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# **Eurasian large mammal dynamics in response to changing environments during the Late Neogene**

**Diana Pushkina**

*Academic dissertation*

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**Supervised by:**

Professor Mikael Fortelius  
Department of Geology  
University of Helsinki

**Reviewed by:**

Dr. habil. Gennady F. Baryshnikov  
Laboratory of Theriology,  
Zoological Institute,  
Russian Academy of Sciences  
Universitetskaya nab., 1  
199034 St. Petersburg, Russia

Dr. Evelyne Cregut  
Muséum Requien  
67, rue Joseph Vernet  
84000 Avignon, France

**Opponent:**

Professor Dr. Doris Nagel  
Institute of Paleontology  
University of Vienna, Austria

*Cover illustration:* A woolly rhino (an attempt) and wild horses of the late Pleistocene,  
painted by the author. © Diana Pushkina

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Yliopistopaino

**Dedicated to my late granny  
Valentina,  
my mom and dad**

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## Abstract

Short and long term environmental changes, variations in climate and vegetation during the late Neogene shaped the geographical ranges of large terrestrial mammals by allowing origination, distribution and dispersal of certain species that make up faunas. Climatic fluctuations were intensified during the latest Neogene, Pleistocene (1.8-0.01 Ma), at the end of which also human presence became more conspicuous. Both climate and humans have been linked to extensive alteration and extinctions in mammalian faunas across the world.

This dissertation consists of a set of papers that examine different periods of the Neogene and associated faunas in northern Eurasia. Major trends in changing environments and climate were studied by means of the tooth crown height (hypsodonty) and dietary structure in herbivorous terrestrial mammals or/and species commonness (locality coverage, abundance proxy). This study was also intended to bring to light a great deal of information contained in Russian literature to fill in the gap between the European literature and not translated Russian records.

Since the middle Miocene (~15-11 Ma), central Asia has been the focal point of the transformation in Eurasia towards more open and dry environment. The drying of the central part of Eurasia hampered the spread of temperate or mesophilic species between western and eastern sides of the continent, and created conditions for origination of the cold and arid adapted grazing fauna in north-eastern Eurasia. Throughout the climatically unstable late middle and late Pleistocene, Europe that was more maritime during interglacials than Siberia, experienced the most drastic faunal alternations between the interglacial *Palaeoloxodon antiquus* and glacial *Mammuthus primigenius* assemblages that permanently inhabited the Mediterranean and Siberia, respectively. During more climatically equable middle part of the middle Pleistocene (Holsteinian interglacial) that was climatically similar to the current Holocene, the interglacial species could have spread eastwards. The origins, dispersal and cohesiveness of the *Palaeoloxodon antiquus* assemblage in Eurasia are examined.

During the latest Weichselian Glaciation (Late Glacial, 15 000-10 500 yr BP, latest late Paleolithic) and Holocene (last 10 000 yr) a rapid warming initiated fragmentation of dry and cold tundra-steppes when increased temperature and humidity produced boggy tundra in the north and forests in the south of the most part of northern Eurasia. The most significant change took place in central Asia influencing the glacial mammoth fauna decline as is seen in southern Siberia from decreased mean hypsodonty and the shift in dietary preferences from grazing towards browsing in herbivorous ungulates along with decreased mean body size in large mammals.

It is difficult to disentangle the role of humans from climate effect in large mammal extinctions in Eurasia at the Weichselian-Holocene boundary because they pretty much coincided. The study is consistent with the idea that Eurasian late Pleistocene extinctions were first climatically driven, after which the impact of rapidly expanding humans must have become more manifest and crucial either by direct hunting or via indirect activities. Only the data for the extinct steppe bison may indicate a disproportionate selection by humans although more sufficient and recently updated data are needed.

**Key words:** Pleistocene, Neogene, Paleolithic, interglacial, glacial, large mammals, distribution, hypsodonty, aridity, precipitation, body size, commonness, extinction, human influence.

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## List of publications

- I. Fortelius, M., Eronen, J. T., Jernvall, J., Liu, L., Pushkina, D., Rinne, J., Tesakov, A., Vislobokova, I. A., Zhang, Z. & Zhou, L. 2002. Fossil mammals resolve regional patterns of Eurasian climate change during 20 million years. *Evolutionary Ecology Research* 4, 1005-1016.
- II. Fortelius, M., Eronen, J., Liu, L., Pushkina, D., Tesakov, A., Vislobokova, I. & Zhang, Z. 2006. Late Miocene and Pliocene large land mammals and climatic changes in Eurasia. *Palaeogeography, Palaeoclimatology, Palaeoecology* 238, 219-227.
- III. Pushkina, D. 2007. The Pleistocene easternmost Eurasian distribution of the species associated with the Eemian *Palaeoloxodon antiquus* assemblage. *Mammal Review* 37, 246-254.
- IV. Pushkina, D. 2006. Dynamics of the mammalian fauna in southern Siberia during the late Palaeolithic. *Vertebrata PalAsiatica* 44(3), 262-273.
- V. Pushkina, D. & Raia, P. Human influence on distribution and extinctions of Late Pleistocene Eurasian megafauna. *Journal of Human Evolution*, accepted.

In papers I and II the main contribution of the author was the compilation of the raw Neogene data from the former USSR, which were also the basis of the author's MSc thesis.

The paper V was written in cooperation with Dr. Pasquale Raia who was in charge of the main statistical analyses.

