

# TUNDRA-STEPPE ENVIRONMENT IN ARCTIC SIBERIA AND THE EVOLUTION OF THE WOOLLY MAMMOTH

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## Introduction

The new concept of woolly mammoth evolution (Lister and Sher, 2001) suggests that the high latitudes of the Siberian Arctic played an important role in the origin of this species (*Mammuthus primigenius*) and its predecessors (of the *Mammuthus trogontherii* level). It is based on morphological comparison of independently dated mammoth samples from Siberia and Europe. The Siberian samples cover the time span of about 1.2 million years. It was shown that the same levels of evolutionary advancement were achieved by mammoths in Arctic Siberia and in Europe but not simultaneously - in Siberia always a few hundred thousand years earlier. It has been suggested that the more advanced Siberian mammoths could repeatedly interact with the populations in the lower latitudes, which would explain a complex pattern of fast morphological innovations in the European mammoths, alternating with the periods of stasis, and sometimes the apparent coexistence of two populations of different level of evolutionary advancement. The supporting background for this model is the early development in the Siberian Arctic of a kind of "periglacial", or tundra-steppe, environment (northern grassland on permafrost), driving the evolution of the woolly mammoth for which it is thought to have provided optimal conditions. This paper presents a more detailed analysis of that environment, evidenced in the last (Weichselian) cold phase, and then examines the relations of key earlier mammoth samples of different ages (Lister and Sher, 2001) to the insect and pollen record.

## The mammoth's environment in the Weichselian of the Siberian Arctic

For the period of the last 50 ka in the Laptev Sea area we have established a correlation between the mammoth's radiocarbon chronology and the character of environment, shown by the composition of fossil insect faunas, with additional support from other proxy evidence (Sher *et al.*, 2001; Schirmermeister *et al.*, 2002). This evidence comes from a very detailed and dated multi-proxy record of the environment in the Mamontovy Khayata section on the Bykovsky Peninsula (Lena River Delta), obtained during the work of the Russian-German Expedition "Laptev Sea System-2000" (1998-2002). This record is compared with the large collection of radiocarbon dates on mammal bones from the Laptev Sea area, from Taimyr to the New Siberian Islands (Sher *et al.*, 2003).

The long record of the Late Pleistocene environment in the Bykovsky section, covering the time span from the lower limit of radiocarbon (50-60 ka or more) to about 12 ka, shows the continuous existence of treeless, grass-and-herb dominated vegetation, and plant and insect communities of tundra-steppe type. Fossil insects, however, as the most sensitive indicators of the past environment, allow us to distinguish at least four periods

in the evolution of the tundra-steppe biome, and presumably the climate, during that time (Table 1). Those changes are well illustrated by two characteristics in the composition of fossil insect assemblages. The first is the proportion of true steppe species, that currently do not occur in tundra; even a few percent of these species indicates summer temperatures higher than present (Alfimov *et al.*, 2003). The second, sum of xerophilic insects, both those currently common in the Arctic (dry tundra inhabitants) and those uncommon or absent there (Kuzmina, this volume), is a proxy indicator of the total extent of various biotopes which were relatively dry, and at the same time better heated, than common modern wet tundra habitats.

LW II - the latest part of the Late Weichselian (=Wisconsin), 15-12 ka (from here on - uncalibrated radiocarbon ages) - demonstrates the last and brief flourishing of tundra-steppe communities. In the pollen record, it is marked by the prevalence of grasses and various herbs, such as Caryophyllaceae, Compositae, and *Artemisia*. Insect assemblages are marked by the highest proportion of all kinds of xerophilic species (averaging 78%), including thermophilic steppe elements (av. 4.2%). This fauna existed in a highly continental and very dry climate with relatively warm summers. Preliminary evaluation of summer temperature ( $T_{VII}$ ) by the Mutual Climatic Range (MCR) method on fossil insects suggests that it was a few degrees higher than present (Sher *et al.*, 2002). The MCR analysis for the 13-14 ka old insect fauna in the Lower Kolyma (Alfimov *et al.*, 2003) reconstructs  $T_{VII}$  as 3° higher than present.

