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Mammoths and the mammoth fauna: introduction to the studies of an extinct ecosystem

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Mammoeten en de mammoetfauna: inleiding tot de studies over een verdwenen ecosysteem – Dit artikel is een inleiding tot de rest van de bijdragen in deze aflevering van DEINSEA, zijnde de verhandelingen van de Eerste Internationale Mammoet Conferentie, gehouden in Sint Petersburg, Rusland, van 16 tot 21 oktober 1995. In de loop van de afgelopen twee eeuwen is de mammoet veranderd van een halfmythisch beest tot een van de best bestudeerde vertegenwoordigers van de 'ijstijdfauna'. Hierdoor weten we meer over mammoeten dan over dinosauriërs en welk ander fossiel taxon dan ook. De hierna volgende bijdragen aan deze bundel presenteren de laatste nieuwe onderzoeksresultaten.

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Now that our planet is at the beginning of the next great climatic change, created by human actions over the past two hundred years, it is fitting that we make new efforts to understand the dramatic effects that such changes may have had on the earth's communities of plants and animals. Some of the most important environmental transformations came about over the last one hundred thousand years - the time of the appearance of anatomically and behaviorally modern humans, and their active dispersal out of the tropics and into the Northern Hemisphere.

We can begin our preparation for future climatic change by examining the glacial epoch, a lengthy interval of unstable climates and paleoenvironments. The last glacial period is one of unusually high mammalian

species diversity. The evidence about life from this glacial interval is often unique and striking. Large accumulations of fossil bones, many still containing fragments of soft tissue, occur within the permafrost in Siberia and Alaska, and are visible as they erode out of streambanks and channels. The number of species represented by these fossils suggests an abundance of living organisms in near-polar habitats during the glacial epoch, foremost among these being the woolly mammoth, *Mammuthus primigenius* (BLUMENBACH, 1799). Today we realize that this extinct beast was one of the northern hemisphere's most widespread inhabitants. The nature of its disappearance and the disappearance of dozens of other species holds valuable lessons for us. The cause of the extinction is

debated, and the conditions leading up to the extinction are only now beginning to come to light. Because of the unsolved questions about its life and final disappearance, it is the mammoth and its associated species whose study will be the most productive, providing us with useful information about the passing of life in the face of environmental changes and human impacts such as those that are now affecting the globe.

THE STUDY OF MAMMOTHS

Two hundred years have passed since mammoth bones were considered to be the remains of mythical giants, and in those two centuries our knowledge of this great creature has increased tremendously. J. Blumenbach and Georges Cuvier provided the mammoth with a scientific name and correctly classified it within the animal kingdom together with its living relatives, the modern elephants (Elephantidae). Scientific interest in the mammoth has never stopped growing since the eighteenth century. In the early 1800s, an adjunct of the Russian Academy of Sciences, M. F. Adams, recovered a complete mammoth skeleton from the delta of the Lena River and brought it to St. Petersburg where it was preserved, measured and mounted. This find still had soft tissue over many bones, including the skin of the face and skull. In the second half of the nineteenth century archaeological excavations explored occurrences of mammoth remains associated with the tools of ancient humans, and discoveries were made of mammoth paintings by Paleolithic artists in the caves of northern Spain and western France. These paintings allowed prehistorians to see the woolly giants through the eyes of long-dead human ancestors. In 1902 a nearly complete frozen carcass of a mammoth from the Beryozovka River in Siberia was delivered to St. Petersburg, where it was subjected to a comprehensive study not only of the bones and teeth, but also of the skin, hair, and internal organs. Plant remains found in the stomach showed for the first time the nature of the mammoth's diet.

Over the past 100 years, mammoths have turned from a half-mythical beast into one of the best studied representatives of the fauna from the glacial period. Evolutionary changes of its dentition through time, the eruption and replacement of molars, variations of tusk sizes and shapes, and skeletal differences based on sex and age have been traced. The skin, hair, muscle tissues, structure of the tongue, blood vessels and the heart, blood cells and proteins, and lipids from brain tissues were studied. The stomach contents of several specimens were analyzed. We know far more about mammoths than about dinosaurs, or any other fossil taxon from the deep past. Its ancestors, history and direction of dispersal have been reconstructed, and the boundaries of its ranges outlined. Taphonomic analyses have been performed on bone accumulations of mammoths, including those from Paleolithic sites where they were used for domestic and ritual purposes. In the last few years work has been conducted on extracting mammoth mitochondrial DNA from remains discovered in the permafrost of northern Asia. Scientific reconstructions of the appearance of the animal are possible, based on our full knowledge of mammoth anatomy and also on the study of ancient paintings and sculpture.

