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Results of the CERPOLEX/Mammuthus Expeditions on the Taimyr Peninsula, Arctic Siberia, Russian Federation

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Abstract

During a series of expeditions organized by CERPOLEX/Mammuthus to the Taimyr region in northern Siberia several mammoth (*Mammuthus primigenius*) carcasses were discovered and subsequently excavated and studied. The oldest specimen is the Arilakh Mammoth (ca. 55,800 BP). Much younger are the Jarkov Mammoth (ca. 20,380 BP) and the Fishhook Mammoth (ca. 20,620 BP), and still much younger are well-preserved Holocene mammoth remains (< 10,000 BP). Some paleobotanical data and descriptions of accompanying fauna provide insight into the ecology of the region during Late Pleistocene times. The faunal collapse at the end of the Pleistocene seems to be the result of increasing temperatures, greater humidity, increased snow cover, formation of insulating plant layers, later thawing of the soil, and a lower herbivore density amplifying the climatic effects.

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1. Introduction

At the second International Mammoth Conference held in May 1999 in Rotterdam (The Netherlands) Buigues and Mol (1999) announced the discovery of the Jarkov Mammoth in the permafrost of the Taimyr

Peninsula, Arctic Siberia. This male individual of the woolly mammoth, *Mammuthus primigenius*, died at an age of 47–49 AEY, on the Taimyr Peninsula, ca. 20,380 BP. In September/October 1999, introducing a new technique, the CERPOLEX/Mammuthus team excavated a huge block of frozen sediment that likely included the remains of the mammoth. On October 17th, this 23-ton block of permafrost was successfully airlifted by an MI 26 helicopter. It was placed in an ice cave system in Khatanga, ca. 250 km south of the locality (Bolshaya Balakhnya River) where the Jarkov Mammoth had been discovered in 1997. The goal of the team is to defrost the frozen block in the safety of the ice cave at a constant temperature of –11 to –15 °C, in order to collect as many data as possible from the

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sediment surrounding the remains. This event in 1999 was the start of the CERPOLEX/Mammuthus programme “Who or What Killed the Mammoths” to contribute to the unsolved questions on the extinctions of the Pleistocene megafauna around 10,000 BP.

2. The Pleistocene fauna of the Taimyr Peninsula

The Taimyr Peninsula in the far north of Siberia is one of the most interesting places where the rich Pleistocene Mammoth Fauna can be found. This fauna is well-known from many sites in the Northern Hemisphere (Europe, Asia and North America). It is generally known that the frozen ground is preserving remains of animals such as woolly mammoth, woolly rhinoceros, steppe bison, reindeer, etc., in excellent condition. Sometimes, soft parts such as skin, fur and underfur, or internal organs are preserved, providing paleontologists with a lot of information on the exterior of these animals that lived on the so-called Mammoth Steppe between 110,000 and 10,000 BP. Good examples are the almost complete mammoth carcasses, amongst others the famous mammoth baby “Dima” and the “Berezovka Mammoth”, both now preserved in the Zoological Museum of Saint-Petersburg. Thousands of studies have been published on the Mammoth Fauna and the Mammoth Steppe by experts from all over the world.

The Mammoth Fauna of Taimyr is of great interest for understanding why most of these impressive animals became extinct around 10,000 BP. At the time, a dramatic climatic change took place and the paleogeography of the world changed accordingly, e.g. Eurasia and North America became separated by the Bering Strait and the Bering Sea. The composition of the Mammoth Fauna in Siberia, Alaska and Europe consists of horses, steppe bison, reindeer, mammoth and other species including the musk-ox. Musk-ox became extinct in Eurasia around 8000 BP, except on the Taimyr Peninsula and in some northern parts of Yakutia, where musk-ox continued living up till around 3000 BP. However, it survived in North America and it became a relict species of the Ice Age, adapted to the extreme cold of the tundra. It is still unknown why the species became extinct.

The first information about the mammoth fauna of the Taimyr Peninsula was received in 1843 when Alexander Theodor von Middendorff (1815–1894) traversed more than 2000 km in this remote area. His expedition found a mammoth skeleton on the River Nizhnaya Taimyra (Middendorff, 1860). It was the first documented find of mammoth remains on Taimyr. Another incomplete mammoth skeleton with some associated soft tissue was found in 1908 on the River Mokhovaya in south-western Taimyr. This was exca-

vated by an expedition of the Russian Academy of Sciences in 1913 (Garutt, 1964). During Soviet time, many paleontological and geological expeditions worked in Taimyr. In 1948, a complete mammoth skeleton was recovered at a tributary of the River Schrenk (Garutt and Dubinin, 1951). This tributary was later named Mamontovaya (Garutt, 1964). The mammoth find in question was not only selected to be the neotype of *Mammuthus primigenius* (Garutt et al., 1990), but also gave birth to a special scientific committee, the Mammoth Committee of the Russian Academy of Sciences. In the late 1970s it was headed by Nikolai Vereshchagin, who organized an expedition in 1977–1978 to excavate a mammoth carcass on the small river of Bolshaya Lesnaya Rassokha, eastern Taimyr (Vereshchagin and Tikhonov, 1990). After this find no representative parts of mammoth carcasses were found in this vast region until 1997.

3. New discoveries of mammoths

3.1. The Jarkov Mammoth

In 1997 the Jarkov Mammoth was discovered by the Jarkov family. It was excavated by CERPOLEX/Mammuthus in 1998 and 1999 (Mol et al., 2001a, b). Since that publication, new investigations took place, including defrosting of the block in the ice cave. We present the following results:

3.1.1. The geology of the block and its environmental interpretation

The block containing the Jarkov Mammoth (Fig. 1) was geologically mapped and studied using field methods (Fig. 2a and b). It contains four sedimentary units (numbered 1–4 below), reflecting different genetic processes and geological origin.

- (1) The lowermost horizon (up to 140 cm thick) is a grayish brown silty clay. At a level below the actual block, it contained fossil plant remains that have been radiocarbon dated to ca. 27,000 BP, corresponding to the final phase of the late Karginisk interstadial (ca. 35,000–25,000 BP). In the eastern section of the block, a gravel interfingers with the clay. This lowermost sedimentary unit is of fluvio-limnic character. The plant remains indicate a relatively warm period. During the Karginisk period, at least the Taimyr lowlands were free of ice. Lake water levels at that time exceeded present ones by up to 30–40 m and vast areas of the Taimyr peninsula were flooded and modern rivers were estuaries (Bolshiyarov and Tikhonov, 2003). The climate was unstable, but generally continentally influenced. Whilst the summer temperatures were comparable to

