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Discoveries of woolly mammoth, *Mammuthus primigenius* (Proboscidea: Elephantidae) and some other Pleistocene mammals on the Taimyr Peninsula

Dick Mol, Alexei N. Tikhonov, Johannes van der Plicht & Dmitry Yu. Bolshiyanov

ABSTRACT**.** We present an overview of the most important discoveries of the woolly mammoth and other Pleistocene mammals from the Taimyr Peninsula, Arctic Siberia, which have contributed much to the understanding of the mammoth fauna and its environment. We also present 25 new radiometric dates on Pleistocene mammals both terrestrial and marine, of which 14 are of the woolly mammoth, recently collected on the Taimyr Peninsula. 14C measurements can be done using two different methods: AMS, i.e. mass spectrometry using milligram-size samples (lab codes UtC and GrA) and conventional radiometry using gram size samples (lab codes IGAN, GIN, LU). For the first time, remains of the Pleistocene bears from this region are reported. We also discuss interaction between climate, environment and megafauna. Dates appear to be consistent with other local proxy studies indicating whether or not conditions were favorable for herbivores on the Taimyr Peninsula.

KEY WORDS: *Mammuthus primigenius*, mammoth fauna, Pleistocene, Taimyr Peninsula, Siberia.

Dick Mol [dickmol@worldonline.nl], CERPOLEX / Mammuthus and Natuurmuseum Rotterdam, P.O. Box 23452, NL-3001 KL Rotterdam, the Netherlands; Alexei N. Tikhonov [tikh@AT8162.spb.edu], Zoological Institute, Russian Academy of Sciences, Laboratory of Mammals, Universitetskaya nab. 1, Saint Petersburg 199034, Russia; Johannes van der Plicht [plicht@phys.rug.nl], Centre for Isotope Research, Radiocarbon Laboratory, University of Groningen, Nijenborgh 4, NL-9747 AG Groningen, the Netherlands; Dmitry Yu. Bolshiyanov [bolshiyanov@aari.nw.ru], Arctic and Antarctic Research Institute, Bering St. 38, Saint Petersburg 199397, Russia.

Находки мамонтов *Mammuthus primigenius* (Proboscidea: Elephantidae) и некоторых других плейстоценовых млекопитающих на полуострове Таймыр

Д. Мол, А.Н. Тихонов, Й. Ван дер Плихт, Д.Ю. Большиянов

РЕЗЮМЕ**.** В статье представлен обзор наиболее важных находок мамонтов и других плейстоценовых млекопитающих на полуострове Таймыр в арктической зоне Сибири. Эти данные дополняют наши знания о мамонтовой фауне и среде ее обитания. Мы также представляем 25 новых радиоуглеродных датировок по плейстоценовым наземным и морским млекопитающим, остатки которых собраны в последние годы на Таймыре и в их числе 14 новых датировок по мамонтам. Впервые публикуются данные по плейстоценовым медведям этого региона. Радиоуглеродные датировки были получены двумя различными методами — способом AMS, методом масс-спектрометра, используя образцы размером в миллиграммах (лабораторные коды UtC и GrA) и обычным методом радиометрии используя образцы размером в граммах (лабораторные коды IGAN, GIN, LU). Обсуждаются также взаимоотношения между климатом, средой обитания и мегафауной. Полученные даты находятся в соответствии с предыдущими исследованиями, показывающими, когда условия обитания были предпочтительны для обитания травоядных млекопитающих на Таймыре.

КЛЮЧЕВЫЕ СЛОВА: *Mammuthus primigenius*, мамонтовая фауна, плейстоцен, полуостров Таймыр, Сибирь.

Introduction

Throughout history, mankind has been puzzled about the abundance of remains of large animals in the north of Siberia. But towards the end of the 18th century, little was known about the "mystical" woolly mammoth, *Mammuthus primigenius* (Blumenbach, 1799). Due to the efforts of the well-known scientific and political figure Vasiliy Tatischev, the Decrees of Tsar Peter I for the search of a complete carcass of a mammoth were prepared in 1720. Peter I had sent an expedition headed by D. Messerschmidt (1724) to Siberia. The successful expedition returned to St. Petersburg with the skull and bones of a mammoth from the Indigirka River in North-

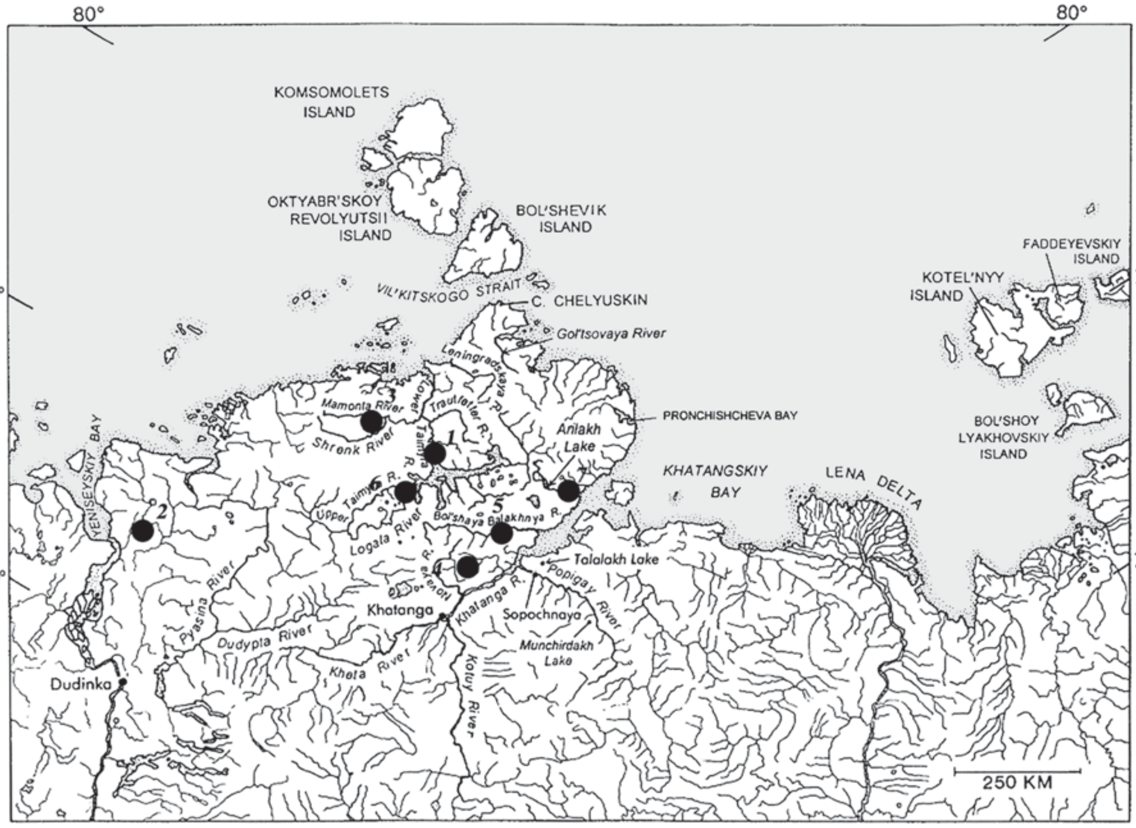

Figure 1. Finds of mammoth skeletons and carcasses on the Taimyr Peninsula, Siberia.
1 — Middendorff Mammoth; 2 — Kutomanov Mammoth; 3 — Taimyr Mammoth; 4 — Khatanga Mammoth; 5 — Jarkov Mammoth; 6 — Fishhook Mammoth; 7 — Markel Mammoth.

eastern Yakutia. Illustrations of these finds were subsequently published in England (1737). Georges Cuvier used these in 1796 for the proof that the mammoth is an extinct elephant species.

The mammoth and the other Pleistocene megafauna have been the focus of mythology building, and controversy surrounds their environmental conditions. With this factual inventory of documented discoveries of mammoth remains, this paper intends to contribute objectively to a better understanding of environmental conditions of the Taimyr Peninsula and North Siberia in the late Pleistocene. We also consider dates in relation to other local proxy studies to see whether or not conditions were favorable for herbivores on the Taimyr Peninsula.

Finally this paper also aims to contribute to solving the questions on the extinction of the Pleistocene megafauna in Siberia around 10,000 BP.