# 1 Introduction

## 1.1 Original idea

This study was suggested by Prof. W. von Koenigswald and originally designed to unite the knowledge from central and western Europe as well as the former USSR republics excluding the Baltic States in order to revise the maximum eastward distribution of the interglacial *Palaeoloxodon antiquus* large mammal assemblage typical of the Eemian interglacial in western and central Europe. In spite of numerous publications in the Russian literature and all kind of fragmentary data that were the subject of thorough attention and importance (Alexeeva, 1980), the need for revision of older sites, stratigraphic correlation of localities between east and west, and a lack of the data from interglacial periods presented difficulties in research. The condition of East European interglacial large mammal fauna remained largely unexplored and unrecognized because it was similar to glacial fauna. The dispersal and cohesiveness of the interglacial *Palaeoloxodon antiquus* assemblage in Eurasia during the second half of the Pleistocene were studied. However, owing to a more thorough research in the former-USSR territory concentrated on the glacial steppe fauna, the dissertation topic was later extended to incorporate steppe-glacial fauna, which was more widespread in Eurasia, and to examine environmental changes and species' eco-morphological adaptations to them.

## 1.2 Climatic changes and mammalian assemblages in northern Eurasia

The evolutionary responses of mammals to climatic change can be assessed by proxies such as tooth height (hypsodonty), body size, taxonomic change, species richness, abundance and commonness, which can in turn be extrapolated into major trends in changing environments and climate (Damuth, 1982; Fortelius *et al.*, 1996; Steininger, 1999; Damuth & Fortelius, 2001; Jernvall & Fortelius, 2002, 2004; Barnosky *et al.*, 2003). Since the middle Neogene (middle Miocene ~15-11 Ma, late Miocene 11-5.3 Ma, Pliocene 5.3-1.8 Ma, Fig. 1) the central part of Eurasia (central Asia) has progressively become more open and dry with drying at times extending into western Europe (latest late Miocene, late Pliocene) (Dorofeev, 1966; Fortelius *et al.*, 1996, 2003, papers I, II). During the latest Neogene (late Pliocene (3.5-1.8 Ma) and Pleistocene (1.8-0.01 Ma)) climate became highly unstable on quite short time scales (Shackleton & Opdyke, 1977; Webb & Barnosky, 1989; Graham, 1990; Sher, 1992; Webb & Opdyke, 1995; Potts, 1996) resulting in a more radical terrestrial faunal exchange probably similar on both sides of the Eurasian continent due to a more pronounced maritime climatic effect (Kahlke, 1986; Guthrie, 1990; van Kolfschoten, 1995; Dong *et al.*, 1996; Zagwijn, 1996; von Koenigswald, 1999; Xue & Li, 2000; Xue *et al.*, 2000; Takashi *et al.*, 2003). Aridification of central Asia must have hampered the spread of temperate or mesophilic species between west and east, and

Time, Ma	Epochs	European Land Mammal				Period
		Mediterranean	Eastern Paratethys	Mega zones	MN zones	
0-0.01 1.8	Holocene Pleistocene	Ionian			MQ1-4	(Quaternary, 1.8-0.0 Ma)
		Calabrian			MN18	
	PLIO-CENE	Gelasian	Akchagyl	Villafranchian	MN17	
		Piacenzian			MN16	
		Zanclean	Balakhnian	Ruscinian	MN15	
					MN14	
	MIOCENE	Messinian	Pontian	Turolian	MN13	
					MN12	
		Tortonian	Maeotian		MN11	
				Vallesian	MN10	
			Sarmat		MN9	
		Serravallian	Konkian	Astaracian	MN7-8	
			Karaganian		MN6	
		Langhian	Chokrakian	Orleanian	MN5	
			Tarkhanian		MN4	
		Burdigalian	Kozakhurian		MN3	
			Sakaraulian		MN2	
	23.8	Aquitanian	Karadzalzganian	Agenian	MN1	

**Fig. 1** Neogene timescale (Steininger, 1999; Popov *et al.*, 2004).

contributed to the origin of the cold and arid adapted grazing fauna in north-eastern Eurasia.

During the late middle and late Pleistocene the glacial and interglacial faunas were interchanging in central and western Europe. The glacial steppe *Mammuthus primigenius* - *Coelodonta antiquitatis* assemblage that occupied vast territories in eastern Europe and Siberia until the beginning of the Holocene spread into central and western Europe during the glaciations (Stuart, 1991; Kahlke, 1999; Sher, 1997). The analogues of this fauna, the arctic-type communities, were already developing in north-eastern Eurasia or Beringia (north-eastern Siberia) since the Pliocene and early Pleistocene (Sher, 1971, 1992; Repenning, 1985; Dubrovo, 1990). The interglacial periods (Holsteinian, Eemian) in central and western Europe were represented by the *Palaeoloxodon antiquus* - *Stephanorhinus kirchbergensis* faunal assemblage, which resided in the Mediterranean during glaciations (Stuart, 1991; von Koenigswald, 1999). This interglacial fauna is considered rather uncommon in eastern Europe and Siberia owing to a more continental climate (Scheglova, 1963; Sher, 1971, 1992, 1997; Kowalski, 1980, 1989; Kalinovskij, 1983; Markova, 1984, 2000). The remains of neither interglacial species nor the Eemian localities have been encountered north of 60°N (Markova, 2000). However, according to the former-USSR literature it appears that many characteristic species of the *Palaeoloxodon* assemblage (or in some cases species closely related to them) occurred further in Eurasia, occasionally with typical glacial and steppe species, at least during the middle Pleistocene, after which they became more restricted to Europe until their final extinction (Vereshchagin, 1959; Kozhamkulova, 1969, 1990; Gromov, 1972; Garutt, 1972, 1986; David & Lungu, 1972; Vangengeim & Sher, 1972; Kahlke, 1975a; Vangengeim, 1977; Alexeeva, 1980; Vereshchagin & Baryshnikov,

1980, 1985; David *et al.*, 1982; Garutt & Vangengeim, 1982; Vangengeim & Zhegallo, 1982; Kalinovskij, 1983; Baryshnikov, 1987; Svistun *et al.*, 1989; Averianov *et al.*, 1992; Khromov *et al.*, 2001).