LW I - the early Late Weichselian, ca. 24-15 ka - was very different. The proportion of all xerophilic insects drops to 10%, steppe insects are totally absent between 23 and 19 ka, and arctic tundra species dominate in most assemblages. Spore-pollen spectra are peculiar for the highest Weichselian content of *Selaginella rupestris* spores. At the same time, they retain high diversity and abundance of various herb families, and the plant macrofossils show a high proportion and diversity of xerophilic plants (Kienast *et al.*, 2001). According to fossil insects, summers were colder than in LW II, but probably still at least as warm as today (Sher *et al.*, 2002).

MW II - the second half of the Middle Weichselian, ca. 34-24 ka. Insect assemblages are of intermediate character between LW II and LW I. Steppe species are almost always present, although the sum of xerophiles averages only 30%. The general interpretation of the ecological composition of the insect faunas is that summers in this period were still dry, but warmer than during LW I. Pollen spectra still combine high levels of various herbs with a large amount of *Selaginella* spores.

MW I - the first half of the Middle Weichselian, ca. 48 (or more) to 34 ka - shows notable variation in the composition of insect assemblages, but generally they have a more xeric and thermophilic appearance than during MW II and LW I. Average proportions of xerophilic species are about 60%, and steppe species are constantly present. Spore-pollen spectra show the highest, though variable, values of *Artemisia* and Caryophyllaceae, but less of Compositae, and very low amounts of *Selaginella*.

Thus, the insect assemblages in the Mamontovy Khayata section demonstrate a significant variation with time, apparently related to changes in summer temperature and humidity. The studied part of the Middle Weichselian (MW I and MW II), despite some variations, reveals a clear trend from warmer to cooler summers, demonstrated by the gradual decrease of relatively thermophilic xerophiles and increase in the proportion of arctic tundra insects. The insect assemblages allow us to consider the MW I

environment as a relatively "warm" variant of tundra-steppe, while the MW II one was "cool" tundra steppe. This cooling trend reached its maximum during LW I (LGM). The dominance of pollen of grass and various herbs, along with the high amount of *Selaginella* spores and the abundance of arctic willow weevil *Isochnus arcticus*, invite a parallel with the modern Wrangel Island environment. A very sharp increase in summer temperature took place around 15 ka, and the LW II environment can be labeled as the "warmest" tundra-steppe for this Arctic region. Permafrost studies and ground ice isotopic analyses show much colder winter temperatures than present during the deposition of the whole Bykovsky Ice Complex (Meyer *et al.*, 2002). Thus, all kinds of proxy evidence indicate the retention of very high continentality of climate through most of the Weichselian succession.

The collection of  $^{14}\text{C}$  dates on mammal bones from the Laptev Sea area has amounted to 380 dates, obtained in the course of the Russian-German Expedition and from published sources; 233 of them are for mammoths, while other species received many fewer dates (including about 60 for horses, 40 for musk oxen and 30 for bison) and do not provide statistically reliable series.

The following distribution of the number of mammoth dates against the timescale can be seen. The number of finite dates on bones older than 40-42 ka is generally low (average 2.8 dates per 1,000 years) for technical reasons (infinite dates are not considered). After that time, the number of dated mammoth bones is more or less steadily high (av. 7.6 per 1,000 years) until about 25 ka, i.e. during the available part of MW I and most of MW II. Then it starts to decrease progressively during the whole LW I with a minimum at 16-17 ka (2 dates). It should be noted, however, that even during the peak of the LGM (18-20 ka BP) mammoth still inhabited the whole area of the Laptev Shelf Land, including the present northernmost islands and Severnaya Zemlya. The number of mammoth dates sharply jumps up after 15 ka, and stays at high levels (av. 7.4 in 1,000 years) until 10,000 y BP, i.e., during LW II. This period (the Late Sartanian) was the last interval with abundant dated records of woolly mammoth (the latest dated mammoth fossils in the region come from the interval 10,000-9,600 y BP, and are so far known from the Taimyr Peninsula only). Interestingly, the same period is marked by the highest number of  $^{14}\text{C}$  dates on *Saiga* fossils in Beringia as a whole (Guthrie *et al.*, 2001), while no dated record of that antelope is known between 25 and 16 ka, i.e., during LW I.