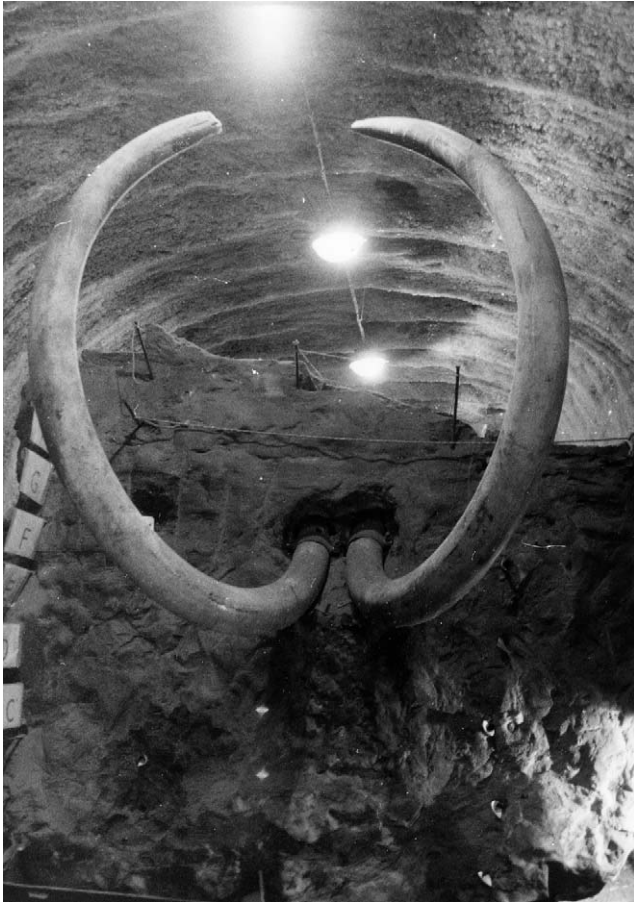


Fig. 1. Sediment block containing remains of the Jarkov Mammoth, stored in an ice cave system in Khatanga (Taimyr), southern section with the artificially fixed tusks of the animal. (Photograph: R.-D. Kahlke, August 2001).

those of the Holocene, the winter temperatures were significantly lower (Melles et al., 2003).

- (2) The next youngest horizon in the block (up to 35 cm thick) is a pale-brown clayey silt, which occasionally exhibits horizontal bedding. The layer is an aeolian sediment, indicating dry and cold climatic conditions of early Sartanian age (ca. 25,000–> 20,500 BP). The vicinity of the site was not glaciated, but exposed to winds during accumulation of this sediment. Chronologically, this horizon corresponds to a period of significantly lower water-levels in Lake Taimyr, contemporaneous with a drop in sea level between 25,000 and 20,000 BP (Bolshiyarov and Tikhonov, 2003).
- (3) The third horizon (up to 25 cm thick), also of early Sartanian age, is a clearly laminated silty fine sand (Fig. 3). Cross-bedding is visible in the western section of the block. The sediment was transported and deposited by shallow water of moderate current-strength. This unit seems to have been produced by reworking of windblown sediment originating from the horizon immediately below. It indicates a

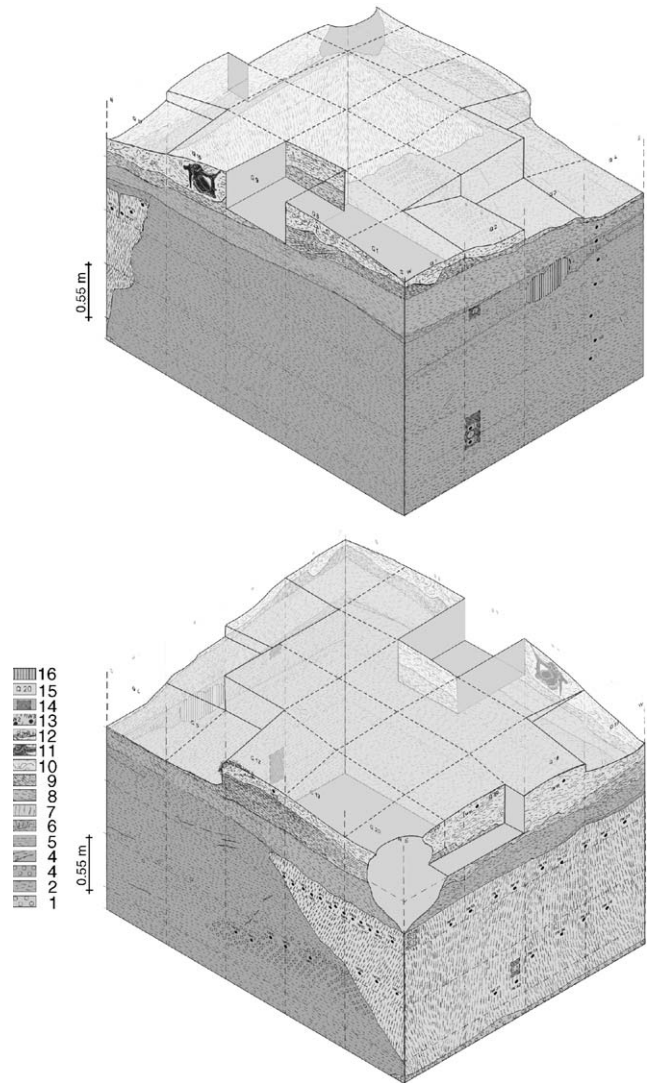


Fig. 2. (a) (top) and (b) (below) Three-dimensional diagrams of the sediment block containing remains of the Jarkov Mammoth (stored in Khatanga/Taimyr) from SW (above) and NE (below), mapped in August 2001. *Explanation:* 1—gravel; 2—grayish brown silty clay = unit (1); 3—gravel interfingering unit (1); 4—ice lenses; 5—layer of segregation ice; 6—discordant ice segregation; 7—ice body; 8—pale-brown clayey silt = unit (2); 9—laminated silty fine sand = unit (3); 10—dark-to pale-brown silty clay with solifluction texture = unit (4), deepest part of the fossil bed of the Jarkov Mammoth; 11—vertebrate skeletal elements (Jarkov Mammoth); 12—exposed mammoth hair; 13—position of samples taken for H₂O analyses (boreholes); 14—position of samples taken for H₂O analyses (peels); 15—excavation square numbers (defrosting); 16—position of the artificially fixed tusks of the Jarkov Mammoth (mapping: R.-D. Kahlke).

depositional setting involving flowing water and most likely was deposited during spring or summer. Units (1)–(3) predate the Jarkov Mammoth and have not produced remains of larger vertebrates.

- (4) The uppermost horizon, containing the dated remains of the Jarkov Mammoth (see below), has

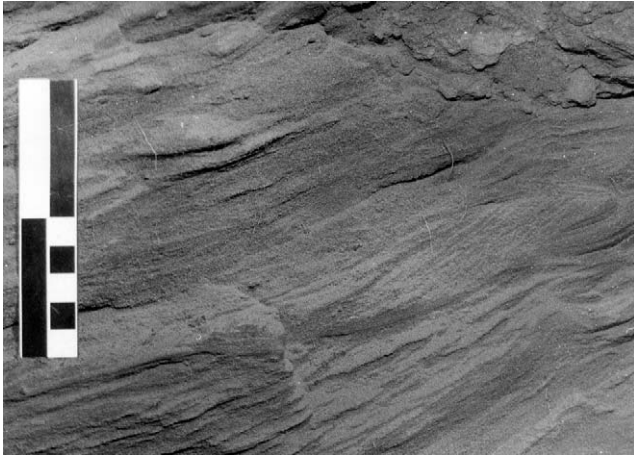


Fig. 3. Jarkov Mammoth block, laminated silty fine sand of sedimentary unit (3) (early Sartanian) directly below the fossil bearing unit (4). Scale: 10 cm. (Photograph: R.-D. Kahlke, August 2001).