The glacial steppe fauna declined after the last Weichselian Glaciation maximum (LGM, 24 000–15 000 yr BP) when climate became warmer and more humid, resulting in vegetation transformation across central Eurasia from a mosaic of open and dry steppe tundra into zonal distribution with boreal forest (taiga) belt (Vereshchagin & Baryshnikov, 1984, 1985; Guthrie, 1984, 1995). The record of the large mammal extinctions in Eurasia ranges over a relatively long period of time, and the human impact is less clear (Grayson & Meltzer, 2002; Stuart *et al.*, 2002, 2004; Stuart, 2005) as it may have been combined with the effects of environmental deterioration and vegetation change after the LGM (Kvasov, 1977; Tormidiaro, 1977; Guthrie, 1990, 1995).

I studied species morphological and ecological characteristics through time to determine environmental and climatic trends. A comparison of species' geographic distributions and commonness between assumed archaeological and paleontological sites was made to untangle the effect people could have on the distribution and survival of the late Pleistocene Eurasian large mammals.

## 2 Material

### 2.1 Locality distribution data

All data on localities, species and chronostratigraphic correlations were obtained from the literature and existing databases, Neogene of the Old World - NOW (Fortelius, M., coordinator, <http://www.helsinki.fi/science/now/>), European Quaternary Mammalia - Pangaea (<http://www.pangaea.de/>, updates of 2001), Marine Oxygen Isotope Stage 3 - OIS-3 (van Andel, 2002) and Paleolithic sites of Northern Asia (<http://sati.archaeology.nsc.ru/pna/>). The Pleistocene data compiled by the author into the NOW database will become available with the publication of this study.

Different sets of localities and species were analysed and published in separate articles. In the first two articles the earlier Neogene periods divided in the Mammal Neogene (MN) zones (Fig. 1) were studied. The detailed information on methodology is described in the papers. Here I present a general overview of data and analyses focusing on the last three papers. The Pleistocene data used for the last three articles were entered into the NOW database, using the standards of the ETE database (Damuth, 1993). The Pleistocene dataset comprises the late middle and late Pleistocene and Holocene sites from western and central Europe and the former USSR as well as several type localities from eastern Europe and the Mediterranean. There are fewer Holocene localities.

The main emphasis is put on the former USSR territory because of often obscure or poorly known literature of the area where the environmental change was initiated. It was also the key survival area of many species that went extinct at the Weichselian - Holocene boundary, and the place of their "last stand" where the human effect could also be detected during their expansion from Europe to Siberia. In the Pleistocene part of the database south-eastern Asia (China, India) and Japan were excluded because of controversial taxonomy for many of their species (Chinese), high endemicity (Japanese) or lack of data. Several Chinese records were used in paper III. In paper IV only archaeological localities, situated in the region of Lake Baikal (50–60° N; 103–117° E) and the Altai Mountains (51–60° N; 84–100° E), were examined. These data were obtained from Vasil'ev *et al.* (2002) and Vasil'ev (2003), who described radiocarbon-based chronology of the late Paleolithic localities and their large mammal fauna in Siberia.

(Abbreviations: N - Northern latitude, E - Eastern longitude.)

## 2.2 Species and assemblages description

The names of the species were used as given in the NOW database. Only large mammals were examined as their overall coverage for north-eastern territories is ample (Damuth, 1982) and they are better comparable across Eurasia. Rodents, lagomorphs, insectivores, marine mammals and primates were excluded to even out the sampling bias because the majority of species in these orders are either small or very rare and recorded less uniformly, or have unique morphological features, thus bound to produce a large amount of regional variation (e.g. hypselodont or high-crowned rootless “ever-growing” teeth found mostly in rodents and rarely among large species like an extinct rhinoceros *Elasmotherium* (Shvyreva, 1980; Kozhamkulova, 1981; Janis & Fortelius, 1988). The late Pleistocene species names were updated on the basis of contemporary species information (McDonald, 1989; Nowak, 1991; Wilson & Reeder, 2005).

In paper III the species that indicated the interglacial assemblage during the second half of the Pleistocene in Europe were traced down to their first appearances in time. Characteristic of the last Pleistocene interglacial Eemian in central Europe were the straight-tusked elephant *Palaeoloxodon antiquus*, Merck’s and narrow-nosed rhinoceroses *Stephanorhinus kirchbergensis* and *S. hemitoechus*, aurochs *Bos primigenius*, hippopotamus *Hippopotamus amphibius*, giant deer or Irish elk *Megaloceros giganteus*, fallow deer *Dama dama*, roe deer *Capreolus capreolus*, wild boar *Sus scrofa* and water buffalo *Bubalus murrensis* (Stuart, 1986, 1991; Currant, 1989; von Koenigswald, 1999, 2003; van Kolfschoten, 2000; Currant & Jacobi, 2001; Bradshaw *et al.*, 2003).