Mammoths of the Taimyr Peninsula

The first information about the mammoth fauna of the Taimyr Peninsula (820,000 square kilometers) in the Far North of Siberia was received in 1843 when Alexander Theodor von Middendorff (1815–1894) traversed more than 2000 km in this remote area. From Dudinka (Western Taimyr), the Middendorff Expedition went through Lake Pyasino, continued upstream on the River Dudypta and then used reindeer for transportation. The expedition reached the lower part of the River Boganida and moved the north and crossed the valley of Upper Taimyra River. Middendorff crossed Lake Taimyr by boat and in the source of the Lower Taimyra River he discovered a skeleton of a mammoth. It was the first documented finding of mammoth remains on Taimyr known to science (Middendorff, 1860).

Baron Eduard Toll has undertaken a number of expeditions in the Arctic Region in the period 1900–1903. Toll reported about the discoveries of a skull and tusks of a woolly mammoth on the northern coastline of the Taimyr Peninsula. The most outstanding further finds of the mammoth carcasses and skeletons in this region are represented on the Fig. 1.

The Kutomanov Mammoth

An outstanding find of the most complete carcass of an adult male woolly mammoth on the River Berezovka (Yakutia) in 1901 excited the Russian public. A couple of years later (1908) C. Yalko found an incomplete carcass of a mammoth with some associated soft tissue in a valley of the River Mokhovaya in southwestern

Figure 2. Skull of the Taimyr mammoth. Participants of expedition L.A. Portenko (left) and B.A. Tikhomirov (center) with Academician E.N. Pavlovskii. Photo: Mammoth Committee.

Taimyr. In the same year the Yenisei Museum received a sample of flesh and wool from this mammoth.

In 1909 the polar researcher N.A. Begichev visited the site of this mammoth and reported its scientific value to the Academy of Sciences. The Academy risked sending an expedition to Taimyr, but realized soon after visiting the site, that the find was less spectacular than the Berezovka Mammoth. Therefore they did not act with expediency. Only in April 1913 did an expedition headed by G.N. Kutomanov arrive at the site. They dug remains of this carcass out of a channel of a stream. From soft tissues, a large piece of skin with wool was dug out. The legs of the mammoth were covered by skin and soft tissue. These legs had been taken away by native people and subsequently fed to dogs (Kutomanov, 1914). The mammoth from the Mokhovaya River is known as the Kutomanov Mammoth. Its cranium and about half of the bones of the post cranial skeleton are stored in the collections of the Zoological Institute in Saint Petersburg, ZIN 31736 (Averianov, 1994). Soft tissues of this specimen were dated by Heintz & Garutt (1964) by 35,800±2700, T-169 (3).

Taimyr Mammoth

The numerous geological and paleontological expeditions in the beginning of the Soviet period occasionally found remains of mammoths on the Taimyr Peninsula, but their scientific and cultural value were not fully appreciated at that time.

Nevertheless, Taimyr was fated to become the starting point in the creation in USSR of the new school of the researchers of mammoths and mammoth fauna of Siberia.

In the autumn of 1948 the staff of the Zoological Institute in Leningrad received information about a carcass of a mammoth in the northwest part of the Taimyr Peninsula. In a valley of an anonymous river (subsequently named Mamontovaya), left inflow of the Schrenk River (basin of Upper Taimyra River), polar explorers S. Zhikharev and A. Korzhikov found the tip of a mammoth tusk protruding from the permafrost. While digging out the tusk, it became apparent that it was still attached to the head of the mammoth with associated remains of flesh and wool. A photographic picture of the discovery and one of the tusks were sent to the Academy of Sciences in Leningrad. The discoverers believed that the trunk and other parts of the mammoth could be found in deeper layers of the site.

Because of this find, professor Y.A. Orlov and colleagues realized the importance of the discovery, and decided that it was necessary to organize a special committee in the Academy of Sciences for the coordination of investigations on this particular mammoth. This commit-

Figure 3. Transportation of the Taimyr Mammoth from the site to Dikson. Photo: Mammoth Committee.

tee would consist of people from different institutes. On December 22, 1948, the Presidium of Academy of Sciences ratified the Committee on the organization of the excavation and delivery to Leningrad of the so-called Taimyr Mammoth, headed by E.N. Pavlovskii (Fig. 2).

The committee developed the plan of sending a multi-disciplinary expedition to Taimyr in the summer of 1949 to salvage the Taimyr Mammoth. It included a survey team, L.A. Portenko (Expedition Chief), geologist A.I. Popov, botanist B.A. Tikhomirov and glaciologist E.P. Shusherina, with the assignment to make a report on site conditions.

On May 26, 1949, the team reached the northern coast of Taimyr by plane, and continued until June 10 by using cross-country vehicles to reach the site. On June 15 the group started to remove the snow cover. The snow was so packed, that it was very difficult to remove. It took until the next day for the workers to reach to the surface of the ground. They used water to melt the sediment in which the mammoth was embedded. On June 18, the cranium, to which one of the tusks was still attached, was taken to a high riverbank to dry out. The excavation continued, exposing the mandibula and bones of the post-cranial skeleton. Some of the ribs and vertebrae were still in anatomical position. Many remains of pieces of skin were salvaged. These parts were in an extremely bad state of preservation. Some remains had been found in a powder resembling dirty chalk. Skin with attached wool and underwool was collected as well. On the next day, the bones of the right forearm were taken out (Portenko *et al*., 1950).

Popov (1950) reports that the excavations were stopped on July 10th because the water level in the excavation area had risen so high, that it was impossible to continue the work. Further excavations were prevented till August 6th. The last bones were taken from the site on August 13th without any soft tissues.

In the middle of October, the excavated materials were transported by plane from the site to Dikson (Fig. 3), and from there to Leningrad. Because of the successful expedition of the survey team, the excavation of the Taimyr Mammoth was closed.

The skeleton of the Taimyr Mammoth was studied by Garutt & Dubinin (1951). The geological age of this mammoth is quite recent, 11,450±250, T-297 (Heintz & Garutt ,1964). The mounted skeleton is on display in the Zoological Museum of the Saint Petersburg (ZIN 27101) (Garutt, 1964). This specimen was recently designated as a neotype of the species of the woolly mammoth *Mammuthus primigenius* (Blumenbach, 1799) (Garutt *et al.,* 1990).

New initiative by N.K. Vereshchagin

After a long period of silence, professor N.K. Vereshchagin gave a new boost to the established Mammoth Committee. His work started at the beginning of the seventies with expeditions to the world famous "mam-

Figure 4. Head of the Khatanga Mammoth, Prof. N.K. Vereshchagin near the find. Photo: Courtesy of Prof. N.K. Vereshchagin.

moth cemetery" of Berelekh in the north of Yakutia. Many thousands of remains of woolly mammoth have been collected and studied by the team headed by Vereshchagin (1977). In 1971 Yakutian scientists excavated a complete skeleton of the Terektyakh mammoth (Guriev *et al*., 1986). In 1972 the almost complete skeleton together with internal organs, amongst others (including the complete stomach) of Shandrin Mammoth was found in the north of Yakutia, and the first complete carcass of a mammoth baby was discovered in the Far East of Siberia, Magadan Province, in 1977. Vereschagin & Tikhonov (1990, 1999) have published a review of every important mammoth discovery on the Russian territory.

Khatanga Mammoth

The Khatanga Mammoth was discovered on the Taimyr Peninsula in 1977 approximately 90 km north of Khatanga. In the spring of 1977 reindeer-raiser P.N. Mikhailov saw a huge mammoth tusk in a fissure of a bank of the River Bolshaya Lesnaya Rassokha (basin of Khatanga River). It was the director of a reindeer state farm V.N. Sobolev who informed the administration of the Taimyr National District. Subsequently, its chairman V.V. Ostapenko, made a preliminary survey at the site and reported about the find to the Mammoth Committee.

In the middle of July 1977, a group of scientists from the Zoological Institute in Leningrad went to Khatanga to organize the protection of the Khatanga Mammoth site preventing its thawing during the summer months. This group excavated frozen sediments and the upper part of the head, nearly completely covered with skin, including the ear, and with the trunk still attached. A front leg appeared also. The partly decayed trunk had pink colored skin. The team had cut it into two pieces (40 and 60 cm in length) and had sent it to a museum in Krasnoyarsk, where it subsequently disappeared. A front foot with nails and skin, some leg bones, and parts of the base of the trunk were all taken to the Zoological Institute.