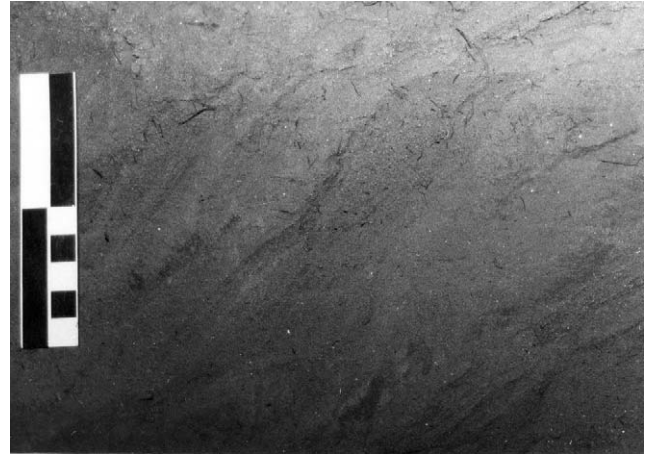


Fig. 4. Jarkov Mammoth block, dark to pale-brown silty clay of the fossil bearing sedimentary unit (4) with solifluction texture. Scale: 10 cm. (Photograph: R.-D. Kahlke, August 2001).

a total thickness up to 160 cm, although only the lowermost part (maximum 40 cm thick) is represented in the block itself, as the overlying part had been removed during the initial excavation. It is formed by a dark to pale-brown silty clay with a texture suggesting solifluction (Fig. 4). In the north-western section of the block, the uppermost part of the laminated sand (3) was also affected by this solifluction. After death and subsequent burial of the mammoth, solifluction processes disarticulated the cadaver and spread the remaining fragments over an area larger than the surface of the block. Intruded plant remains indicate a major solifluction event at about 2000 BP. Climatic interpretations of insect remains sampled from the mammoth bearing horizon (4) could be related to this period.

In the northern section of the block, ice is exposed (up to 120 cm thick) (Fig. 5). The ice is contemporary with, or younger than, the lowermost sediment layer (1). The Jarkov Mammoth cadaver was buried at least 300 km from the North Taimyr ice marginal zone (NTZ sensu Alexanderson et al., 2001, 2002), which was formed by the youngest advance of a relatively thin ice sheet that originated from the shelf of the Kara Sea inundating the area of current Taimyr Peninsula from the north/northwest during the last global glacial maximum (LGM).

3.1.2. Remains of the Jarkov Mammoth

The following remains (followed by the CERPOLEX/Mammuthus catalogue number) of the Jarkov Mammoth have been excavated: left tusk (2001/341), right tusk (2001/342), maxilla with M3 sin. et dext. (2001/339), mandibula (2001/340) (Fig. 6), vertebra thoracalis (2001/323), costae (2001/324 to 2001/337), radius dext. (2001/321 + 2001/338), ulna dext. (2001/322). The block

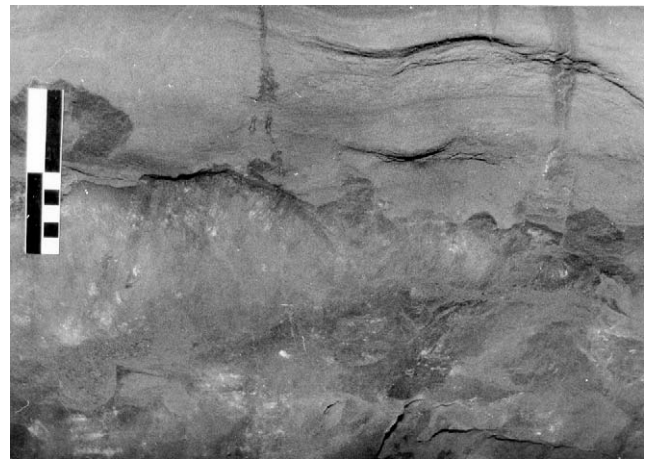


Fig. 5. Jarkov Mammoth block, ice body in the northern section of the block, discordant covered by sedimentary unit (2). Scale: 10 cm. (Photograph: R.-D. Kahlke, August 2001).

contains many unnumbered skeletal parts and soft tissue. The block is numbered 2001/XXXXA. These remains are stored in the ice cave in Khatanga. Samples of both bones and hair/wool (Fig. 7) have been taken for DNA research by Ross MacPhee (American Museum of Natural History, New York) and by Regis Debruyne (Muséum National d'Histoire Naturelle, Paris). Several samples of the tusks were drilled out by Daniel Fisher (Ann Arbor, Michigan) for analysis. Results will become available in the near future. About 15% of the upper layer of the block has been defrosted so far. The sediments from the block are stored in frozen condition in the ice cave.

3.1.3. Paleoecological results

Microfossils (pollen, algae, fungal spores) were studied in sediment samples taken from between



Fig. 6. Top: Mandibula with m3 sin and dext of a small old (female) woolly mammoth, *Mammuthus primigenius* (coll. Natuurmuseum Rotterdam, s.n.), collected on the Taimyr Peninsula. The jaw was dated by means of ^{14}C at Groningen University and proved to be 9920 ± 60 BP (Laboratory # GrA-17350). Below: The mandibula of the Jarkov Mammoth, *Mammuthus primigenius*, (2001/340) with m3 sin and dext. (Photograph: CERPOLEX/Mammuthus, Francis Latreille).

the hairs of the Jarkov Mammoth. The analysis of microfossils was combined with the identification of fruits, seeds and vegetative plant remains. The pollen spectra are dominated by Poaceae, *Artemisia* and *Papaver*. Also macrofossils of these taxa were present. Mosses such as *Racomitrium lanuginosum*, *Pogonatum* cf. *Pogonatum urnigerum* and cf. *Polytrichum piliferum* indicate dry, sandy or stony environments, with cryogenic phenomena as well as disturbance as a consequence of trampling or grazing. The vegetation reconstruction based on the recorded microfossils and macroremains indicates a steppe (cool and dry climatic conditions), and this fits well with the reconstructions based on palynological studies of lake sediments in Taimyr (Hahne and Melles, 1999; Andreev et al., 2002).