EXTINCTION

Many different hypotheses have been proposed for the cause of the extinction of the mammoths and the so-called mammoth fauna (the associated species of large and small mammals), ranging from the deluge and cosmic cataclysm theories to extermination by primitive hunters. Other fauna that coexisted with mammoths have also been studied in detail: as competitors for plant food resources (rhinoceros, bison, horse, saiga), and as enemies (cave lion, hyena, bear, wolves, wolverines) that could attack young or weakened animals and that would also consume the mammoth carcasses. At present it is clear that many species of the mammoth fauna were bound by intricate ecological relationships and that life for one species of the community, particularly in win-

tertime, may have depended on the life of other species. Mammoths undoubtedly had a decisive role in maintaining or shaping community structure and relationships. Modern elephants are sometimes considered to be gardeners or active habitat managers, opening up woodlands and increasing community diversity by their feeding habits, such as tree-felling and debarking, by their trampling, and by the sheer volume of plant parts eaten every day. They also dig out water holes in dry riverbeds, thus making the water available to other animal species during dry seasons. In these and other ways elephants affect the survival and well-being of other animals and plants, and it seems reasonable to expect that mammoths behaved in similar far-reaching ways. If elephants were to be removed from their natural communities, perhaps unexpectedly severe ecological adjustments would occur, leading to system-wide changes affecting all forms of plants and animals. The role of mammoths in extinct ecosystems may be better understood once we gain a fuller picture of the roles that modern elephants play in Africa and Asia.

THE FUTURE OF MAMMOTH STUDIES

The accumulation of information on mammoths and the conditions of their existence creates more and more new questions that touch upon different themes, such as the intraspecific systematics of *Mammuthus primigenius*, features of physiological and ecological adaptation to an extremely rigorous set of conditions in periglacial and arctic landscapes, genetic polymorphism of the species, clarification of its mode of life, details of its death, its fate after death, the nature of the interactions between mammoths and primitive man, and ultimately, the causes and time of the taxon's demise. The issue of the protection of the most important localities of fossil remains of mammoth fauna now has become topical. Of particular importance is the organization of expeditions to uncover new frozen carcasses, and the preservation of tissues in their frozen

state which may eventually lead to the future restoration of mammoths as a zoological species by means of hybridization of a living somatic cell with a mature unfertilized ovicell of the modern elephant. At present, this possibility appears to be a fanciful abstraction, but scientists continue to try. The necessity to discuss the collected data, and the development of new methods and directions of research about mammoths and the mammoth fauna were determining factors in organizing the First International Mammoth Conference.

THE PRE-EMINENCE OF RUSSIA IN THE STUDY OF MAMMOTHS

Fossil remains of mammoths have been found throughout the huge territory of Europe, Russia, China, and North America, but their greatest concentration can be found in the northern part of Eastern Siberia. The number of mammoth tusks discovered, for instance, in the Liakhov Islands is so large that they remain an object of commercial trade in that area. Remarkable collections containing mammoth teeth, bones, and soft tissues have been accumulating in museums of St. Petersburg and Moscow for many years. A Mammoth Museum was recently established in Yakutia, with many new specimens added to its collections annually. The richness of fossil collections that have accumulated in museums from all over Russia, as well as ample opportunities for field research in mammoth localities of different types, from tundra permafrost to steppe loess, have determined the tradition of the Russian paleozoological school. Efforts of scientists from different regions of Russia are coordinated by the Russian Mammoth Committee at the Russian Academy of Sciences which was established in 1948 by E. Pavlovski, a Member of the USSR Academy of Sciences. Six Russian Coordinating Meetings on the Study of Mammoths and the Mammoth Fauna have been held. It therefore seemed logical that the First International Mammoth Conference should be held in Russia.

