagyl	
	Middle	Late
	Akkulaevo	Voevodskoye
Succinea cf. *oblonga* Drap.		+
S. pfeifferi Rossm.	+	
Succinea sp.	+	+
Pupilla muscorum L.	+	
P. cf. mutabilis Steklov	+	
Vertigo sp.		+
Retinella sp.		+
Vallonia pulchella (Müll.)	+	
V. costata Müll.	+	
Vallonia sp.	+	
Bradybaena fruticum Müll.	+	
Helicella sp.	+	+
Strobilops costata Cless.		+
Iphigena sp.	+	+
Scalaxis sp.	+	

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Table 5
Late Pliocene water molluscs of the Southern Fore-Urals.

Species	Late Pliocene		
	Akchagyl		
	Middle		Late
	Zilim-Vasylyevo	Akkulaevo	Voevodskoye
Limnaea stagnalis L.		+	
Limnaea sp.		+	+
Radix auricularia L.		+	
R. pereger Müll.		+	+
R. ovata Drap.		+	
Radix sp.		+	+
Galba sp.		+	+
Stagnicola (Galba) palustris Müll.		+	+
Planorbis planorbis Müll.		+	+
Planorbis sp.			+
Paraspira spirorbis L.		+	
Anisus vortex L.		+	
Gyraulus albus Müll.			+
G. laevis Alder.			+
G. gredleri var. *rossmaessleri* Auers.		+	
Gyraulus sp.		+	
Bathyomphalus contortus L.		+	
Armiger crista L.		+	+
A. crista var. *inermis* Lindh.		+	
Planorbarius corneus L.		+	
Valvata antiqua Sow.	+	+	+
V. cristata Müll.		+	
V. pronaticina Lindh.		+	
V. naticina Menke	+	+	
V. kubanica Krest.	+		
V. piscinalis Müll.	+	+	+
V. piscinalis antiqua Sow.	+	+	
V. pulchella Müll.	+	+	+
Valvata sp.	+	+	+
Viviparus proserpinae Bog.		+	
V. mangikiani Bog.		+	
V. mangikiani singularis G. Ppp.		+	
V. turritus Bog.		+	+
V. cf. *turritus* Bog.		+	
V. bashkirikus G. Ppp.		+	
V. romaloi Cob.		+	+
V. tiraspolitanus Pavl.	+	+	
V. tiraspolitanus subcrassus Lung.		+	
V. limatus G. Ppv.		+	+
V. aff. *bithynica* Mang.		+	
V. sinzovi Pavl.		+	
V. pseudoachatinoides Pavl.	+	+	+
V. achatinoides Desh.		+	
Viviparus sp.		+	
Lithoglyphus naticoides Ferus.		+	
L. decipiens Brus.		+	
L. decipiens oblongus G. Ppp.		+	
L. decipiens kinelicus G. Ppp.	+		
L. acutus G. Ppp.		+	+
L. neumayri Brus.		+	
Bithynia vucotinovici Brus.		+	
B. vucotinovici longa G. Ppp.		+	
B. tentaculata L.	+	+	+
B. tamanensis G. Ppp.		+	
B. spoliata Sabba		+	
B. alta G. Ppp.		+	
B. croatica Brus.		+	
Bithynia sp.	+	+	
Clessiniola (Baschkiria) julaevi G. Ppv.		+	+
C. (Baschkiria) julaevi concinna G. Ppv.		+	
C. aff. *utvensis* Andrus.		+	
Clessiniola sp.		+	+
Caspia turrita G. Ppv.		+	+
C. turrita subcylindrica G. Ppv.		+	
Caspia sp.		+	+
Caspiella roseni G. Ppv.		+	+
Caspiella (?Nematurella) sp.			+
Corbicula fluminalis Müll.		+	
Micromelania sp.		+	
Amphimelania impressa Bog.		+	
Pisidium amnicum Müll.	+	+	+
P. personatum Malm.		+	
P. supinum A.Schm.		+	
Pisidium sp.		+	
Sphaerium aff. *scaldianum* (Norm.)		+	
S. rivicola Lam.		+	
Sphaerium sp.		+	+
Dreissena polymorpha Pall.	+	+	+
D. polymorpha Pall. var. *angustiformis* Kolesn.		+	+
D. rostriformis Desh.		+	
D. pontocaspia Andrus.		+	
D. isseli Andrus.		+	
D. eichwaldi Andrus.		+	
D. incrassa Andrus.		+	
Dreissena sp.		+	+
Rugunio samarica Andrus.		+	
R. caspia Tshep.		+	
Ritia orintalis Tshep.		+	
Potamoscapha akchagylica Tshep.		+	
Unio cf. *hybrida* Bog.			+
Bogatschevia tamanensis Ebers.		+	
Aktschagylia subcaspia Andrus.		+	+
Aktschagylia subcaspia - ossoskovi		+	+
A. ossoskovi Andrus.		+	+
A. karabugasica Andrus.		+	
Aktschagylia sp.		+	+
Cerastoderma dombra dombra Andrus.		+	+
C. dombra pseudoedule Andr.		+	+
C. dombra vogdti Andrus.		+	+
Cerastoderma sp.		+	+