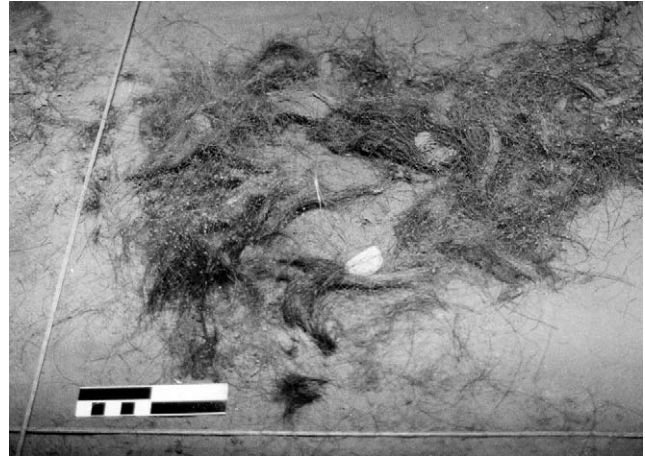


Fig. 7. Jarkov Mammoth block, sedimentary unit (4) surface exposure, excavation square 11 with mammoth hair recovered by defrosting, scale: 10 cm. (Photograph: R.-D. Kahlke, August 2001).

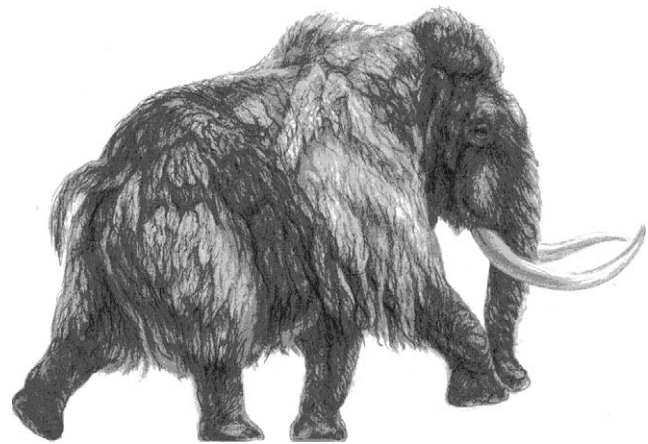


Fig. 8. Reconstruction of the Fishhook Mammoth, *Mammuthus primigenius*. (drawing by A.J.M. Kennis, 1999).

But some mosses (*Calliergon giganteum*, *Drepanocladus aduncus*, *Rhizomnium pseudopunctatum*) and the alga *Pediastrum* indicate that some wet sites also were present in the predominantly dry landscape of Taimyr. The abundance of ascospores of the dung-inhabiting fungi *Sporormiella* (Davis, 1987) and *Sordaria* type (Van Geel, 2001; Van Geel et al., 2003) is a clear indication of a high population density of herbivores.

3.2. Fishhook Mammoth

The Fishhook Mammoth (Fig. 8) is a $20,620 \pm 70$ BP old woolly mammoth carcass (Mol et al., 2001b; MacPhee et al., 2002). It was discovered in the estuary of the Upper Taimyra River, in 1990 and some parts of the carcass were removed in 1990 and 1992. After the site had been flooded for 8 yr, it was rediscovered in 2000. In May 2001 the remains were excavated under

extreme cold conditions as a part of the CERPOLEX/Mammothus program “Who or What Killed the Mammoths”. Ground-penetrating radar (GPR) technique was firstly used to accurately locate the bones and tissue of the carcass. The remaining parts of the carcass (Fig. 9), including soft tissue (Fig. 10), fur and underfur were extracted from the frozen ground together with the surrounding sediments to learn more about the environment and the time of death of the Fishhook Mammoth. One block of approximately 1100 kg with a hind part of the Fishhook Mammoth was taken to the ice cave in Khatanga where it is stored under controlled conditions. The expedition and the first results on the investigations on the Fishhook Mammoth were published by Mol et al. (2001b). The block was cleaned in the summer

of 2000. Part of the skeleton is still in anatomical position (Fig. 11), among others, 6 vertebrae thoracalis, 2 vertebrae lumbalis, and 16 ribs are exposed. It became clear that a lot of soft tissue is preserved in this block of frozen sediment, including remains of the stomach (Fig. 12) and remains of the intestinal tract and its contents of digested food remains (Fig. 13).

The second aspect of GPR application consisted of 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 perspectives for



Fig. 9. Fishhook Mammoth excavation in May 2000. Remains exposed during the excavation. (Photograph: CERPOLEX/Mammothus, Dick Mol, May 2000).



Fig. 10. Fishhook Mammoth, *Mammothus primigenius*, some of the bones have soft tissue attached. (Photograph: CERPOLEX/Mammothus, Francis Latreille).



Fig. 11. Fishhook Mammoth block, stored in an ice cave system in Khatanga (Taimyr), last two thoracic and first lumbar vertebrae together with hair of the animal. Scale: 25 cm. (Photograph: CERPOLEX/Mammuthus, Philippe Cabaret).



Fig. 12. Fishhook Mammoth block, thick layers of remains of the gut content. (Photograph: CERPOLEX/Mammuthus, Philippe Cabaret).

using GPR in expeditions in the far north of Arctic Siberia. Grandjean et al. (2003) 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 gut content may be strongly biased by the food preference of the mammoth and therefore cannot be considered as indicative of 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* (0.2%), Asteraceae liguliflorae (+), 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



Fig. 13. Fishhook Mammoth block, remains of the intestinal tract and its contents. It is interesting that some internal organs can be seen, such as some oval-shaped intestine filled with digested food remains, greatest diameter 6.5 cm. Scale: 15 cm. (Photograph: CERPOLEX/Mammuthus, Philippe Cabaret).

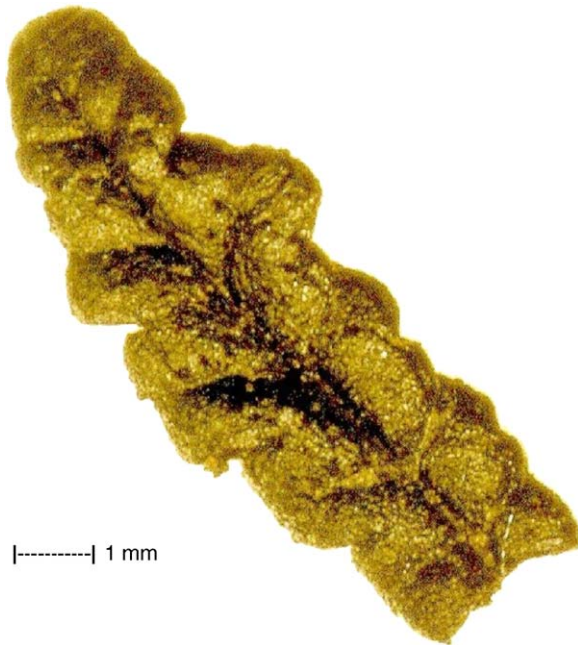


Fig. 14. *Dryas* leaf fragment from the gut sample of the Fishhook Mammoth. (Photograph: Jan Peter Pals, University of Amsterdam).