In paper V only the large herbivores that belonged to the two best known faunal assemblages in Europe and Siberia and largest carnivores that accompanied them in Eurasia during the second half of the Pleistocene and Holocene were included. The glacial assemblage was composed of the woolly mammoth *Mammuthus primigenius*, woolly rhinoceros *Coelodonta antiquitatis*, steppe bison *Bison priscus*, musk ox *Ovibos moschatus*, reindeer *Rangifer tarandus* and saiga antelope *Saiga tatarica* (Stuart, 1991; Alexeeva, 1980; Baryshnikov, 1987; Sher, 1997; Kahlke, 1999). The horse *Equus ferus* (including *E. caballus*, *E. ferus*, *E. gmelini*, *E. latipes*, *E. lenensis*) and red deer *Cervus elaphus* were not unambiguous indicators of any assemblage (von Koenigswald, 2003) but were abundant herbivores across Eurasia and were included along with the moose *Alces alces*, kulan *Equus hemionus* and the Pleistocene ass *Equus hydruntinus*. Other ungulates that occurred regionally (e.g. in mountainous habitats) and/or could have discrepancies in scientific names were excluded, such as sheep, goats, antelope *Spirocerus kiakhtensis*, or extinct yak *Bos baikalensis*. In paper V the species were also categorised as the extinct or extant in nature in Eurasia.

The carnivores were separated in some analyses, because they represent the secondary trophic level and a rival to humans, which could increase their extinction vulnerability (Purvis *et al.*, 2000; Carbone & Gittleman, 2002; Cardillo *et al.*, 2004) or possibly decrease it since humans were less interested in hunting carnivores than herbivores (see for paper V results). The largest among carnivores were the hyena *Crocuta crocuta*, lion *Panthera leo*, cave bear *Ursus spelaeus*, brown bear *Ursus arctos*, grey wolf *Canis lupus*, red fox *Vulpes vulpes*, Arctic fox *Alopex lagopus*, Corsac fox *V. corsak*, dhole *Cuon alpinus*, European lynx *Lynx lynx*, leopard *Panthera pardus*, wolverine *Gulo gulo* and European badger *Meles meles*.

## 2.3 Chronostratigraphic correlations

The Pleistocene fossil record localities were chronostratigraphically correlated on the basis of marine oxygen isotope record (OIS) (or MIS - marine isotope stage), chronometric dating (radiocarbon, AMS - accelerator mass spectrometry, TL - thermoluminescence, ESR - electron spin resonance, uranium  $^{238}\text{U}$ -series), paleomagnetic polarity and chron correlations, continental mammalian biostratigraphy, and archaeology (human cultural stages) (Vangengeim, 1977; Gerbova & Krasnov, 1982; Azzaroli *et al.*, 1988; Stuart, 1991; Kahlke, 1999; van Kolfschoten, 2000; Currant & Jacobi, 2001; Khromov *et al.*, 2001; Lister & Sher, 2001; Stuart & Lister, 2001; Vangengeim *et al.*, 2001; Vasil'ev *et al.*, 2002; Lister *et al.*, 2005; Sher *et al.*, 2005). (Fig. 2)

The Pleistocene localities were divided into six succeeding age groups: 1) late middle Pleistocene (late Early Paleolithic sites 400-130 ka); 2) Eemian interglacial (early Middle Paleolithic or early Mousterian sites 130-115 ka); 3) early and middle Weichselian Glaciation (late Middle Paleolithic or late Mousterian sites and early Late Paleolithic or Aurignacian sites 115-24 ka); 4) late Weichselian or Last Glacial Maximum (LGM) (middle Late Paleolithic sites 24-15 ka); 5) latest late Weichselian or Late Glacial (LG) (latest Late Paleolithic or Magdalenian sites 15-10 ka); and 6) Holocene (Mesolithic and Neolithic sites less than 10 ka). The oldest age group consisted of the Khazarian and Singilian faunal complexes, correlated with the early Saalian and Holsteinian pollen phases (Azzaroli *et al.*, 1988; Khromov *et al.*, 2001; Vangengeim *et al.*, 2001). This division was performed to better correlate the localities across Eurasia because a more detailed temporal division was not always available.

In paper IV the dates varied from about 34 000 to 10 500 yr BP  $^{14}\text{C}$  representing the early, middle and latest Late Paleolithic. On the basis of the fossil insect faunal zones in East Siberian Arctic (Sher *et al.*, 2005) the localities dated 34 000-24 000 yr BP and correlated with the late Oxygen Isotope Stage 3 (OIS3) were representing the early Late Paleolithic or late middle Weichselian; 24 000-15 000 yr BP, early OIS2 localities - the LGM; and the late OIS2 localities - the LG. A similar division of the Weichselian was applied by Beck (1996) to study late Pleistocene extinctions in North America.

In paper V the Eemian stage (OIS5e) was excluded from analyses because it could be mixed with the earlier interglacial (OIS7) or later deposits, many of which appeared to be often mistaken for the Eemian (Schreve & Thomas, 2001). We analysed two datasets and described in the article the results of the second conservative database. In the first database, localities were placed into the six above mentioned age groups depending on the majority of their temporal ranges or dates, accompanied by the localities' description. In the second the Late Paleolithic localities were directly dated and the earlier archaeological sites were either dated or correlated with the OIS and Pleistocene/Weichselian stages. In the first dataset as "archaeological" we took the sites that were attributed to a human cultural stage or where human artifacts were found. The rest of localities were treated as "paleontological". In the second dataset we more conservatively counted all indications of human presence for indication of human hunting (even if they were carnivore generated accumulations) and treated these sites as the archaeological. Even when an archaeological site belongs to a cultural stage it may be essentially paleontological because it can contain remains of species that were never hunted by humans in any form but collected by non-human related processes or predators. Thus, a slight bias increasing human impact on large mammal fauna could be present (especially during the later periods, see for paper V), because humans could have reworked some bones from the earlier sites that could be either paleontological or archaeological.