The next year a new team, headed by Vereshchagin, was formed, and a second expedition on the Khatanga Mammoth took place. The cranium of the mammoth (Fig. 4), many remains of soft tissues, separate bones of the skeleton including the tibia/fibula and well preserved hind foot were excavated and taken to the same institute (Vereshchagin & Nikolaev, 1982). Arslanov *et al*. (1980) dated this specimen as older than the limit of the radiocarbon method 53,170 (LU-1057).

The Jarkov Mammoth

In the summer of 1997, a family of Dolgans (a nomadic people living on the Taimyr Peninsula) named Jarkov (Fig. 5), discovered a 30-cm piece of a mammoth tusk protruding from the tundra, ~12 km south of the River Bolshaya Balakhnya (73°32′N; 105°49′E). The Jarkovs dug out the tusk, and to their surprise, they discovered the second tusk, too. Both tusks were still in anatomical position, relative to the cranium. The excavation activities of the Jarkovs damaged the cranium, maxilla, and mandible, which were also in relative

Figure 5. S. Jarkov with frozen ground embedded by wool of the mammoth. Photo: F. Latreille.

Figure 6. B. Buigues excavating the remains of the Jarkov Mammoth in 1998. Photo: F. Latreille.

anatomical position to each other. Only the tusks were removed; all bones were left in the permafrost. This mammoth was nicknamed the Jarkov Mammoth.

A team from CERPOLEX/Mammuthus excavated the remains of the cranium in May 1998 (Figs. 6 and 7). Next to the cranium were a small piece of meat, skin, and

Figure 7. Excavation of the block with the remains of the Jarkov Mammoth in September 1999. Photo: F. Latreille.

Figure 8. Airlifting of the Jarkov Mammoth block with attached tusks. Photo: F. Latreille.

large portions of fur and underwool all of which were saved. The party employed a ground-penetrating radar system to see if more remains of the mammoth were present in the frozen ground. Immediately north of the cranium, anomalies in the permafrost were visible on the radar. The anomalies were interpreted as potential remains of the Jarkov Mammoth carcass. It was decided to extract those remains in an unusual way: in September–October 1999, a huge block of frozen sediment that likely included the remains of the mammoth, was excavated.

On October 17th, 1999, an MI 26 helicopter successfully airlifted a 23-ton block of permafrost from the frozen tundra of the Taimyr Peninsula (Fig. 8). In this 13.5-m^3 block of soil, remains of the Jarkov Mammoth were embedded. This event in 1999 was the start of the CERPOLEX/Mammuthus program "Who or What Killed the Mammoths" to contribute to the unsolved questions of the extinction of the Pleistocene megafauna around 10,000 BP.

The Jarkov Mammoth's tusks (Tab. 1; Fig. 9) are well preserved. They are spirally twisted and reach nearly 3 m in length, indicating that they belong to an adult, male woolly mammoth, *Mammuthus primigenius*.

The third molars in both the maxillae (left and right M3) and mandible (left and right m3) are preserved. The anterior parts of both molars are worn to the base of the crown. The stage of wear of the m3 is equivalent to Laws' Age Group XXV, which means that the Jarkov Mammoth had an age of approximately 47±2 African Elephant Years (AEY) at the time of its death.

Figure 9. The Jarkov Mammoth block in the ice cave in Khatanga. Photo: F. Latreille.

Table 1. Measurements (in cm) of the tusks of Jarkov Mammoth.

Measurement	right tusk	left tusk
Maximum length (outer curve)	294	298
Diameter	13.5–14.5	13.5–14.6
Weight	45 kg	47 kg

Table 2. Radiometrical dates of the Jarkov Mammoth.

Laboratory Number	Radiocarbon age (^{14}C yr. BP)	Sample
UtC 8137	19,910±130	bone
UtC 8138	20,380±140	hair
UtC 8139	20,390±160	skin

Remains of the Jarkov Mammoth excavated by the first CERPOLEX/Mammuthus expedition (1998) have been radiometrically dated at the R. J. van de Graaff Laboratory, Utrecht University, The Netherlands, by means of the accelerator mass spectrometry method (AMS) (Tab. 2).

In September–October 1999 about 1 m^2 of the top of the block was melted in the field, for which purpose ordinary hairdryers were used. A large portion of fur and under fur of the Jarkov Mammoth was exposed. It was noted that the under fur was extremely long, up to 12 cm. The team agreed that this might be the winter coat of the mammoth.

It was also decided to defrost the frozen block in the safety of the ice cave at a constant temperature of –15°C, in order to retrieve the mammoth remains, as well as any micro- and macro-organisms trapped in the surrounding sediments.

Microfossils (pollen, fungal spores, algae) and macrofossils (fruits, seeds, remains of flowers, vegetative plant remains, bryophytes) were found in sediment samples from two loci studied by Van Geel, Pals and Van Reenen (Mol *et al.,* 2001). The preservation of these fossils is excellent and a variety of taxa are present. Poaceae, *Artemisia* and *Papaver* dominate the pollen spectra. Also macrofossils of these taxa are present in our samples. The overall picture based on interpreting these fossils, is a landscape dominated by steppe vegetation as a consequence of dry and cool climatic conditions. Moreover, pollen diagrams produced recently from Lake Deposits elsewhere in the Taimyr area demonstrated that vegetation during the Late Weichselian glacial maximum was typical for a steppe. In addition, on a local scale, mosses such as *Racomitrium lanuginosum*, *Pogonatum* cf. *urnigerum* and a hair-cap moss resembling *Polytrichum piliferum* are indicative of a rather dry, sandy, or stony environment, with cryogenic phenomena as well as biodisturbance as a consequence of trampling or grazing. We consider the abundant presence of spores of the dung-inhabiting fungus *Sporormiella* as clear indication of the presence of herbivores.

Among the microfossils and macro remains there are also indicators for wet conditions (e.g., the alga *Pediastrum*; the mosses *Drepanocladus aduncus*, *Calliergon giganteum*, *Rhizomnium pseudopunctatum*). The Jarkov Mammoth may have been covered by mud after solifluction, so that the mammoth and the associated plant remains were soon under permafrost conditions.

To learn more about the life and death of the Jarkov Mammoth, a small sample of the left tusk near its base was extracted. Just under the pulp cavity surface is the last dentin deposited before the animal's death; extending outward from this inner surface, in the sample recovered, was 16 mm of a deposit of dentin laid down during the few years preceding death. This tusk sample was embedded in epoxy resin and cut transversely, producing three 5-mm thick slabs. One of these slabs was thin-sectioned for structural analysis and the other two were sampled to document changes in dentin composition during the last few years of this animal's life. The death of the Jarkov Mammoth occurred at the end of the winter, just before the onset of its vigorous spring growth.

Compositional profiles through the last three years of life traced isotope variation in carbonate oxygen, carbonate carbon, collagen carbon, and collagen nitrogen. The oxygen-isotope profile showed seasonally varying values that confirmed the annual increments (identified in thin section), with minimum values corresponding to mid-winter and rising values through spring and early summer. This pattern is in phase with expected variation in the composition of local precipitation, suggesting that winter precipitation, presumably snow, was ingested, but that the snow volume was so small that its melting did not dominate springtime surface-water composition. Carbon isotope values were variable, but all consistent with ingestion of C3 vegetation. Nitrogen isotope values suggest brief periods of late-winter nutritional stress about two years before death and in the final months of life, but this was probably a short-term response to seasonal food shortage. In the episode about two years before death, this stress quickly reversed with the onset of spring. The terminal episode of stress was less severe and probably not associated with the cause of death. Year-to-year contrasts in oxygen-, carbon-, and nitrogen-isotope profiles suggest a biennial (about once every two years) migration between lower latitude environments that had a less "open" vegetation structure and slightly greater moisture availability and the higher latitude mammoth steppe, where this animal finally died.

Fishhook Mammoth

In 1990, Alexander Stolyarov, a citizen of Khatanga, Taimyr Peninsula, discovered a nearly complete carcass of a woolly mammoth, *Mammuthus primigenius*, in the delta of the Upper Taimyra River, near Lake Taimyr (74°08′5″N, 99°38′0″E). Stolyarov removed the two remarkably preserved tusks and, allegedly, sold them to someone in Krasnoyarsk.