The chronological variations in the number of radiocarbon dates is subject to many factors, such as collecting biases, occurrence of sediments of a certain age, changes in taphonomic conditions, etc. In our case, however, we can assume that the changing number of radiocarbon dates broadly reflects former mammoth abundance for the following reasons. The distribution of dates has similar pattern in four large areas around the Laptev Sea, with varying geology and collecting history; an increasing number of dates through almost 15 years of research (Sher and Sulerzhitzky, 1991; Lavrov and Sulerzhitzky, 1992) has not changed the major features of that pattern; and the sedimentary characteristics of continuous successions, such as Bykovsky, show no major shifts which might imply serious changes in taphonomic conditions, e.g. their worsening during the LGM. Finally, comparison of the mammoth radiocarbon chronology in the Laptev Sea area with the environmental record on the Bykovsky Peninsula shows a correlation between the number of mammoth dates, the proportion of xerophilic insects, and the presence of steppe species.

Both of the peaks in the number of mammoth dates correspond to periods with a relatively high proportion of xerophilic insects and the presence of steppe species. A high diversity of insect fauna implies a richer vegetation mosaic, including more extensive areas with better heat supply, occupied by presumably more productive grassland. The number of mammoth dates starts to decrease at the same time as the proportions of those insect groups, reaching its lowest point soon after the period of total absence of steppe species. This pattern allows us to infer that all varieties of tundra-steppe insect assemblages indicate environments tolerable to the woolly mammoth, but that the less diverse insect faunas of the LGM, lacking the most thermophilic beetle species, may suggest less productive, probably just sparser, vegetation, and large grazers seem to have responded by reducing their numbers.

### **Early to Middle Pleistocene environments and mammoth evolution**

It is interesting to apply this model of relationships between insect faunas (as environmental proxies) and mammoth populations, to the Early and Middle Pleistocene samples used by Lister and Sher (2001) in their study of mammoth evolution (<http://www.sciencemag.org/cgi/content/full/294/5544/1094/DC1> for site details). We have examined insect samples from the same sites where most of the key mammoth fossils were found (Table 1).

All insect and mammoth localities in Table 1 have pollen records. In agreement with the insect evidence, they mostly portray grass- and herb-dominated vegetation, although a more complex variation of pollen spectra is observed, especially in the ancient samples. The earliest recorded appearance of steppe insects in northeastern Siberia comes from even older horizons (ca. 1500-2000 ka) (Sher, 1997; Kiselyov, 1981), but no proboscidean fossils of that age have so far been found there. For the subsequent at least 1-1.5 million years, the evolution of mammoths in Arctic Siberia was inseparably linked with a tundra-steppe environment, represented in the fossil record by insect, plant and pollen remains. That resulted from the high continentality of the climate that supported mostly treeless grassland vegetation with various cryoxerophilic and some steppe elements. The periods of decreased continentality (increasing humidity and extensive formation of boggy terrain) were relatively short, and did not result in total disappearance of tundra-steppe communities, just in some reduction of their spatial distribution (Kiselyov, 1981). As far as we know, none of those periods is comparable to the early Holocene with its devastating effect on the tundra-steppe biome. None of our model samples was found to correspond to a more impoverished insect fauna, similar to that of LW I, although this does not mean that such periods of climate and environment did not occur earlier.

Table 1. Insect assemblages corresponding to evolutionarily important mammoth samples from northeastern Siberia (based on Kiselyov, 1981, 1994; Kuzmina, 2001; Sher *et al.*, 2003, and geological publications cited in these papers). The Bykovsky succession, though providing no morphologically important mammoth fossils, is correlated with the "Ice Complex" sample from a wide region, from which the latest mammoth samples (Lister and Sher, 2001) were drawn.