In associations from the end of the Late Holocene these species disappeared (Ustjevoi cave, Gumerovskyi cave, Ziganskyi cave, Lemeza I) and the fauna consists of modern species of small mammals, which are extant in the mountainous part of the Southern Urals.

6. Molluscs

Mollusc shells were not evenly distributed in Pliocene deposits. The Upper part of the Akkulaevo (Middle Akchagyl) is better characterized by molluscs than other Pliocene suites. Molluscs were rare in alluvial and limnian deposits of the Upper Akchagyl (Tables 4 and 5).

The Davlekanovo period of the Lower Eopleistocene is characterized by a variety of molluscs species.

In the Pleistocene and Holocene deposits molluscs have often been found in lacustrine deposits of interglacial periods (Tables 6 and 7).

Two mollusc complexes could be determined in the Late Pliocene deposits.

The Middle Akchagyl mollusc complex was found in the localities Akkulaevo, Sultanbekovo, Sultanaevo, Yulushevo, Karmaskaly and others (Yakhimovich et al., 1965, 1972, 1977, 2000).

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Table 6
Land molluscs for some Pleistocene and Holocene intervals.

Species	Quaternary										
	Pleistocene									Holocene	
	Eopleistocene		Neopleistocene								
	Early	Late	Early	Middle		Late				Late	
	Davlekanovo	Karmasan	Chui-Atasevo I	Belaya	Elovka	Mikulino	Saigatka	Tabulda	Kudashevo	Subboreal	Subatlantic
Succinea pfeifferi Rossm.			+		+		+	+			
S. putris L.					+					+	+
S. oblonga Drap.	+		+	+			+	+	+		
S. cf. *oblonga* Drap.	+										
Succinea sp.				+		+		+			
Vertigo substriata Jeff.	+										+
Cochlicopa lubrica Müll.							+	+			
Cochlicopa lubrica columna Cles.			+								
Vallonia costata Müll.	+		+	+		+	+	+	+	+	+
V. pulchella Müll.			+					+			
Vallonia sp.									+		
Pupilla muscorum L.			+	+				+	+		
Zenobiella rubiginosa Schm.			+	+	+	+		+			
Vitrea cristallina Müll.			+		+			+			
V. contracta West.					+	+	+				
Chondrula tridens Müll.					+			+			
Nesovitrea pura Alder.					+			+			
Euomphalia strigella Müll.								+		+	
Bradybaena fruticum Müll.								+			+
Scalaxis sp.			+								

The maximum of the Akchagyl transgression was reached in this period and the Caspian Sea extended far to the north. The development and change of biocoenosises could be well traced. The influence of fresh water (rivers, different types of lakes) on the marine and brackish water communities has been noted in the Southern Fore-Urals. Representatives of different ecological groups could be found together in one taphocoenosis. The Upper part of the Akkulaevo is characterized by a rich species variety of fresh water molluscs such as Unionidae and Viviparidae of the Levantine type, *Bithynia*, *Valvata*, *Lithoglyphus* and others, and brackish water molluscs (*Cerastoderma*, *Aktschagylia*, *Clessiniola*) which existed in the warm climate.