Mammoth consisted of a mass of unidentifiable grassy material. Among the identifiable remains were leaves of *Dryas octopetala* (dryad) (Fig. 14), *Salix* sp. (willow), *Betula nana* (dwarf birch), *Vaccinium* species, a catkin of *Alnus fruticosa* (alder), and needles of *Larix* (larch) (Fig. 15). The sample also contained a large number of

mosses, as well as some inflorescences of *Polygonum viviparum* (Fig. 16) and seeds/fruits of about 15 taxa of other herbs, amongst others *Pedicularis sceptrum-carolinum* (Fig. 17). Among these are at least four species of grasses (Fig. 18), two Cyperaceae (sedges), two Juncaceae (rushes) and *Papaver radicum* (arctic poppy). Furthermore, excrements of lemmings were found as well as several remains of Coleoptera (beetles).

The conclusion from the paleoecological analysis may be summarized as follows: the Fishhook Mammoth had been grazing a moist, open vegetation dominated by grasses, with a lot of mosses in the ground cover. However, the presence of vegetation types of dry ground, as well as border scrub of forest tundra is also reflected by the plant remains. The find of *Larix* (Fig. 15) is especially interesting, because the site where the Fishhook Mammoth was found is situated at about 200 km north of the present timber line.

3.3. 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 were found, together with the mandibula and some other parts of the skeleton. Other remains are still hidden in the permafrost at the locality near Cape Sablera. The tusks are spirally twisted and one of them is missing a small portion of the tip. The length



Fig. 15. *Larix*, needle tip from the gut sample of the Fishhook Mammoth. (Photograph: Jan Peter Pals, University of Amsterdam).



Fig. 16. *Polygonum viviparum* from the gut sample of the Fishhook Mammoth. (Photograph: Jan Peter Pals, University of Amsterdam).

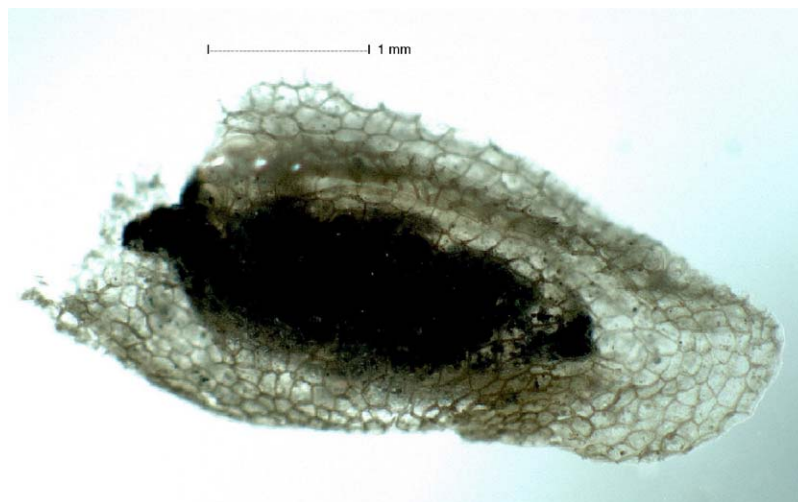


Fig. 17. *Pedicularis sceptrum-carolinum* from the gut sample of the Fishhook Mammoth. (Photograph: Jan Peter Pals, University of Amsterdam).

measurements are: ca. 283 cm for the right one and ca. 253 cm for the left. The diameter for both tusks at the beginning of the pulpa cavity is 10 and 11 cm. The pulpa cavity is not deep, and the length, diameter and curvation of the tusks point to an old male individual. The preservation of the ivory is excellent. The mandibula with the molars m3 sin. et dext., indicate that the animal died at an age of 40–42 AEY. The state of preservation of the mandibula and its molars is

excellent. An expedition to the site is planned for the near future to take out the other remains of the Nikolai Mammoth.

3.4. Holocene Mammoths

Holocene woolly mammoths have been reported from the Taimyr Peninsula by [Sulerzhitsky and Romanenko \(1997\)](#). The youngest specimen dates 9670 ± 60 BP

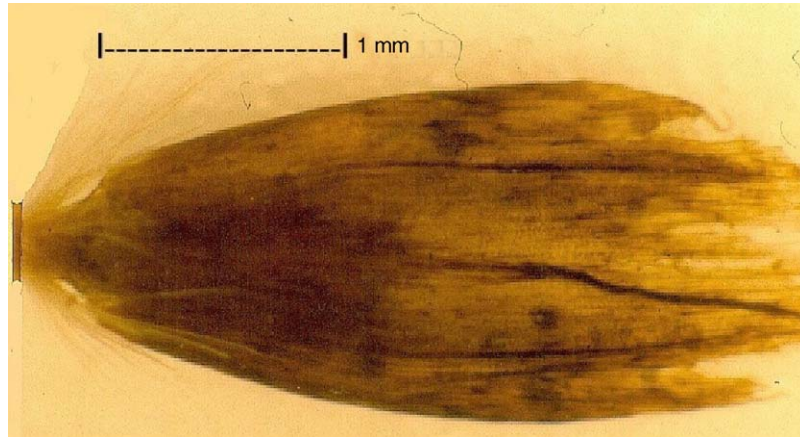


Fig. 18. *Calamagrostis* sp. from the gut sample of the Fishhook Mammoth. (Photograph: Jan Peter Pals, University of Amsterdam).

(GIN-1828). The youngest bone of a woolly mammoth, collected by us on the Taimyr Peninsula, is a lower jaw that is now being kept in the Natuurmuseum Rotterdam. This jaw (Fig. 6) 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 9920 ± 60 BP (Laboratory # GrA-17350/DM5, 13δ : -22.80%). This result shows that the woolly mammoth occurred on Taimyr until the beginning of the Holocene. A short description of the specimen and comparison with other small mammoth remains was published by Reumer and Mol (2001).

4. Taimyr megafauna investigations

Vereshchagin (1959) published a paper on the Late Pleistocene megafauna of the Taimyr Peninsula. He listed the following species and the percentages of recovered skeletal remains for these species: polar fox *Vulpes lagopus* (14.3%), hare *Lepus timidus* (3.9%), mammoth *Elephas primigenius* (11.7%), horse *Equus caballus* (27.2%), bison *Bison priscus priscus* (1.3%), *Bison priscus* subsp. indet. (3.9%), musk-ox *Ovibos moschatus* (14.3%), reindeer *Rangifer tarandus* (20.8%), narwhal *Monodon monoceros* (1.3%), beluga *Delphinapterus leucas* (1.3%).

In the 2000, 2001 and 2002 field campaigns by the team of CERPOLEX/Mammuthus collected thousands of fossil bones at several localities on the Taimyr Peninsula. A total of 623 items have so far been described in our catalogue (as by August 2002; several numbers bear sub-numbers); mammoth *Mammuthus primigenius* (395 specimens = 63.41%), musk-ox *Ovibos moschatus* (103 specimens = 16.54%), horse *Equus* cf. *caballus* (57 specimens = 9.15%), reindeer *Rangifer tarandus* (34 specimens = 5.45%), bison *Bison priscus* (26 specimens = 4.17%), moose *Alces alces* (5 specimens = 0.8%) and wolf *Canis lupus* (3 specimens = 0.48%).