In 1992, a Japanese team visited Khatanga by invitation of Yuri Karbainov, Director of the Taimyr Nature

Figure 10. Excavation of the block with the remains of the Fishhook Mammoth. Photo: F. Latreille.

Reserve. This team arrived in autumn when the carcass and surroundings were completely covered with snow. In Japan, the year 1992 was declared the "Year of the Mammoth". The Japanese team visited the carcass site by helicopter and began to uncover parts of the frozen carcass. Although the specimen and the ground were frozen, they managed to excavate the skull, vertebrae, ribs, and part of a scapula. Their findings also included a lot of mammoth hair, skin, and muscle.

Later in the week, the Japanese returned to the site with a "steam machine" to thaw the mammoth. Much of the carcass remained frozen in the ground, but the team removed the cranium, a humerus, a partial ulna, a complete ulna and a femur. The team brought femur and some of the meat and skin of this specimen to Japan, and left other bones at the museum of the Nature Reserve in Khatanga. Many soft materials — skin and muscles were cut by axe and later thrown away. The unsophisticated "excavations" of this Japanese team and their Russian hosts raised an outcry from scientific circles worldwide. When the Japanese team returned to the site the following year (1993), on this occasion with the representative of the Mammoth Committee, the entire site had been — and remained — flooded naturally by the river. Still, a lot of material, including some skin and muscle, was left in the permafrost at the carcass site.

The cranium of the Fishhook Mammoth is high-domed and heavily damaged (lacks tusks and molars); broken maxillae demonstrate that both M3s were broken out after the specimen was unearthed. Molar alveoli indicate that small molar remnants (M3) were present on both sides, indicating that the mammoth was a very old individual, at least 55 African Elephant Years (AEY). Both M2s were lost prior to the animal's death. Maximum diameter of tusk alveoli is 14 cm; maximum width of cranium at eye sockets is 73 cm (top) and 65 cm (bottom); maximum width of posterior cranium is 73 cm. All collected skeletal remains of the Fishhook Mammoth indicate that it is a very old individual. The so-called Fishhook Mammoth stood approximately 255 cm at shoulder compared to some other mammoths (see table 3). The Fishhook Mammoth was a male individual based on (1) large cranium, (2) diameter of the tusks, and (3) size of known post-cranial skeletal elements. The cranium is on display in the Museum of the Nature Reserve in Khatanga.

In August 2000, S. Pankevitch rediscovered the Fishhook mammoth carcass remains where they were first discovered in 1987. Because the area was flooded, Pankevitch searched with his fishing equipment: he was

Table 3. Comparison of the shoulder height (in cm) of the Fishhook Mammoth to two other specimens of *Mammuthus primigenius*.

Measurement	Fishhook	Kemel *	Adams **
Maximum height of back	ca.255	258	320
Humerus length	89	91	100
Ulna length	79	66.6	77

* Found in 1899, now in the collection of Geological and Mineralogical Museum of Kazan University, Kazan.

** Found in 1799 in delta of Lena River, Russia; now in the Zoological Institute, Russian Academy of Sciences, Saint Petersburg.

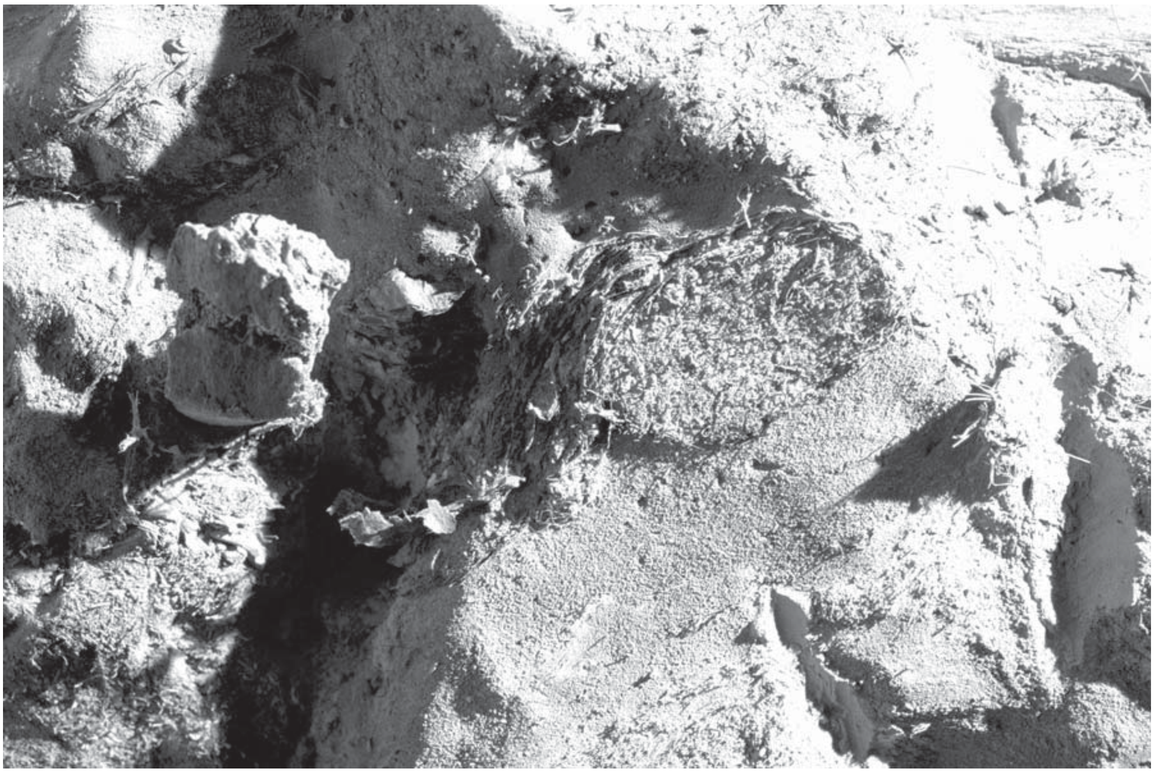

Figure 11. Cross section of intestine in the block of the Fishhook Mammoth. Photo: F. Latreille.

successful! On his fishhook, Pankevitch caught a muddy strand of mammoth hair. Hence the mammoth was nicknamed the Fishhook Mammoth.

Small drilled samples of the long bones of Fishhook were taken by MacPhee and Flemming (AMNH) for DNA research and radiocarbon dating. The ^{14}C-AMS date (Beta Analytic, FL; November 2000) for the Fishhook Mammoth is 20,620±70 years BP.

In October 2000, a small expedition led by Bernard Buigues (CERPOLEX/Mammuthus) set out to study the Fishhook Mammoth site. Parts of the carcass were exposed at the surface: a portion of the vertebral column (lumbar vertebrae in anatomical position), parts of the pelvic bones, muscles, and an abundance of hair.

In May 2001 the remains were excavated under cold conditions (Fig. 10). The ground-penetrating radar (GPR) technique was used to locate the bones and tissue of the carcass accurately. Then the remaining parts of the carcass, including soft tissue, fur and underfur were extracted from the frozen ground together with the surrounding sediments to learn more about the environment at the time of death of the Fishhook Mammoth. A block of approximately 1100 kg with a hind part of the Fishhook Mammoth was airlifted and put on a truck that drove it to the ice cave in Khatanga where it is stored under controlled conditions. The block was cleaned in the summer of 2001. Part of the skeleton is still in anatomical position, among others, 6 thoracic vertebrae, 2 lumbar vertebrae, and 16 ribs. It became clear that a lot of soft tissue is preserved in this block of frozen sediment, including remains of the stomach, the intestinal tract and its contents. It is interesting that some internal organs can be seen in this block, such as some intestines still filled up with digested food remains (Fig. 11).

The second aspect of using the GPR application, consisted in sounding the block with the Fishhook Mammoth remains in order to define the detailed distribution of the bones and tissue, which is valuable information for researchers in charge of excavation work. The results of using GPR for paleontological research in the permafrost were published by Grandjean *et al.* (2003). The encouraging results open up various possibilities for using GPR in expeditions in the Far North of Arctic Siberia. Grandjean *et al.* demonstrated that the GPR technique operated at 900 MHz is well suited to sounding the upper few meters of permafrost. Even though radar penetration is not very deep due to the dielectric properties of the permafrost, it is sufficient to locate mammoth or other mammal remains within the layer where it is technically possible to extract them.