The Unionidae have been described by Chepalyga (Yakhimovich et al., 1983). Such genera as *Bogatschevia*, *Rugunio*, *Ritia*, *Psilunio* (*P. lascarevi* Milos., *P. pavlovici* Milos., *P. crassus* Milos., *P. milosevichi* Tshep., *P. andrussovi* Tshep., *P. popovi* Tshep., *P. elongatum* Tshep.), *Potamida* (*P. neustruevi geometrica* (Bog.), *P. agydelica* Tshep., *P. tamanensis riphaei* G. Ppv., *P. bashkirica* Sidnev, *P. altecarinata* (Pen.), *P.* cf. *lenticularis samarica* (Andrus.), *P. triangulata* Tshep., *P. inflata* Tshep., *P. rectungularis* Tshep., *P. trapezoidea* Tshep., *P. circula* Tshep., *P. andrussovi* G. Ppv., *P. ufensis* Tshep.), *Ebersininaia (E. jahimovitchae* Tshep., *E. orbicularis* Tshep., *E. robusta* Tshep., *E. bashkirica* Tshep., *E. romboidea* Tshep., *E. uralica* Tshep., *E. salavati* Tshep., *E. sculpta* Tshep., *E. neustruevi* Andrus.), *Unio (U. metochiensis* Milos., *U. hybrida* Bog., *U.* cf. *hybrida* Bog., *U. hocaensis* Milos., and *U. praecrassoides* Sidnev) became extinct at the end of the Pliocene. Some other fresh water species were also members of the complex: Limnaeidae, Valvatidae, Planorbiidae, Sphaeriidae which became widespread in the Pleistocene and Holocene.

The Late Akchagyl mollusc complex was found in the locality Voevodskoye. The Upper Akchagyl deposits were formed in a brackish water basin. Molluscs were represented by brackish water (*Aktschagylia*, *Clessiniola*, *Cerastoderma*) and fresh water species (*Dreissena*, *Unio*, *Sphaerium*, *Valvata Planorbis* and others). Species of the Levantine type disappeared at the end of the Akchagyl when it became colder and reappeared in the first part of the Eopleistocene.

Microcondylia, *Unio*, *Bogatschevia*, *Pseudosturia*, *Viviparus*, *Corbicula*, *Bithynia*, *Valvata*, *Lithoglyphus*, *Planorbis*, *Pisidium* occurred in the first half of the Eopleistocene.

Two mollusc complexes could be determined in Pleistocene deposits: Lower–Middle Neopleistocene and Upper Neopleistocene–Holocene. These complexes are represented by fresh water and land molluscs. Almost all species are hydrophilic and inhabited moist places. The small sizes of the shells indicate cold conditions during glaciations and an insufficiently warm climate of interglacials. A composition with *Succinea oblonga* Drap. characterized glacial deposits of the Late Pleistocene.

7. Comments

The main feature of the Quaternary history of the fauna and flora development in the Southern Urals region lies in the fact that the ice caps were absent in different glacial periods. The changes of the palaeoenvironment were not so sharp as in the adjacent northwestern territories. Biota of the region has been formed under the influence of the European and Asiatic elements.

As a result of many years of investigations we may conclude the following. Late Pliocene, Late Neopleistocene and Holocene deposits in the Southern Urals region have been biostratigraphically studied in detail. Eopleistocene, Early and Middle Neopleistocene deposits have been studied fragmentarily.

There were several reasons for this situation. During some geological periods, deposits were eroded because of uplift of the territory, which took place in the Quaternary. During quick sedimentation in interglacial periods the thick strata do not have enough fauna and palaeobotanic remains necessary for stratigraphic correlations and a reconstruction of the palaeoenvironment.