**Fig. 2** A summarising stratigraphical table of northern Eurasia.



### 3 Methods

#### 3.1 Morphological (hypsodonty, precipitation, diet, body size)

Hypsodonty is a term denoting molar crown height in herbivorous mammals. The extent of the development of the molar crown height indicates an adaptation to higher rates of tooth wear experienced in open and dry habitats (Flerov, 1962, Fortelius, 1985; Janis & Fortelius, 1988, A. Lister, personal communication, 2002). The values of the hypsodonty classes are usually attributed to each species according to the ratio of height to length or sometimes the ratio of the molar width to height (Janis & Fortelius, 1988). I followed the classification of Fortelius *et al.* (2003), where teeth are considered brachydont or low-crowned when the ratio of height to length (or dorsal-ventral to anterior-posterior ratio) is below 0.9 – class 1, mesodont or medium-crowned with the ratio from 0.9 to 1.2 – class 2, and hypsodont or high-crowned with the ratio higher than 1.2 – class 3. Individual values were not recorded.

In paper IV the mean hypsodonty value was translated into precipitation in mm per year to compare the precipitation values derived from hypsodonty with precipitation values estimated from other paleoindicators. Mean hypsodonty (H) at a locality divided by the number of the large species is related to mean annual precipitation (P) by the formula  $\log_{10}P = -1.27(\log_{10}H) + 1.36$  (Damuth & Fortelius, 2001). Although the absolute rainfall estimates are regarded as very approximate due to various factors, the relative difference is considered significant to be able to detect general trends in the rainfall change (Damuth & Fortelius, 2001; M. Fortelius, personal communication, 2005).

Diet for each species was ordinated into the grazers as 1, mixed grazers-browsers as 2, browsers as 3. The diet values were assigned to species not only from hypsodonty but also on the basis of their dental wear patterns (Fortelius *et al.*, 1996; Fortelius & Solounias, 2000).

Body size depends on wide variety of factors, including resource availability and climatic conditions, physiological and biomechanical factors (Damuth & MacFadden, 1990; Blackburn & Gaston, 1994, 1998). Instead of the actual body masses, mostly the body length categories were examined, where the body length of 10 cm - 1 m was assigned to 2; 1 m - 2 m to 3; 2 m - 5 m to 4; and over 5 m to 5. Except in paper V we used a body size limit of approximately 7 kg.

Molar crown height (hypodonty), body size and diet for each species were mainly taken from the NOW database (<http://www.helsinki.fi/science/now/>) and literature sources for both extant (McDonald, 1989; Nowak, 1991; Wilson & Reeder, 2005) and extinct species (Ukrainseva, 1985, 1991; Smith *et al.*, 2003) as the majority of late Pleistocene species are similar to the Holocene ones. Unclear cases were left out or used as unidentified species only at the generic level where possible.

#### 3.2 Ecological (commonness or locality coverage, rarity)

Commonness or locality coverage is the proportion of species presence in localities during a certain period (Jernvall & Fortelius, 2004). Commonness of a species remains at a fossil locality or in an assemblage is an alternative to abundance in ecological studies of modern communities, because it is likely that a species abundant at some sites within a given region will be present at most of them. It was suggested that the common species (or species present in  $\geq 25\%$  of localities) strongly indicate the general evolutionary trends because they are the ones that make the most use of the habitats and resources available (Jernvall & Fortelius, 2002, 2004) and thus are better adapted to the prevailing environment.

Commonness estimates were proved to be rather robust (Jernvall & Fortelius, 2004), especially when used within one temporal unit. A misidentification of several individuals will not significantly

change the results because it is represented by proportion (or percentage).

In paper V we combined commonness of several species belonging to a certain assemblage or group (e.g. herbivore, carnivore, extant, extinct) to reveal the main trends between and within the groups. The differential length of time units or their partial overlapping should not significantly affect the commonness results because the relative statistical differences between the extinct and living species or between archaeological and paleontological sites are notably large. The effects on commonness of the two most relevant taphonomic factors: body size and preservation in caves versus open environments, were also tested with respect to the species distribution. The species with different geographic ranges, more northwards than humans or species with distribution similar to humans, can produce substantial latitudinal differences in commonness as they are expected to become rarer at the periphery of their ranges (Lawton, 1993; Brown *et al.*, 1995; Blackburn *et al.*, 1999) thus being able to decrease “northern” species commonness values within archaeological sites. We also calculated a human preference (HP) factor for each time-period as the difference in commonness between archaeological and paleontological sites for each species. Higher than expected commonness at archaeological sites (higher HP) was considered human selection and exploitation of these animals. If the extinct species were highly “preferred”, humans could be associated with extinction of the large mammals in Eurasia. If the extant species were more abundant in the human-occupied localities it would suggest against human influence on extinction of the Pleistocene large mammals.

## 4 Results based on articles (I-V)

One of the main results of this study is the overall drying trend that was initiated in central Asia starting from the middle Miocene. The drying extended westwards and possibly eastwards during the late Miocene, at times during the Pliocene, and continued almost through the whole of Pleistocene. The opposite large scale transformation towards more humid conditions began across Eurasia during the latest Pleistocene (Late Glacial) and Holocene and most significantly affected central Asia as the most continental core. Similar change towards climatic warming and amelioration could have also occurred to some extent during the Holsteinian interglacial.

(I) Herbivore hypsodonty and precipitation values inferred from it corresponded well to the modern precipitation maps, thus, demonstrating congruence to other continental-wide studies of modern and past climates. The global aridity of the late Miocene appears to have been related to the major phase of uplift of the Himalayas and Tibetan Plateau and the intensification of summer monsoon, in contrast to the regional effect in China, where these events produced a reversal to more humid conditions.

(II) Aridification resulted in transgression of open-adapted faunas westwards along the east-west gradient, which later in Europe changed into the north-south oriented. The east-west gradient in large herbivore communities' distribution in Europe appears to have been driven primarily by precipitation during the late Miocene (early- middle Turolian, MN11-12). The north-south gradient during the latest Miocene and Pliocene (starting from late Turolian, MN13) was driven by temperature related effects of humidity enabled by the underlying climatic and tectonic effects (Tibetan Plateau uplift, intensification of summer monsoon).