The pollen spectrum of the sampled gut content of the Fishhook Mammoth was completely dominated by grasses (97.8 % Poaceae). Some clusters of unripe grass pollen were found in the pollen slides. This may indicate that the animal died in the flowering season of the grasses. The pollen spectrum from the intestines content may be strongly biased by the food preference of the mammoth and therefore cannot be considered as indicative for the regional vegetation pattern. Nevertheless, the conclusion can be made that the landscape was very poor in trees. Apart from grass pollen, also low amounts of other herbaceous plants were recorded: *Artemisia*

Figure 12. Tusks and mandibula of the Nikolai Mammoth. Photo: D. Mol.

(0.2%), Asteraceae (+), Caryophyllaceae (1.0%), Ranunculaceae (0.5%), *Rumex acetosa* type (0.2%), Liliaceae (0.2%), and *Polemonium* (+). Some ascospores of the dung-inhabiting fungus *Sporormiella* illustrated by van Geel (2001) were found. The matrix of the gut sample from the Fishhook Mammoth consisted of a mass of unidentifiable grassy material. Among the identifiable remains were leaves of *Dryas octopetala* (dryad) *Salix* sp. (willow), *Betula nana* (dwarf birch), *Vaccinium* species, a catkin of *Alnus fruticosa* (alder), and needles of *Larix* (larch). The sample also contained a large number of mosses, as well as some inflorescence of *Polygonum viviparum* and seeds/fruits of about 15 taxa of other herbs, amongst others *Pedicularis sceptrum-carolinum*. Among these are at least four species of grasses, two Cyperaceae (sedges), two Juncaceae (rushes) and *Papaver radicatum* (arctic poppy). Furthermore, excrements of lemmings were found as well as several remains of Coleoptera.

The conclusion from the paleoecological analysis may be summarized as follows: the Fishhook Mammoth had been grazing moist, open vegetation dominated by grasses, with a lot of mosses in the ground cover. However, the plant remains also reflect the presence of vegetation types of dry ground, as well as border scrub of forest tundra. The find of *Larix* is especially interesting, because the site where the Fishhook Mammoth was found is situated at about 200 kilometers north of the present timberline.

The Markel Mammoth

A nearly complete skeleton of a woolly mammoth, *Mammuthus primigenius*, was collected during the August 1999 field trip of the CERPOLEX/Mammuthus program. A Dolgan family named Poratov mainly excavated the skeleton on the tundra of the Taimyr Peninsula. The location of the Markel Mammoth is situated on the north bank of the mouth of Novaya River about 15 meters above the water level of the river. The skeleton was covered by approximately one meter of sediments.

The hunters who found and removed the tusks protruding from the tundra destroyed the cranium of the Markel Mammoth. Hence the tusks are lost for scientific exploration. The expedition has found only fragments of the cranium and one molar (M3). The upper molar is indicating an individual age of more than 50 AEY. The fusion of the epiphyses and the diaphyses of the long bones, namely the caput femoris of the left and right femora also indicate an old age for this animal. The vertebral column is almost complete but has been damaged by excavating activities. Of great interest are some thoracic vertebrae, which are fused by extra bone growing indicating illness.

Measured radiocarbon age on the right ulna of the Markel Mammoth, show an age of 32,570±280 BP (Beta-148650). A 14C date on a vertebra (GrA-17439) gives a measured radiocarbon age of 41,580±1190/-1040 BP. MacPhee *at al*. (2002) leave the possibility open that these results might indicates that more than one individual is present in the collection of bones attributed as the Markel Mammoth. The expedition members have double-checked all skeletal remains of the Markel Mammoth and reconfirm that none of these parts is a replicate. A new radiocarbon date is required to solve the problem of the thousands of years discrepancy of the two radiocarbon dates.

The Nikolai Mammoth

Another (partial) skeleton of a woolly mammoth was found during the 2002 field campaign by Nikolai Rudenko, working with the CERPOLEX/Mammuthus team. On the west bank of Lake Taimyr, a pair of tusks was found (Fig. 12), together with the mandibula and some other parts of the skeleton. Other remains are still hidden in the permafrost at that location near Cape Sabler. The measurements are: c. 283 cm for the right tusk and c. 253 cm for the left one. The diameter for both tusks at the beginning of the pulp cavity is 10 and 11 cm. The pulp cavity is not deep, and the length, diameter and curvature of the tusks point to an old male individual. The mandibula with the molars m3, indicate that the animal died at an age of 40–42 AEY. An expedition to the site is planned for the near future to take out the other remains of the Nikolai Mammoth.

Holocene mammoths

Holocene woolly mammoths have been reported from the Taimyr Peninsula by Sulerzhitskii & Romanenko (1997). The youngest record dates 9670±60 BP (GIN-1828). The youngest bone of a woolly mammoth, collected by us on the Taimyr Peninsula, is a lower jaw. This jaw appeared to be of an extremely small specimen, probably an old female individual. The jaw was dated by means of ^{14}C at Groningen University and proved to be 9,920±60 BP (Laboratory No.GrA-17350/DM5). This result shows that the woolly mammoth occurred on Taimyr up to the beginning of the Holocene. A short description and comparison with other small mammoth remains was published by Reumer & Mol (2001).

Most northern mammoths in the world

The most northern remains of the woolly mammoth in the world have been recovered from the Severnaya Zemlya Islands (October Revolution Island), north of the Taimyr Peninsula. Radiocarbon dates towards the end of the Pleistocene (ca. 12,000–10,000) have been published by Makeev *et al*., (1979) and Kuzmin *et al*., (2003). We reproduce the results of the 14C investigations here (Tab. 4).

Table 4. Radiometrical (^{14}C) dates of *Mammuthus primigenius* from October Revolution Island (different specimens).

Tusk	11,500±60 BP	LU-610
Tusk	19,270±130 BP	LU-654B
Molar	19,970±110 BP	LU-688
Bone	25,030±210 BP	LU-749B

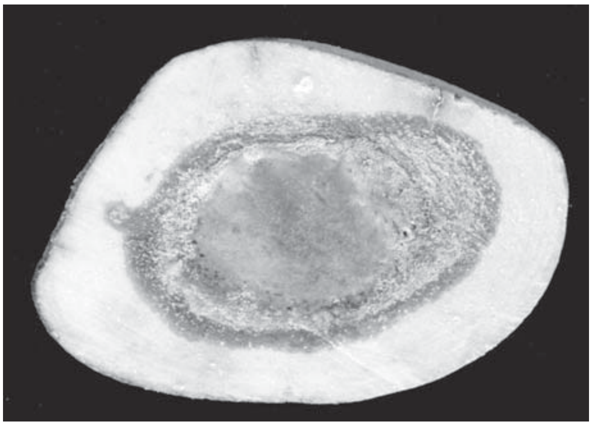

Figure 13. Marrow inside a mammoth ulna. Photo: F. Latreille.

Other extreme northern remains of mammoths have been collected by the CERPOLEX/Mammuthus program on the continental part of Taimyr, on the banks of the Leningradskaya River 76°24′784″N, 101°37′846″E.

These remains have been washed out of the sediments when the water level was high but still are in a very good state of preservation. A right ulna of a mature individual of the woolly mammoth was cut open and in the interior of the shaft the marrow could be noticed in an excellent preservation (CERPOLEX/Mammuthus collection 2003/733) (Fig. 13).

Other interesting finds

Reindeer (*Rangifer tarandus*)

During the summer of 2001, dry weather conditions led to a rapid lowering of the water level of Lake Taimyr. In August of that year, on the northwestern shore of the lake and 3 km NE of Cape Sabler (74°31′N, 100°30′E), an almost complete *Rangifer tarandus* skeleton was discovered in silt sediments of the defrosted lake bottom. The stomach contents were radiocarbon dated at Groningen University to 13,040±80 BP (AMS date GrA-19245). The skull, which includes a poorly developed antler fragment and the mandible, was excavated, as were the extremities with an almost complete set of hooves including the after claws. Parts of the coat and the contents of the intestinal tract were also found. This specimen bridges the previously existing chronometric gap in radiocarbon dated *Rangifer* finds from Taimyr between 20,250 and 8,700 BP and supports the theory

Figure 14. Musk-oxen on in the Taimyr tundra. Photo: F. Latreille.

that this species has occurred at Taimyr, without interruption, since at least 36,000 BP (MacPhee *et al.,* 2002).