Several remains of small mammals (including hare *Lepus timidus*) and of birds have been collected but have not yet been identified.

4.1. New results

- (1) New for the Late Pleistocene *Mammuthus* Fauna 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).
- (2) The most abundant species in the list of Vereshchagin (1959) is the horse (*Equus caballus*), followed by reindeer (*Rangifer tarandus*), musk-ox (*Ovibos moschatus*) and the polar fox (*Alopex lagopus*) and then the woolly mammoth (*Mammuthus primigenius*).
- (3) 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*), horse (*Equus* cf. *caballus*), etc. (see above).
- (4) 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 (Fig. 19).
- (5) The woolly rhinoceros, *Coelodonta antiquitatis*, common in Eurasian faunas, together with the woolly mammoth, is unknown from the Late Pleistocene of the Taimyr Peninsula, as is the case for North America. A well-preserved cranium of the woolly rhinoceros, which is stored in the Historical and Natural History Museum of Dudinka (south-western 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



Fig. 19. Neuro-cranium with horn cores, atlas, epistropheus and third cervical vertebra of a partial skeleton of a musk-ox (*Ovibos moschatus*, # 2001/430 A–E, male) in situ (collection numbers), recovered 1.5 km SW of Cape Sablera at the bank of Lake Taimyr. Scale: 25 cm. (Photograph: R.-D. Kahlke, 9th August 2001).



Fig. 20. Set of hooves of a reindeer skeleton (*Rangifer tarandus*, # 2002/471) after excavation, recovered 3 km NE of Cape Sablera at the bank of Lake Taimyr. Scale: 10 cm. (Photograph: R.-D. Kahlke, 8th August 2001).

Coelodonta populations to Taimyr, as was suggested by Kahlke (1999) for the comparable record from north-eastern parts of Yakutia.

- (6) The steppe bison, *Bison priscus*, lasted in eastern Taimyr until the beginning of the Holocene. The youngest radiocarbon date is 8810 ± 60 BP (B-148623) for a well-preserved horn sheath.
- (7) MacPhee et al. (2002) presented 75 new 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*.

The collections of CERPOLEX/Mammuthus are stored in the ice cave in Khatanga, Taimyr Peninsula at -11 to -15°C . In our opinion this is the best place to keep these Late Pleistocene faunal remains in the best state of preservation for future research (radiocarbon dating, DNA research).

5. Other interesting finds

5.1. *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 Sablera ($74^\circ 31' \text{N}$, $100^\circ 30' \text{E}$), an almost complete *Rangifer tarandus* skeleton was discovered in silty sediments of

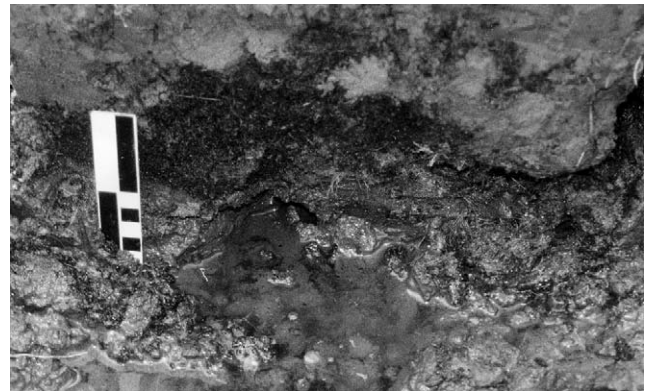


Fig. 21. Exposed part of the digestive tract of the reindeer (*Rangifer tarandus*, # 2002/471) filled with food remains (dark area right of the scale) during excavation, 3 km NE of Cape Sablera at the bank of Lake Taimyr. Scale: 10 cm. (Photograph: R.-D. Kahlke, 8th August 2001).

the defrosted lake bottom. The find (CERPOLEX/Mammuthus collection number: 2002/471) represents the first fossil reindeer skeleton known so far from Taimyr, and probably from Arctic Siberia in general. The stomach contents were radiocarbon dated at Groningen University to $13,040 \pm 80$ BP (AMS date GrA-19245). The anatomical arrangement of the skeletal elements indicates they have not been disturbed by either cryogenic or solifluction processes. 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 (Fig. 20), parts of the coat and the contents of the intestinal tract (Fig. 21). This specimen bridges the previously existing chronometric gap in radiocarbon dated *Rangifer* finds from Taimyr between 20,250 and 8700 BP and supports the theory that this species has

occurred at Taimyr, without interruption, since at least 36,000 BP (see MacPhee et al., 2002).

The pollen spectrum of a sample of plant remains in the stomach was dominated by grasses (Poaceae 54.3%) and *Artemisia* (30.9%), indicating an open steppe landscape. However, birch (*Betula*) pollen reached 7.4% and many small wood fragments of cf. *Betula* in the pollen slides indicate that shoots of birch were also used as a food source. Other taxa recorded in the pollen slides were Cyperaceae (5.9%), Ranunculaceae (0.4%), *Salix* (0.3%), *Alnus* (0.3%) and *Valeriana* (+). Remains of the algae *Pediastrum* and *Botryococcus* will have entered the stomach with drinking water. Spores of the fungus *Sporormiella* indicate the presence of dung in the area where *Rangifer* was grazing and may even reflect a relatively high population density of mammals (Davis, 1987).

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*, ehippia 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*, *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.

6. First insight into the ancient DNA of the woolly mammoth femur (2002/473 Arilakh) and other mammoths

6.1. Methodological background

Preservation of DNA in mammoth carcasses or isolated bones has been a source of many developments in sequencing of ancient DNA for the last 10 yr (Greenwood, 2001). Independent studies have revealed that, notwithstanding that specimen age plays an obvious role in DNA preservation, three categories of other factors have to be taken into account: (1) taphonomy and fossilization, (2) preservation conditions through time, and (3) recent conservation. In the first category we include environmental conditions of the deposit and quickness of burial. Nature of the deposit, erosion and climatic variations belong to the second category, while the third one includes the treatments and conditions of conservation following the “discovery” of the material. The conditions for fossilization are most of the time speculative because, with few exceptions (like the Jarkov or Fishhook

Mammoth carcasses), most of the mammoth discoveries are isolated bones exposed as a result of solifluction and/or erosion. Usually these conditions can be correlated to the completeness of the carcass, a nearly complete mammoth indicating a very fast burial into the frozen ground, away from scavengers and oxydation processes. As for the conditions of preservation since the late Pleistocene, we might consider that they have been similar for all specimens kept in permafrost with temperature varying between -15 and -30 °C. This means that “class (2)” criteria may be disregarded as a whole in a comparative approach of Siberian mammoth DNA conservation. Recent preservation (3) is a parameter to be evaluated for different mammoths or different tissues submitted to several treatments.