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Table 7
Water molluscs from some Pleistocene and Holocene intervals.

Species	Pleistocene												Holocene	
	Eopleistocene			Neopleistocene										
	Early		Late	Early	Middle			Late					Late	
	Dema	Davlekanovo	Karmasan	Chui-Atasevo I	Belaya	Gornova	Elovka	Mikulino	Saigatka	Tabulda	Kudashevo		Subboreal	SubAtlantic
Limnaea stagnalis L.				+										+
Limnaea sp.										+				
Radix auricularia L.						+								
R. pereger elongata Cless.	+													
Stagnicola palustris Müll.				+	+	+				+			+	
Stagnicola sp.					+									
Galba truncatela Müll.				+										
Planorbis planorbis Müll.	+			+	+	+		+		+			+	+
Planorbarius corneus L.	+			+		+								
Paraspira spirorbis L.				+	+					+	+			
Gyraulus albus Müll.					+	+	+		+				+	+
G. laevis Alder.				+	+					+			+	+
Gyraulus sp.							+			+				
Armiger crista Drap.					+	+							+	+
Hippeutis riparius Westler														
Acroloxus lacustris L.													+	+
Bathyomphalus contortus L.										+				+
Valvata antiqua Sow.	+				+									
V. piscinalis Müll.	+	+		+	+		+	+					+	+
V. piscinalis antiqua Sow.				+						+				
V. naticina Menke				+										
V. pulchella Müll.	+	+		+	+	+			+					
Bithynia vucotinovici Brus.	+													
B. tentaculata L.	+			+										
B. leachi (Shepp.)	+			+										
B. spoliata Sabba	+													
B. croatica Brus.	+													
B. tamanensis G. Ppv.	+													
Bithynia sp.	+			+	+									
Viviparus cf. *bashkirikus* G. Ppp.	+													
V. achatinoides Desh.				+										
V. romaloi Cob.	+													
V. tiraspolitanus Pavl.	+													
V. tiraspolitanus subcrassus Lung.	+													
Viviparus sp.				+	+									
Lithoglyphus naticoides Ferus.	+			+										
L. decipiens Brus.	+	+												
L. decipience oblongus G. Ppv.				+										
L. decipiens gracilis (Mang.)	+													
Lithoglyphus sp.				+	+			+						
Clessiniola julaevi G. Ppv.	+	+		+				+			+			
Clessiniola sp.	+	+												
Corbicula fluminalis (Müll.)	+			+										
Pisidium amnicum Müll.	+			+	+	+				+			+	+
P. cosertanum Poli.				+	+								+	+
P. supinum A. Sch.					+									
Pisidium sp.	+	+					+							
Sphaerium aff. *Scaldianum* (Norm.)	+													
S. rivicola Lam.	+	+		+	+		+			+			+	+
S. corneum L.					+									
Dreissena polymorpha Pall.	+	+		+	+		+			+	+			
Dreissena sp.			+											
Potomida ex gr. *sturi* (Hörnes)	+													
P. neustruevi geometrica (Bog.)	+													
Unio ex gr. *crassus* Phil.	+													
U. praecrassoides (Sidnev)														+
U. pavlovi G. Ppv.	+													
U. chasaricus Bog.		+												

(*continued on next page*)

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Table 7 (*continued*)

Species	Pleistocene											Holocene	
	Eopleistocene			Neopleistocene									
	Early		Late	Early	Middle			Late				Late	
	Dema	Davlekanovo	Karmasan	Chui-Atasevo I	Belaya	Gornova	Elovka	Mikulino	Saigatka	Tabulda	Kudashevo	Subboreal	SubAtlantic
U. apsheronicus Alz.		+											
Unio sp.				+				+					
Microcondylaea apsheronica Tshep.		+											
Bogatschevia scutum Bog.		+											
B. subscutum Tshep.		+											
Pseudosturia caudata (Bog.)		+											
P. brusinaiformis (Mod.)		+											
Aktschagylia ossoskovi Andrus.	+												
Aktschagylia sp.	+												

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