The matrix of the macroscopic plant remains from the stomach consisted of a mass of small twigs, mainly *Betula* and *Salix*, together with very few grass remains and some mosses. The assemblage of macroscopic remains reflects different types of environment: open water (fruits of *Potamogeton* sp., *Ranunculus* subg. *Batrachium*, *Hippuris vulgaris*, ephippia of *Daphnia* sp.), mesotrophic bank vegetation (*Menyanthes trifoliata*, *Potentilla palustris*, *Carex aquatilis*), but also vegetation of higher, drier ground, as indicated by *Cassiope tetragona*, *Dryas octopetala*, and *Minuartia rubella.* The conclusion that the reindeer used shoots of shrubs as a food source is corroborated by the finds of catkins and achenes of *Alnus*, fruits and bud scales of *Salix*, and *Betula* seeds.

The Pleistocene mammoth fauna of the Taimyr Peninsula

Along with study of finds of the mammoth on Taimyr, some attention was also given to other representatives of mammoth fauna. Most numerous among them are the horse, reindeer, bison and musk-ox. Discovery of the Holocene musk-ox living 3000 years back on Taimyr (Vereschagin, 1959b, 1971) has forced researchers to reconsider the theory of extinction of the mammoth fauna on the boundary between the Pleistocene and the Holocene. Subsequently the Holocene mammoth, horse and bison were added to the evidence of the more recent

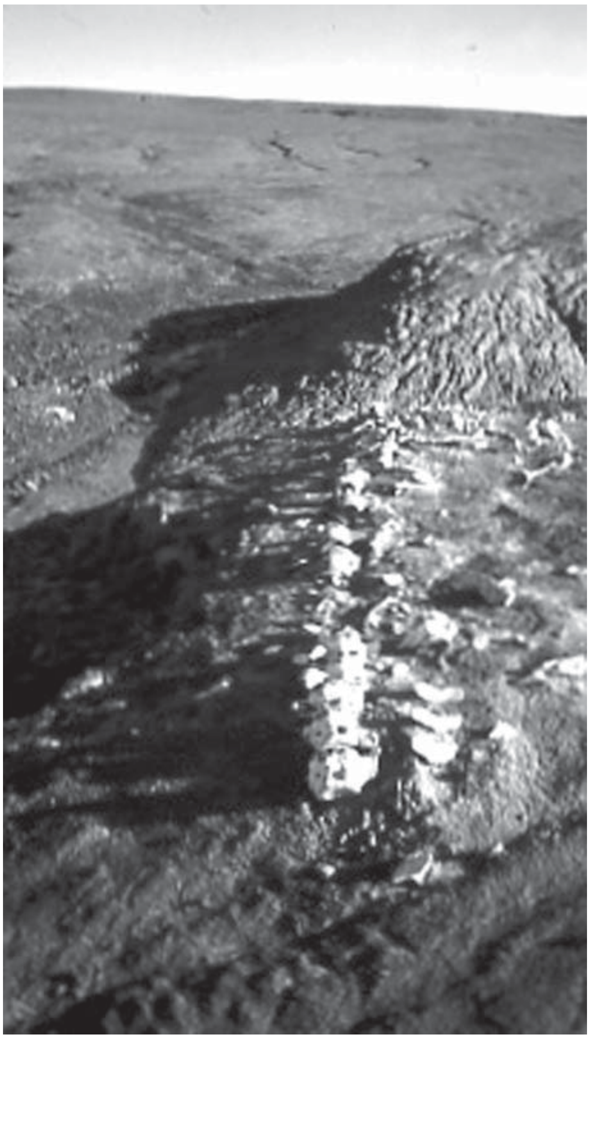

Figure 15. Skeleton of the Pleistocene narwhal (October Revolution Island). Photo: B. Buigues.

musk-ox. All this allows us now to speak about original refugia of the Late Pleistocene fauna on the Taimyr Peninsula.

Vereshchagin (1959a) published a paper on the Late Pleistocene megafauna of the Taimyr Peninsula. He listed the following species and the percentages of skeletal remains recovered for each species: *Vulpes lagopus* (1.25%), *Lepus timidus* (3.75%), *Mammuthus primigenius* (16.25%), *Equus caballus* (31.25%), *Bison priscus priscus* (1.25%), *Bison priscus* subsp. indet. (3.75%), *Ovibos moschatus* (12.5%), *Rangifer tarandus* (27.5%), *Monodon monoceros* (1.25%), and *Delphinapterus leucas* (1.25%).

In three field campaigns by the team of CERPOLEX / Mammuthus thousands of fossil bones at several localities on the Taimyr Peninsula have been collected (Fig. 16). A total of 623 items (by April 2003) have so far been described in our catalogue (as by August 2002; several numbers bear sub-numbers); *Mammuthus primigenius* (395 specimens, 63.41%), *Ovibos moschatus* (103 specimens, 16.54%), *Equus caballus* (57 specimens, 9.15%), *Rangifer tarandus* (34 specimens, 5.45%), *Bison priscus* (26 specimens, 4.17%), *Alces alces* (5 specimens, 0.8%), and *Canis lupus* (3 specimens, 0.48%). Several remains of small mammals and birds have been collected but have not yet been identified.

New for the fauna of the Late Pleistocene of Taimyr is the moose, *Alces alces* (for radiocarbon dates see MacPhee *et al*., 2002). These finds represent the northernmost record of fossil moose in the northern hemisphere (compare Kahlke, 1999).

The most abundant species in the list of Vereshchagin (1959a) is the horse (*Equus caballus*), followed by reindeer (*Rangifer tarandus*), woolly mammoth (*Mammuthus primigenius*) and musk ox (*Ovibos moschatus*). The most common species, collected during the field campaigns in the period 2000–2002 by CERPOLEX/ Mammuthus, is the woolly mammoth (*Mammuthus primigenius*), followed by the musk ox (*Ovibos moschatus*), and horse (*Equus caballus*).

Compared to other regions of the northern hemisphere, e.g. Western Europe, *Ovibos moschatus* was very common during the Late Pleistocene in the far north of Siberia (now reintroduced on Taimyr Peninsula; Fig. 14).

The woolly rhinoceros, *Coelodonta antiquitatis*, common in Eurasian faunas, together with the woolly mammoth, is absent on the Taimyr Peninsula and from North America during the Late Pleistocene. A well-preserved cranium of a woolly rhinoceros, which is stored in the Natural History Museum of Dudinka (southwestern Taimyr), was not collected on the peninsula. Ice free landscapes, saturated with moisture, in combination with long periods of high lake and river levels and frequent flooding of large parts of the peninsula, possibly prevented the regular immigration of *Coelodonta* populations to Taimyr, as was suggested by Kahlke (1999) for the comparable record from north-eastern parts of Yakutia.

There are no reliable records of the saiga antelope during the Late Pleistocene of Taimyr. On one occasion, a skull of this bovid was reported to be collected somewhere on the peninsula. It was to be delivered to an anonymous person in Khatanga. It became lost to science. It seems that saiga was extremely rare on Taimyr or even absent for the same reasons as for the woolly rhinoceros. The closest known find to the saiga is a skull from the basin of the Olenek River in northwestern Yakutia.

Among carnivorous animals of Taimyr, the most abundant remains belong to canids, wolf and polar fox. An almost-complete skull of a wolf with mandibula was dated by AMS 16,310±50 BP and 16,670±70 BP (MacPhee *et al*., 2002). It is remarkable that the cave lion (*Panthera spelaea*) is not known on Taimyr. This can be a sign of rarity of its prey in comparison with adjacent territories of Yakutia. The nearest record of *Panthera spelaea* is in north western Yakutia, close to the border with East Taimyr.