6.2. Material and methods

Here we focus on the quality (in terms of maximal size of amplifiable mitochondrial DNA; Debruyne et al., 2003) of the DNA of several mammoths. Experiments applied in the isolated femur of a young mammoth, the so-called Arilakh Mammoth, collected near Lake Arilakh (east of Lake Taimyr) as reference 2002/473 (Fig. 22), and in the flesh and radius bone (2001/482) of the Fishhook Mammoth (Fig. 23; all specimens collected by the CERPOLEX/Mammuthus program).

The Arilakh Mammoth, is dated ca. 50,000 BP (see below), as well as the complete carcass of the Lyakhov Mammoth preserved at the French National Museum of Natural History. Interestingly, a previous study has shown that no mtDNA fragment longer than 200 bps could be amplified from the Lyakhov Mammoth. Bone and bone marrow of specimen 2002/473 then have been collected in order to establish the range of mtDNA fragment that could be retrieved.

Samples taken from the bone and the marrow were put in ethanol 70% prior to sending to the laboratory, where they were kept at -20 °C until treatment. Our preliminary results show how posterior conservation of fossil material might play a decisive role in the recovery of exploitable DNA. DNA extractions were performed with a modified phenol/chloroform extraction protocol (Hassanin et al., 1998) for bones and marrow and with a CTAB protocol for soft tissues (Winnepenninckx et al., 1993). Sequenced fragments have been checked for authenticity through the program BLASTN (Altschul et al., 1997).

6.3. Results

First, our analyses have confirmed that bone as well as marrow contain DNA of high molecular weight through a modified phenol/chloroform extraction protocol (Hassanin et al., 1998), although concentration appears to be slightly greater in bone. Profiles of raw



Fig. 22. Cross-section of the isolated femur of a young mammoth, the so-called Arilakh Mammoth, collected near Lake Arilakh (East of Lake Taimyr), # 2002/473. Greatest diameter: 12.4 cm. (Photograph: CERPOLEX/Mammuthus, Francis Latreille).

DNA extracts are provided for several samples (Fig. 23). They show that the DNA content for the marrow of the Arilakh mammoth appears excellent relative to the DNA from Fishhook Mammoth (which is itself as good or better than the other specimens assayed). It also shows that within Fishhook Mammoth samples, extracts from bone yielded much better results than soft tissues, accordingly to the prevalent DNA pattern of preservation described in ancient material (Hofreiter et al., 2001).

The template DNA were submitted to PCR amplifications of different mitochondrial cytochrome *b* fragments ranging 100 bp up to 800 bp. Positive results have been observed for different fragment sizes up to 620 bp (that is to say, three-fold the maximum length obtained for the Lyakhov Mammoth bone, see Table 1). As expected, soft tissue samples did not provide well-preserved DNA. Fragments up to 240 bp could be authenticated for the Fishhook Mammoth tissues, while nothing comparable could be obtained for the skin of the Jarkov Mammoth. Nevertheless, the bones from the same specimens were amplified more successfully, providing fragments up to 620 and 240 bp, respectively (Table 1). The best amplification results were obtained for the marrow of specimen 2002/473 and for the bone of 2001/384, both providing positive PCR up to 620 bp. However, when we discovered that the DNA content of the core bone for Arilakh Mammoth could not produce results as good as its marrow, we suspected contamination.

When sequenced, the fragments amplified from the marrow resulted in artefacts or in best cases, in DNA fragments that could not be aligned with the cytochrome *b* of mammals. By comparing to available sequence databanks (genbank, EMBL), we examined the contamination of bacterial DNA. We support the view of contamination by a recent exogene source, due to the nature of material and of its preservation (this piece was discovered by a fisherman a few months prior to being put into the ice-cave), and also because the bacterial contaminant was not retrieved in extracts from the core bone.

These results provide a first insight in mtDNA preservation within the mammoth collection of CERPOLEX/Mammuthus and lead us to consider that the current conservation of samples in the ice-cave should be encouraged. This is important, considering that the repeated amplifications and sequencing of mammoth DNA fragments ranging 400–600 bp is quite unusual for available material, and may enable sequencing of phylogenetic meaningful markers relying on longer sequences. However, the time from sample collection to placement in the cave should be reduced to a minimum in order to limit rapid alteration of the material and contamination from extant sources of DNA.

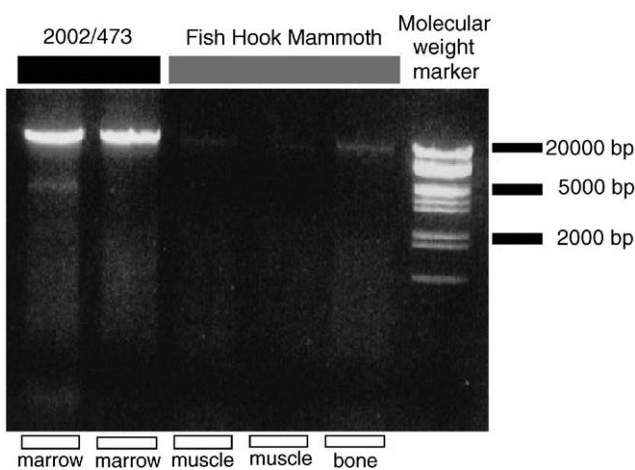


Fig. 23. Modified phenol/chloroform extraction protocol analyses have confirmed that bone as well as marrow contain DNA of high molecular weight (Hassanin et al., 1998), although concentration appears to be slightly greater in bone (Picture: Regis Debryne).

Table 1
Differential fragment size amplified through different specimens and tissues

Specimen label	Tissue	240 bp	320 bp	380 bp	460 bp	620 bp
Mammoth 2002/473	Femur marrow	—	C	—	C	C
Mammoth 2002/473	Femur core bone	X	X	X	—	—
Fishhook 2001/384	Radius bone	X	X	X	X	X
Fishhook	Muscle	X	X	—	—	—
Jarkov 2001/322	Lunatum bone	X	—	—	—	—
Jarkov	Hair	—	—	—	—	—
Lyakhov Mammoth	Sesamoid bone	—	—	—	—	—
Lyakhov mMammoth	Skin	—	—	—	—	—

Positive mammoth sequences are displayed by “X”. “C” depicts a positive results in PCR stage proven to be contamination by exogene (recent) DNA. “—” is shown for negative experiments. Results for the Lyakhov Mammoth are displayed for comparison.

Table 2

Lab no.	Method	Material	¹⁴ C activity (¹⁴ a%)	¹⁴ C age (T, BP)
GrA-21232	AMS	Marrow	0.010 ± 0.100	> 49,500
GrA-21293	AMS	Marrow	0.000 ± 0.080	> 51,700
GrN-27409	Conv.	Marrow	0.231 ± 0.086	48,800 ⁺³⁷⁰⁰ ₋₂₅₀₀
GrN-27520	Conv.	Collagen	0.121 ± 0.068	> 47,900

Concerning the possible exogene contamination we propose a plausible explanation relative to the differential preservation of these mammoths. As previously advocated, it is likely that the initial burial of the Lyakhov Mammoth proceeded under optimal conditions so that the limited results obtained for this specimen, in comparison to 2002/473, should result from the differences in conservation of this material. While the Lyakhov Mammoth was excavated between 1908 and 1910 and kept in ambient conditions since then, the femur 2002/473 was placed in frozen conditions just a few months after its discovery.