Mammoth samples from Lister and Sher (2001)	Corresponding insect assemblages	Locality	Important mammoth specimens in situ	Age, ka	Sum of xerophilic insects, %	Proportion of true steppe species, %
"Ice Complex"	LW II, 6 samples	Bykovsky		12,5-15	78.0	4.2
	LW I, LGM, 4 samples	Bykovsky		19-22	10.4	0.0
	MW II, 4 samples	Bykovsky		ca 25-30	29.7	2.9
	MW I, 4 samples	Bykovsky		ca 42-48	58.5	2.8
	The base of the Ice Complex (series ANV & ANN, 7 samples)	Achchagiy-Allaikha, Lower Indigirka	+	ca 150-200	58.9	9.0
"Late Middle Pleistocene"	Utkin Beds, 4 samples	Maliy Anyuy River, Kolyma Lowland	+	ca 200-400	60.0	5.4
	Khomus Suite, lower part, 1 sample (6000 insect individuals)	Bolshoy Khomus-Yuryakh R., Indigirka Lowland		ca 400-600	64.4	14.0
"Late Olyorian"	Akanian Horizon, Loc. 35, 2 samples from the mammoth site	Bolshaya Chukochya R., Kolyma Lowland	+	ca 700-800	52.6	3.1
"Early Olyorian"	Chukochyan Horizon, Loc. 23, 4 samples	Bolshaya Chukochya R.	+	1000-ca 1200	59.7	2.5
	Chukochyan Horizon, Loc. 6, 4 samples	Krestovka R., Kolyma Lowland	+	ca 1000-1400	75.6	9.3

Permafrost made a very early appearance in Arctic Siberia (at least 2.5 million years ago), and a peculiar, extremely continental climate, with very cold winters and short, but relatively warm and dry summers, supported continuous tundra-steppe communities. The long existence of mammoth in this environment resulted in its successful adaptation to these habitats. Under such conditions, they reached successive stages of morphological advancement much earlier than their southern relatives. During certain periods of the Pleistocene, when similar (periglacial) environments developed in temperate latitudes, the northern mammoths had the potential for southward and westward dispersals. Our analysis supports the idea that the arctic Siberian mammoths repeatedly contributed to the evolutionary advancement of the whole lineage in Eurasia (Lister and Sher, 2001), and probably in North America too.

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## SYSTEMATIC POSITION OF THE CAVE LION (*Panthera spelaea*)

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The large lion-like cat is one of the important members of the Mammoth fauna, which was widespread during the late Pleistocene in northern Eurasia and America. The history of the lion-like cats dates back to the Villafranchian with the earliest record in the African locality Laetoli at ca. 3.5 Ma. The earliest European occurrence of this group of felids is established in the Italian site Isernia dated at about 0.7 Ma (Turner and Antón, 1997). Unfortunately, the relationships of the middle Pleistocene European lion *Panthera fossilis* and the late Pleistocene *P. spelaea* are currently not clear because of the insufficient knowledge of the ancient form.

The cranial morphology and systematic position of Eurasian cave lion have been debated over a long time. The majority of studies showed close affinities of *P. spelaea* with the extant lion, rather than the tiger. Moreover, the European paleontologists have treated *P. spelaea* as a subspecies of *P. leo*, whereas the Russian students usually distinguished it as a separate species.

In the present study, remains of *P. spelaea* from the Upper Pleistocene deposits of the Smolensk area (Russian Plain) and northern Kolyma lowland (Northern Siberia) are compared and discussed. This material is represented by new complete skulls of adult males with almost equal basicranial lengths of 307 mm for the Smolensk specimen and 305 mm for the Kolymian one.

The discussion is based on the detailed morphological and the metrical cranial analysis. It suggests a close affinity of the two studied forms from geographically distant regions