The most interesting finds of carnivorous mammals are those of ursids. Three bones of bears in our collection represent brown and polar bears, and one of them identified by us as a right fourth metatarsal of *Ursus maritimus* with GPS coordinates: 76°23′463″N, 102° 01′396″E (Leningradskaya River in the Far North of the Peninsula) has been radiocarbon dated (GrA 19290: 12,500±70 BP). Our colleague, G. Baryshnikov, from the Zoological Institute, Saint Petersburg ascribed this metatarsal to a huge brown bear, *Ursus arctos*. Because metapodials are not very distinct in both species, we are looking forward to recovering more materials on future expeditions to solve the problem of identification. In any case, the metatarsal belongs to *Ursus arctos*, and we are dealing with the most northern distribution of this species in Eurasia and probably in the Holarctic. An extremely large epistropheus, which was collected at Cape Sabler, was identified as *Ursus arctos*.

Wolverine, *Gulo gulo*, should be present in the fauna of Taimyr as other moderate and small sized carnivorous animals, but so far, records of Pleistocene wolverine of Taimyr are unknown.

Two species of marine mammals are reported (Vereshchagin, 1959a) from the Late Pleistocene of Taimyr: narwhal *Monodon monoceros* and beluga *Delphinapterus leucas*. Both species probably were distributed here in the interstadial periods. The radiocarbon date for narwhal tusk (approximately 15 cm in the base of the tusk was collected on the River Schrenk, 4 km upstream of the mouth of the River Mamonta, ZIN 24188) shows a Karginskyi interglacial time (29,760± 220, B-137967), whereas the Taimyr Lake at this time was connected with the Kara Sea. On the Severnaya Zemlya Islands (October Revolution Island), ten skeletons of narwhals were recently discovered *in situ* and larger parts of the skeletons are still in anatomical order (Fig. 15). Radiocarbon dates on tusks are beyond the limit of reliable radiocarbon dating.

The steppe bison, *Bison priscus*, lasted in the area of eastern Taimyr until the beginning of the Holocene. A keratin horn sheath was collected by us in the basin of Popigay River (East of the Khatanga River). This is the youngest radiocarbon date is 8,810±60 BP (B-148623)

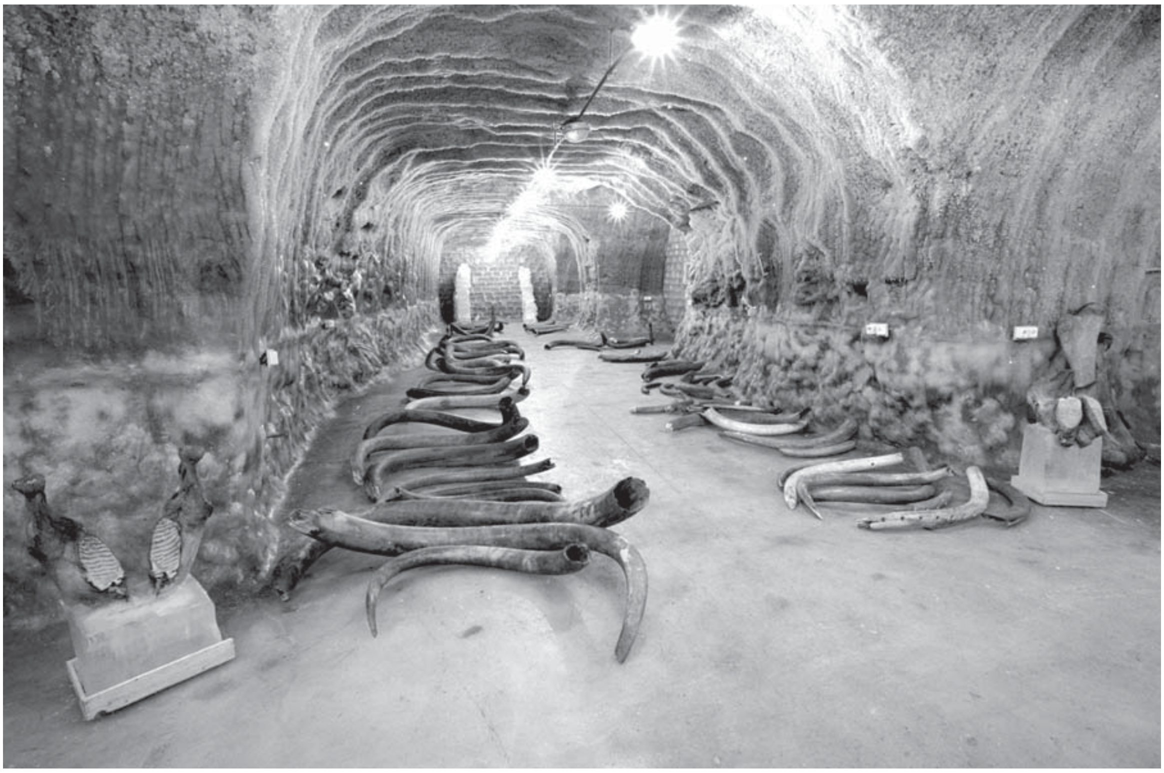

Figure 16. Mammoth remains collected byCERPOLEX/Mammuthus team in the ice cave in Khatanga (Underground Mammoth Museum). Photo: F. Latreille.

for *Bison priscus* in the far north. In general the remains of *Bison priscus* are rare on the Taimyr Peninsula.

Radiocarbon dates

MacPhee *et al.* (2002) presented 75 radiocarbon dates, including 46 dates for the woolly mammoth, based on the late Quaternary mammal remains recovered in the eastern Taimyr Peninsula and adjacent parts of the northern Siberian lowlands, which included*Mammuthus primigenius*, *Bison priscus*, *Ovibos moschatus*, *Alces alces*, *Rangifer tarandus*, *Equus caballus*, and *Canis lupus.*

Forty-nine AMS dates were taken on megafaunal remains collected by CERPOLEX/Mammuthus in 1999 and 2000. Of these, 30 are dates on mammoth remains; the rest are on musk-ox, bison, reindeer, canid and moose. The mammoth dates range from "infinite" ages in excess of 50,000 radiocarbon years before present (BP) to 10,270±40 BP. Sixteen of the dates are in excess of 30,000 BP, which is of interest because we selected for dating only those specimens that seemed in the best condition, which we assumed would mostly be very young. The youngest date is approximately 600 years older than the most recent mammoth date from the Taimyr Peninsula (9670±60 BP; GIN 1828), based on a tusk from the Nizhnyaya Taimyra River which flows out of Lake Taimyr 60 km north of Cape Sabler. The large number of well-preserved specimens of substantial age indicates how well organic remains are preserved at this latitude.

A new set of dates which were done recently on the materials collected at the end of XX century on Taimyr by D. Bolshiyanov makes a good addition to the representative massive of radiocarbon dates from this region (Tab. 5).

On integrating the new AMS dates on mammoth with previous catalogues of Russian dates for the Taimyr Peninsula (Kind & Leonov, 1982; Sulerzhitskii & Romanenko, 1997), an interesting pattern emerges. Dates are roughly evenly distributed except for three prominent gaps for which there are few or no dates: several thousands years prior to 35,000 (mid-Kargian interstadial), 18–14,000 (immediately after Last Glacial Maximum); and after 10,000 (beginning of Holocene). An unpaired t-test of the grouped data was significant, suggesting that the gaps are real. The last gap is easily explained — mammoths became extinct (except for the Wrangel population) just after 10,000 BP in Eurasia. But mammoth populations recovered after the other two gaps; they must represent periods when the Taimyr was not a favorable habitat for mammoths, or when taphonomic conditions were different. If mammoth populations were able to recover during interstadial conditions as well as after the coldest phase of the late Weichselian/upper Zyryansk (Sartan) stadial, it seems unlikely that climate change alone can explain their complete loss from the mainland around 10,000 BP (MacPhee *et al.,* 2002).

Owing to data accumulated in the last few years, including new paleontological finds, radiocarbon dates on mammoth remains, description of the structure of

Table 5. New radiocarbon dates, mainly from the banks of the Taimyr Lake.