(III) Despite the unconditional dominance of the glacial steppe species across much of northern Eurasia throughout most of the Pleistocene (Kahlke, 1975b; Vereshchagin & Kuzmina, 1984; Markova *et al.*, 1995), the mesophilic species could spread further eastward during the middle period of the middle Pleistocene (e.g. Holsteinian). The Holsteinian interglacial was apparently more climatically equitable in continental Siberia and China than either before or after (Howard, 1997;

Prokopenko *et al.*, 2002; Molodkov & Bolikhovskaya, 2006; Qiu, 2006). The species typical of the interglacial European *Palaeoloxodon antiquus* assemblage appear to have occurred as far as the Lake Baikal region and the Russian Far East. These species or closely related forms (across the Urals) were independently encountered in various faunal associations dissimilar to central and western Europe. Several now-extinct species of the *Palaeoloxodon* assemblage disappeared in Siberia and central Asia earlier than in Europe and the Caucasus and became fragmented into smaller biogeographical zones, with possibly similar species on both sides of the continent. In a small biogeographic region of central and western Europe these species formed an unvarying *Palaeoloxodon antiquus* assemblage and responded together to climatic and environmental changes alternating with the glacial woolly mammoth assemblage.

(IV) The fauna of the late Paleolithic sites in southern Siberia (the region of Lake Baikal and Altai Mountains) indicated a considerable environmental change starting after the LGM. Decreasing hypsodonty, decline in body size and a shift towards browsing, more prominently portrayed by the common species, suggested a response to the climatic warming and increasing humidity. This rather dry environment of mountainous regions with open habitat and a continental climate, where species are often ecologically and morphologically adapted to severe climatic conditions like the tundra-steppe, e.g. Tibetan Plateau mountain desert (Baryshnikov & Markova, 1992), was becoming more humid and, probably, forested as a consequence of the Late Glacial warming. The precipitation values derived from hypsodonty are comparable with the precipitation values derived from other paleoindicators in showing the relative change of mammals adjusting to environment. With altitude hypsodonty increases and precipitation decreases. The deviation in their relationship might be also increasing with altitude that can be related to lower evaporation in cooler regions. Steeper decreasing trends in commonness of the mammoth and perissodactyls opposed to milder or increasing trends in artiodactyls at the Paleolithic sites can be partially associated with exploitation by humans. However, these trends also reflect the species decline in nature in response to climate change and may indicate differences in their digestive strategies. For example, caecal fermenters needed more food variety than ruminants, which is consistent with their late Weichselian or Holocene extinction or survival (Guthrie, 1984; Barnosky *et al.*, 2004). Humans, who were rapidly expanding in area and numbers, could regionally strain the species populations more and lead to their disappearance from southern Siberia.

(V) The comparison of commonness patterns between archaeological and palaeontological sites indicated significant differences between the extinct and living species during the early and middle Weichselian Glaciation. People appear to have hunted the most abundant prey. Yet, contrary to the hypothesis of human-induced extinction, the species with the highest relative commonness at archaeological sites (high human preference HP residuals) appeared to be those still living. The only exception is the extinct steppe bison *Bison priscus*, the only abundant prey that appears to have been negatively influenced by humans. By the Holocene humans became able to compete with large carnivores for their existence and defend their homes. After the LGM the large steppe-glacial species were already suffering from the deterioration and contraction to the north of their preferred habitat, whereas humans appeared to have shown little interest in the now-extinct species, even when we used a conservative archaeological approach that should have increased human influence on extinct fauna. It is possible that regionally and later during the Holocene human overexploitation added to the stress of the declining mammalian populations even more to lead quicker to their extinction in northern Eurasia. The beginning of the decline in many extinct species in northern Eurasia appeared to be more associated with the climatic environmental effects.

## 5 Discussion

### 5.1 Mammalian eco-morphological adaptations and general environmental trends

Large scale studies of eco-morphological relative variations in mammals were shown to be concordant with results from contemporary climate research, modelled climatic reconstructions and other geological continental-scale evidence of past climates (Webb & Barnosky, 1989; Webb & Obdyke, 1995; Fortelius *et al.*, 1996, 2003, papers I, II; Barnosky *et al.*, 2003). Mammals and, especially their teeth (size, shape and height), can well depict the main trends in changing environments both geographically and through time. Morphological modifications in tooth height (hypsodonty increase) in herbivores indicated one of the major trends in Eurasia during the middle-late Neogene, precipitation decrease that was set in motion in central Asia and expanded in Eurasia (papers I, II). During the Pleistocene (latest Neogene), when climatic variation occurred very fast, the large mammals' response was not always imminent and hypsodonty proxy is not expected to work well because of low evaporation in cool conditions (M. Fortelius, personal communication, 2006). At the times of climatic change when species ranges shift and ecological and climatic differentiation is weakened the mammal response can seemingly produce no change or a mixture (e.g. in hypsodonty), probably indicating the period of species dispersal (transit) (paper II), which might point at changing species characteristics in space and time that are not consistent enough to be detected (e.g. periods of the Pleistocene, unpublished study). However, when a rather small geographic and time scale was applied at the very end of the Weichselian Glaciation and during the Holocene (paper IV for southern Siberia) the commencement of the opposite climatic shift towards humidification is clearly visible. And this change is congruent with studies on other paleoindicators (Velichko, 1984; Savina & Khotinsky, 1984; Grichuk, 1984; Frenzel *et al.*, 1992).