7. ¹⁴C content of the Arilakh Mammoth (2002/473)

A piece of bone from the Arilakh Mammoth (2002/473; Fig. 22) was submitted to the Groningen Radiocarbon laboratory. We performed 4 measurements of the ¹⁴C content. First, bone marrow was sampled. The sample material underwent standard chemical pretreatment (Mook and Streurman, 1983), and was combusted into CO₂. A few ml of this CO₂ was first transformed into graphite and analyzed by the AMS facility (Van der Plicht et al., 2000), to relatively quickly obtain an initial date. This AMS analysis was done in duplo. The large gas sample was also measured by the proportional counters in the conventional laboratory (Van der Plicht et al., 1992). The usual datable fraction for bone, however, is bone collagen. From a piece of about 10 g of bone, collagen was extracted following the method

developed by Longin (Mook and Streurman, 1983). The results of the ¹⁴C measurements are shown in Table 2.

The errors quoted are 1sigma (1σ). The Radiocarbon ages are reported in BP, the timescale defined for ¹⁴C. It turns out that the measurements are very close to the detection limit (ca. 50,000 yr) for the ¹⁴C method. Three measurements (both AMS marrow dates, and the collagen) show infinite age on the ¹⁴C timescale; one measurement (conventional marrow) shows a finite age. The problem is how to interpret these results: is the age of the mammoth around say 50,000 BP, or infinite on the ¹⁴C timescale (i.e. in theory any age above 50,000)?

In order to discuss this question, we first have to explain some ¹⁴C conventions. The Radiocarbon ages (T) are calculated from the so-called ¹⁴C activities (¹⁴a), which are the actually measured quantities. The ¹⁴C activity is the relative radioactivity, measured relative to the standard radioactivity, and ranges between 0 and 1 (or 0% and 100%; Mook and Van der Plicht, 1999). The standard activity corresponds to 100% (which in turn corresponds to 1950 AD or 0 BP); the background corresponds to no activity, or 0%. These activities are also shown in Table 2. The activities are the result of a measurement, and therefore have a measurement error. The errors shown in Table 2 are 1sigma (1σ) errors, which in statistical theory is a way of expressing that the chance that the true result is within the ±1σ range is 68%. One can also quote 2σ errors, which means that this chance is 95%.

The ¹⁴C ages T are calculated from the ¹⁴C activities ¹⁴a from the simple formula $T = -8033 \ln ^{14}a$, which is the inverse form of the exponential decay law of

radioactivity. The number 8033 is $T_{1/2}/\ln 2$, with $T_{1/2} = 5568$ yr (the conventional ^{14}C half-life). For ^{14}C ages which are not so old, the measured activity plus error $^{14}a \pm \sigma(^{14}a)$ easily translates into an age $T \pm \sigma(T)$. For old samples, however, the errors in T become asymmetric. This is, for example, the case for GrN-27409. For measurements close to the dating limit the error estimation becomes problematic. For example, the result for GrA-21232 is: $^{14}a = 0.01 \pm 0.10\%$ (see Table 2), so that the 1σ range includes negative activities. These do not exist, and correspond to ages which are infinite. For this reason, the following convention has been established, based on the sigma value $\sigma(^{14}a)$ of the ^{14}C activity ^{14}a (Olsson, 1989).

Also note that when $\sigma(^{14}a) < ^{14}a < 2\sigma(^{14}a)$, an age limit should be given despite the fact that $\sigma^+(T)$ and $\sigma^-(T)$ can be calculated. The reason is that for these cases $2\sigma(T)$ is infinite because $^{14}a - 2\sigma(^{14}a)$ is negative. The bottom part of Table 3 is the “normal” situation where activities are not negative, and is included here for completeness. Following these conventions, the ^{14}C ages in Table 1 have been calculated based on the activities and their errors.

This convention is explained in order to further interpret the results measured for the Arilakh Mammoth. Normally, i.e. for ages which are not too old, the ages can be averaged when we have multiple measurements. The average age is then determined with better precision. For the Radiocarbon ages given in Table 2, this is obviously impossible. For such cases, one has to average the measured activities ^{14}a . From this averaged value one can then calculate the averaged ^{14}C age, again taking into account the conventions from Table 3. The final results for the Arilakh Mammoth are shown in Table 4. After calculating the weighted average for the 4 measured results, the resulting error now becomes

significantly smaller. The averaged $^{14}a > 2\sigma(^{14}a)$, so that the (average) ^{14}C age is now very old but finite. The calculated ages are rounded off to the nearest 100.

We conclude that the ^{14}C age of the Arilakh Mammoth is $55,800_{-2900}^{+4500}$ BP. The errors quoted are 1σ . This means that the probability that the true age lies within the range 52,900–60,300 BP is 68%. For 2σ (or 95% probability), this range is 50,900–71,300. Thus, the chance that the true age is older than 71,300 BP is 2.5%; also the chance that the true age is younger than 50,900 BP is 2.5%.

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

Several continuous sedimentological 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 and Melles, 1997, 1999; Niessen et al., 1999; Siegert et al., 1999; Kienast et al., 2001; Andreev et al., 2002, 2003). These 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 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 an understanding of the high 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 steppe to moist tundra at the start of the Holocene had strong effects on the habitat conditions of the large herbivores. Snow cover during winter was thin or even absent

Table 3

When	... Then take for ^{14}a	... To calculate age T
$^{14}a < 0$	$^{14}a^* = 2\sigma(^{14}a)$	$T > -8033 \ln ^{14}a^*$
$^{14}a < \sigma(^{14}a)$	$^{14}a^* = ^{14}a + 2\sigma(^{14}a)$	$T > -8033 \ln ^{14}a^*$
$^{14}a < 2\sigma(^{14}a)$	$^{14}a^* = ^{14}a + 2\sigma(^{14}a)$	$T > -8033 \ln ^{14}a^*$
$^{14}a > 2\sigma(^{14}a)$	$^{14}a \pm \sigma(^{14}a)$	$T = -8033 \ln ^{14}a$ $\sigma^+(T) = -8033 \ln (^{14}a - \sigma(^{14}a))$ $\sigma^-(T) = -8033 \ln (^{14}a + \sigma(^{14}a))$
$^{14}a \gg 2\sigma(^{14}a)$	$^{14}a \pm \sigma(^{14}a)$	$T = -8033 \ln ^{14}a$ $\sigma^+(T) = \sigma^-(T) = \sigma(T)$

Table 4

	^{14}C activity (%)	^{14}C age (BP)
Averaged result	0.096 ± 0.041	$55,800_{-2900}^{+4500}$

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, and those species are easily damaged by grazing. The moist-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 agent causing the crash of the megafaunal populations, but the effects of increased temperatures and precipitation—as is evident from the pollen records from Taimyr—were an important factor in the megafaunal collapse at the Pleistocene/Holocene boundary. The climate change at the start of the Holocene contributed to 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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