Taxon/specimen	Locality	Date
Mammuthus primigenius, woolly mammoth, tusk (CM-DM 1)	Oskar Peninsula	GrA 19275: 28,370±200 BP
Mammuthus primigenius, woolly mammoth, tusk (CM-DM 2)	Oskar Peninsula	GrA 19271: 28,350±200 BP
Mammuthus primigenius, woolly mammoth, tusk (CM-DM 3)	Oskar Peninsula	GrA 19284: 34,680 (+350, –340) BP
Mammuthus primigenius, woolly mammoth, tusk, (CM-DM 9)	Baskura Peninsula	GrA 19523: 32,180 (+210, –200) BP
Mammuthus primigenius, woolly mammoth, radius/ulna, (CM-DM 10)	Baskura Peninsula	GrA 19310: 14,050±70 BP
Mammuthus primigenius, woolly mammoth, cranium, (CM-DM 13)	Delta of the Upper Taimyra River	GrA 19238: 24,460±200 BP
Mammuthus primigenius, woolly mammoth, vertebra thoracalis, (CM-DM 15)	Delta of the Upper Taimyra River	GrA 19311: 24,990±150 BP
Mammuthus primigenius, woolly mammoth, tusk, (CM-DM 16)	Delta of the Upper Taimyra River	GrA 19231: 10,230±60 BP
Mammuthus primigenius, woolly mammoth, tusk, (CM-DM 17)	Delta of the Upper Taimyra River	GrA 19526: 24,980±130 BP
Mammuthus primigenius, woolly mammoth, mandibula, (CM-DM 18)	Delta of the Upper Taimyra River	GrA 19273: 24,740±150 BP
Mammuthus primigenius, woolly mammoth, DP4, (CM-DM 20)	Between rivers Ayatari and Tareya	GrA 19279: 16,570±160 BP
Mammuthus primigenius, woolly mammoth, tusk, (CM-DM 21)	Toll's Bay	GrA 19528: 35,760 (+280,–270) BP
Mammuthus primigenius, woolly mammoth, vertebra thoracalis, (CM-DM 22)	Cape Sabler 2	GrA 19264: 13,919±70 BP
Rangifer tarandus, reindeer, femur, (CM-DM 24)	Cape Sabler 4	GrA 19241: 18,260±120 BP
Rangifer tarandus, reindeer, radius/ulna (CM-DM 19)	Delta of the Upper Taimyra River	GrA 19239: 175±45 BP GrA 19527: 95±40 BP
Rangifer tarandus, reindeer, radius/ulna (CM-DM 11)	Delta of the Upper Taimyra River	GrA 19880: 780±60 BP
Rangifer tarandus, reindeer, metatarsal (CM-DM 5)	Cape Sabler, Lake Taimyr	GrA 19522: 135.0±0.6 %
Ovibos moschatus, musk-ox, cranium (CM-DM 6)	Severnaya River	GrA 19285: 46,620±1310 BP
Ovibos moschatus, musk-ox, metacarpus (CM-DM 12)	Delta of the Upper Taimyra River	GrA 19236: 22,740±170 BP
Bison priscus, steppe bison, vertebra thoracalis, (CM-DM 14)	Delta of the Upper Taimyra River	GrA 19524: 41,200 (+440, –410) BP
Equus caballus, horse, vertebra cervicalis, (CM-DM 23)	Delta of the Upper Taimyra River	GrA 19274: 22,010±120 BP
Equus caballus, horse, femur (CM-DM 8)	Baskura Peninsula	GrA 19289: 27,950±190 BP
Equus caballus, horse, humerus (CM-DM 7)	Baskura Peninsula	GrA 19287: 26,640±170 BP
Equus caballus, horse, metacarpal (CM-DM 4)	Cape Sabler, Lake Taimyr	GrA 19235: 38,750 (+1050, –930) BP

Quaternary deposits and relief of the Taimyr Lake basin, it is possible to note an interesting relationship. The correlation between flow fluctuation of the lake and presence of mammoths on its banks is striking. Favorable conditions for mammoths arose in the following time intervals: 10–14; 16–18; 20–21; and 20–25 thousands years ago. These were times of low water level in the lake. The majority of dated mammoth bones are known from the last interval. Until now there have been no dates between 14–16; 18–20; and 25–27 thousands years ago from this region. Those were times of high water levels. The water level of the lake fluctuated greatly at the end of the Late Pleistocene. The highest points during the Karginskyi transgression exceed the recent one by 30–40 m. At that time the vast territories of Taimyr lowland were flooded. Rivers became estuaries, and Pyasina River and Taimyra River as two estuaries were united in one basin. At the same time some species of fresh water organisms from Baikal Lake penetrated to the Pyasina River and Taimyr Lake.

During the Sartan glaciation (the last of the Late Pleistocene) some areas on Taimyr Peninsula were covered by glaciers. But the glaciers did not form a glacial shield because they were made up of vast fields of "dead" ice and small glacial domes which were formed on uplands that rose more than 100 m. The glaciers formed and disappeared very quickly so in between them the fauna may have survived. In the earliest stages of the Late Pleistocene, the Taimyr Peninsula was a region of marine sedimentation and as a result of this, the glacial shields were absent at that time.

Traces of glaciation synchronous with marine transgression were found only on the Byrranga Mountains. Mammoths did not live on the banks of Taimyr Lake before 40–50,000 years ago. Evidently the distribution of mammoths was limited by at least two factors: rises in water level in the sea and lakes, and expansion of glaciers.

Late Pleistocene vegetation and climate in Taimyr lowland and the interaction between vegetation and megafauna

Several continuous sedimentary records from lakes were studied in order to reconstruct the vegetation and climate of Late Pleistocene (Middle and Late Weichselian) and Holocene lowland Taimyr (Hahne & Melles, 1997, 1999; Niessen *et al.*, 1999; Siegert *et al.*, 1999; Kienast *et al.*, 2001; Andreev *et al.*, 2002, 2003). Those studies are of considerable value for understanding the environment of the Late Pleistocene fauna and the interrelation between fauna and vegetation (Guthrie, 2001). The pollen diagrams from lake sediments show that most of Taimyr was unglaciated since Middle Weichselian time. Based on geological data Möller *et al*. (1999) and Niessen *et al*. (1999) found no evidence for extended glaciation during the last glacial maximum. Only the northern and northwestern coastal lowlands were covered with a thin ice cap (Alexanderson *et al*., 2002). Dryness prevented the formation of large ice sheets (Svendsen *et al*., 1999). The vegetation during the Weichselian was dominated by taxa indicating dry, cold steppe conditions (mainly grasses and *Artemisia*). Tundra plants were of minor importance and mainly occurred at humid sites. During two less cold, more humid Middle Weichselian interstadials, there was a temporary increase of Larch, Birch and Alder, but the pollen records during those phases still reflect a rather open landscape. After the transition from the Late Weichselian to the warmer and more humid Holocene, as indicated in Ice cores (GISP II) a remarkable and dramatic change took place. The herbaceous steppe vegetation declined and shrub and tree Birches and Alder expanded, together with tundra species.

For understanding the population density and final collapse of the Late Pleistocene megafauna of Taimyr, insight into the interaction between climate, vegetation and herbivores is essential (Guthrie, 1990, 2001). The climate-induced transition from dry tundra-steppe to moist tundra at the start of the Holocene had strong effects on the life conditions of the large herbivores. Snow cover during winter was thin or even absent during the dry climate of the Late Weichselian, and thus food remained available for grazing animals. Thick snow covers were problematic for the herbivores after the transition to the Holocene. The change in humidity played another important role: the dryness of the Weichselian period had positive effects on the length of the growing season, while, after the transition to the Holocene, plant growth could only start during late spring, after the thick snow cover had melted. Intensive grazing during the Weichselian had strong effects on the vegetation, because of the accelerated nutrient cycling (recorded fungal spores point to high production of dung). In addition, grazing stimulates grass species (Poaceae) because they have their growing points just near their roots. Many tundra plants have their growing points at the end of their stems, for which reason those species are easily damaged by grazing. The moisture-demanding and less palatable tundra plants could expand only after the early Holocene decline of the herbivore population density. Wet conditions and low grazing pressure caused the development of thick (insulating) layers of plant remains on top of the soils, which hampered early and deep thawing of the soils and thus also resulted in nutrient-poor conditions. Climate change probably was not the only factor causing the crash of the megafaunal populations. The effects of increased precipitation — as is evident from the pollen records from Taimyr — will have been an important factor in the megafaunal collapse at the Pleistocene / Holocene boundary. The climate change at the start of the Holocene was a major factor in the observed vegetation change, but the climate effect was amplified as a consequence of the reduced population density of large herbivores.

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