On how short scales can the studies of the general environmental tendency be performed? What determines the resolution depends on what ecological and morphological (eco-phenotypical) indicators in species are used and how rapidly they can change in response to climate and environment. In fossil communities the outcome also depends on the available stratigraphic resolution. Analyses such as commonness can be done geographically within one to numerous generations. In this study I used thousands of years' units and numerous generations' commonness (papers IV, V). The smaller the territorial division and time unit will be, the more commonness study will be essentially the same as abundance study. Restricted to the length of at least 2-3 generations commonness/abundance study will show a temporal trend (or a part of it). Adjustment of morphological attributes (an increase in crown height or a change in crown shape) under the pressure of environmental circumstances is a much longer process (Barnosky *et al.*, 2003; Lister, 2004). Morphological changes become evident in populations after a climatic change that lasts over 100 years (e.g. global warming) (Barnosky *et al.*, 2003). In mammoths it took several interglacial and glacial cycles (300-500 000 years) to select for dental specializations (increase in lamellar frequency, decrease in tooth size) and speciation from *Mammuthus trogontherii* to *M. primigenius* (Lister & Sher, 2001; Lister *et al.*, 2005). The rate of evolutionary divergence in mammals is usually longer than 1 Myr (Barnosky *et al.*, 2003). There are some examples of fast evolving species (Kurtén, 1955, 1964) but rarely among the mammals (Orr & Smith, 1998). However, the rate of appearance of a new genetic variation within a given species appeared to be largely determined by the global population numbers of a considered species (Makarieva & Gorshkov, 2004). During the Pleistocene the speciation rate was greater than during previous periods and most modern mammal species and their adaptations were finally created during the Pleistocene (Dynesius & Jansson, 2000; Lister, 2004).

Body size changes can be noticed geographically (Mayr, 1963) within a generation among the individuals in contemporary species. In the fossil record, though, this change can be interpreted from the change in species bone dimensions (e. g., elongation, increase, decrease (Kurtén, 1968)). There are a number of biological rules that describe the association between body size and climate. According to Cope's rule mammal size increases over geological time (Hone & Benton, 2005). Bergmann's rule suggests that mammals with a wide distribution should be smaller in warmer areas and larger in colder areas. Allen's is the rule of shorter appendages in cold climates. The last two are usually applied geographically. The body size decrease indicated in the common mammals in southern Siberia (paper IV) suggests a possibility of temporal application of Bergmann's rule. Although here it was associated with several species and the body size decrease along with the climatic warming occurred at the expense of the loss of the largest species. Body size and climate correlation rules (Bergmann's, Allen's) may also be applied in terms of a temporal change, however, not directly. A relative trend can be noticed if the environmental conditions perform a consistent directional effect. For instance, Allen's rule was demonstrated in fossil community studies on many of the Holocene mammals that have limbs with elongated distal parts in comparison to their Pleistocene counterparts (Arctic fox, tundra reindeer in the Urals) associated with the snow depth increase (Kuzmina, 1970).

## 5.2 Species individual and community response, refugia

The environmental fragmentation, different timing in the last appearances and changes in spatial distribution of species (related to climatic oscillations) in the whole of Eurasia from western Europe to the former-USSR add regional variation to mammal communities. The *Palaeoloxodon antiquus* interglacial assemblage that could have spread eastward from western Europe during the middle period of the middle Pleistocene became fragmented into smaller biogeographical zones on both sides of the continent with possibly analogous species or subspecies. Recent studies have shown that in northern Eurasia the region of the Urals may be a loose barrier, across which the species experienced speciation or subspeciation into other closely related forms (Lister, 2004). The species with a wide distribution are more prone to speciation closer to the peripheries of their ranges (Mayr, 1963; Lister & Sher, 2001).

It was suggested that species tended to react to climatic and environmental changes rather individually in their own space-time distributions following their own limiting gradients and developing disharmonious distribution patterns (Graham & Lundelius, 1984; Webb & Barnosky, 1989). However, mammalian faunas apparently can maintain more cohesion than previously believed, because individual species (with similar ecological requirements) responded to climatic changes in a similar way tightly correlated with simple ecological gradients (Lyons, 2003, 2005). Therefore, despite regional variation trends associated with temperate fauna can be discerned. For example, the distribution of mesophilic species associated with the *Palaeoloxodon antiquus* interglacial assemblage in western and central Europe can indicate possible forest refugia in northern Eurasia during the second half of the Pleistocene (paper III). Occurrence maps of these species (paper III) are congruent with the river valleys and forested regions on the vegetation maps (Grichuk, 1984; Frenzel *et al.*, 1992). It has been noted that the river valleys seasonally and during the warming could accommodate temperate species (Garutt, 1972, 1986). Apart from the Mediterranean and the Balkans (Croatia, Slovenia, Bulgaria) (Malez, 1986; Stuart, 1991; Spiridonov & Spassov, 1998; von Koenigswald, 1999, 2003), the refugia for thermophilous fauna during the late Pleistocene are known also from more northern regions of south-eastern Europe like Hungary (Stewart & Lister, 2001) and, probably, Romania (Kahlke, 1987, 2001). The regions with the longest persistence of the temperate

and/or extinct species that could have served as their refugia existed in the Caucasus (Baryshnikov, 1987; Baryshnikov *et al.*, 1989), the Ural Mountains (Stuart *et al.*, 2004), southern Russia (Volga river region), the vicinity of Lake Baikal and the Russian Far East.

Species can exist for millions of years. The species that appeared during the Holsteinian could have survived up to now not even expanding species lifetime potential (suggested 2 Myr (Vrba, 1993; Johnson, 1998) or 2.5 Myr (van Dam *et al.*, 2006)). *Bos primigenius* and *Megaloceros giganteus* survived in Europe till the later Holocene. There are indications that the latest giant deer finds are represented by rather large individuals (Stuart *et al.*, 2004) unlike in species on the verge of extinction (e.g., Alaskan horses that demonstrated a decline in body size prior to their disappearance in America (Guthrie, 2003), and possibly dwarf mammoths on Wrangel Island (Vartanyan *et al.*, 1993), although there are views that dwarfism has little to do with extinction (Raia & Meiri, 2006)).

### 5.3 Humans and climate

It is not a novelty that in Eurasia humans appeared to be not decisive factor in large mammal extinctions that were rather induced by climatic fluctuations, especially at their beginning (Owen, 1860; Wallace, 1911; Kvasov, 1977; Tormidiaro, 1977; Vereshchagin & Baryshnikov, 1984; Guthrie, 1984, 1990, 1995; Stuart, 2005; Kosintsev, 2007). It is likely that the predation efficiency of human colonisers has been greatly exaggerated. Searching for any major discrepancies we offered a broad faunal analysis between paleontological sites and sites with human bones or artifacts applying methods robust in expressing general trends or most notable differences. It is difficult to determine when *Homo* species evolved as the “hunter” from the “hunted upon” (Hart & Sussman, 2005). Therefore, we used the conservative method that should have inclined towards the recognition of human influence in the faunal extinction. Remarkably, our main findings suggest that we cannot make hasty conclusions concerning human impact on all large mammal extinctions. The database does not have enough resolution in the Mediterranean and European localities where humans appeared much earlier but linking some of the large interglacial species demise to humans during earlier times is just as intricate. The case of *Bison priscus*, the only extinct species possibly associated with human influence, needs further clarifications. Certainly, on such a large territory the aurochs *Bos primigenius* or possibly other newly evolving bison species (Ricciuti, 1973) can be mistaken for the extinct steppe bison. According to Shapiro *et al.* (2004) the decline in bison population was related to some sufficient ecological stress, which, however, can be related to the bison increased occurrences at the Paleolithic sites (papers IV, V) as it was the major game species in Siberia (Vasil’ev, 2003).

According to our results, humans were generalized albeit effective predators who could efficiently concentrate on the most abundant prey species, most of which still exist today. During the Holocene, human effect could have become more significant, for example, in medium-sized species. The largest mammals were the most affected by the late Pleistocene extinctions. The extinction rate for medium-sized mammals, conversely, increased only slightly (Graham & Lundelius, 1984). After rapid environmental climatically induced changes, larger species could have become extinct or transformed into new smaller species (or subspecies) via ecological replacement (Guthrie, 1990) but the decline of medium-sized gregarious species, can, perhaps, be associated with humans (hunting or altering environment) later during the Holocene.

## 6 Conclusions

Throughout the Neogene, mammalian communities and individual species responded to climatic fluctuations and environmental transformations via their different strategies in ecological and morphological adaptations that can be studied.

One of the major trends indicated by mammals in Eurasia is the drying of its central part since the middle Miocene that later extended across Eurasia. The middle part of the middle Pleistocene was climatically more equable than adjacent periods allowing for the mesophilic species to possibly overcome arid barriers in central Asia.

Even with some stratigraphical and/or nomenclatural confusion and errors, individual species response could enable the dispersal and persistence of some of the *Palaeoloxodon antiquus* assemblage species, typical to the Holsteinian and the Eemian in central and western Europe, further in continental Siberia and China.

Eco-morphological changes in southern Siberia at the end of the Weichselian Glaciation demonstrated the global changes that were dramatically initiated in central Asia as the most continental core and brought the demise of the unique steppe-glacial assemblage in northern Eurasia. However, several representative species of both glacial and interglacial assemblages have survived up to now.

The patterns of faunal change and speciation associated with local and global climatic changes are complex. For better quantitative comparisons of faunal associations and species geographical variation across Eurasia comprehensive systematic reviews across Eurasia as well as cross-continental bio-stratigraphic updating are further needed. A commonness study on shorter Holocene periods with better discrimination between the new evolving species at the Weichselian-Holocene boundary that my data did not permit in great detail are of great interest.

The results are mainly consistent with previous studies on Pleistocene-Holocene extinctions in Eurasia. The decline of now-extinct large mammals appears to have been triggered climatically for many of them (possibly except for the extinct steppe bison) with most probable human impact later during the Holocene.

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## Paper I

**Fossil mammals resolve regional patterns of Eurasian climate change  
during 20 million years**

Fortelius, M., Eronen, J. T., Jernvall, J., Liu, L., Pushkina, D., Rinne, J.,  
Tesakov, A., Vislobokova, I. A., Zhang, Z. & Zhou, L., 2002  
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# II

## Paper II

### **Late Miocene and Pliocene large land mammals and climatic changes in Eurasia**

Fortelius, M., Eronen, J., Liu, L., Pushkina, D., Tesakov, A., Vislobokova, I. & Zhang, Z. 2006

*Palaeogeography, Palaeoclimatology, Palaeoecology* 238, 219-227

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Paper III

**The Pleistocene easternmost Eurasian distribution of the species associated  
with the Eemian *Palaeoloxodon antiquus* assemblage**

Pushkina, D. 2007

*Mammal Review* 37, 246-254

III

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Paper IV

**Dynamics of the mammalian fauna in southern Siberia during the late  
Palaeolithic**

Pushkina, D. 2006

*Vertebrata PalAsiatica* 44(3), 262-273

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Chinese Academy of Sciences  
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IV

Paper V

**Human influence on distribution and extinctions of Late Pleistocene**

**Eurasian megafauna**

Pushkina, D. & Raia, P.

*Journal of Human Evolution*, accepted 2007

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