THE FIRST INTERNATIONAL MAMMOTH CONFERENCE

The First International Mammoth Conference took place October 16-21, 1995, at the Zoological Institute of the Russian Academy of Sciences, in St. Petersburg. Collections of the Zoological Institute include extremely rare specimens such as the carcass and skeleton of an adult mammoth from the Beryozovka River (1902), two mummies of mammoth calves from the permafrost of the Kirgilyakh River in the Kolyma River basin (1977) and from Yuribeteyakha River in the Yamal Peninsula (1988), and two complete skeletons of mammoths from the Lena River (1806) and from Mammontovaya River in the Taimyr Peninsula (1948; adopted as the neotype for *Mammuthus primigenius*). The opportunity to see these unique specimens and also a worldwide interest in the study of mammoths and the mammoth fauna brought together in St. Petersburg 100 specialists from 12 countries, including four from the USA, two from the United Kingdom, one from the Netherlands, two from France, two from Germany, one from Finland, one from Austria, one from Poland, one from Ukraine, one from Georgia, four from Japan, and 80 from Russia (from the cities of St. Petersburg, Moscow, Ekaterinburg, Yakutsk, Novosibirsk, Rostov-on-Don, Stavropol, Kursk, and Samara). Forty-two reports and 18 posters were presented at the conference. Financial support for the First International Mammoth Conference was provided by the Russian Basic Research Foundation.

The gargantuan task of arranging and conducting the Symposium fell to the Organizing Committee who include: its President, Dr. Alexander Alimov (Russia), Vice President Dr. Nikolai Vereshchagin (Russia), Scientific Secretary Dr. Irina Kuzmina (Russia), Dr. Larry Agenbroad (USA), Dr. Gennady Baryshnikov (Russia), Dr. Gerhard Bosinski (Germany), Dr. Anatoly Derevianko (Russia), Dr. Igor Fokin (Russia), Dr. Ann Forsten (Finland), Dr. Vadim Garutt (Russia), Dr. Peter Lazarev (Russia), Dr. Adrian Lister (Great

Britain), Dr. Victor Mikhelson (Russia), Dr. Roald Potapov (Russia), Dr. Nikolai Praslov (Russia), Dr. Leonid Rekovetz (Ukraine), Mikhail Sablin (Russia), Dr. Jeffrey Saunders (USA), Alexei Tikhonov (Russia), Dr. Savelii Tomirdiaro (Russia), Dr. Valentina Ukraintseva (Russia) and Dr. A. Velichko (Russia). Staff members of the Mammalogy Laboratory, Zoological Institute, who contributed to the success of the Symposium were Alexei Abramov, Galina Nuraeva, Nikolai Orlov, Sonya Kuzmina, Ekaterina Tsytsulina, and Svetlana Sukhoruchenko. The mammoth task of interpreting the Russian presentations into English, and the English presentations into Russian was performed by Tatyana Platonova. Her skills made the sharing and exchange of information a success for all participants. Eighty-nine abstracts of the papers presented at the Mammoth Symposium were published in English in the Russian Journal 'Cytologia', 1995, Vol.37(7), pp. 659-719. The collection of papers to follow includes only a sample of those presented at the Symposium. Dr. Gary Haynes and Janis Klimowicz edited the papers for colloquial style, format, spelling, grammar, and correct references, and Dr. Jelle W.F. Reumer did the final editing. Our thanks are also due to Ms. Tatyana Platonova (Zoological Institute, RAS), who translated a number of papers from Russian into English.

We wish to express our gratitude to our Dutch colleagues and Editors of the journal DEINSEA, Rotterdam, who kindly gave us the opportunity to publish this collection of papers. The appearance of this volume sets the stage for the Second International Mammoth Conference, to be held May 16-20, 1999, in Rotterdam.

THE PAPERS TO FOLLOW

The 14 papers in this collection represent a small but fair cross-section of the oral presentations at the St. Petersburg conference. Three papers are from North American authors, perhaps a bit too well represented compared to the others, while six are from Russians and five

are by authors from other European countries, including the United Kingdom.

The papers by Haynes, Bahn, Lioubine, and Saunders are concerned with sites and assemblages that show interactions between humans and mammoths. Haynes's contribution provides theoretical and empirical evidence that New World Paleoindian dispersals were accelerated by Columbian mammoth-hunting, while Bahn's and Lioubine's papers examine variability in visual depictions of woolly mammoths from Upper Paleolithic sites in the Old World. Saunders's paper is a morphometric analysis of a Clovis site's Columbian mammoth bones, and discusses mammoth taphonomy, mortality, and social organization.

Lister's paper discusses topics of proboscidean biology and behavior, and shows that the scheduling of skeletal maturation in the woolly mammoth is as patterned and predictable as in the other species. The paper by Agenbroad, Morris & Roth describes a recent find of pygmy mammoth in California's Channel Islands, and offers some ideas about the ancestry of the small mammoths. The paper by Foronova & Zudin applies some rather unconventional ideas and methods to the study of the mammoth's evolutionary lineage in Eurasia, pointing out the variability and adaptability of earlier forms to oscillating cold and warm climates. Mol, van den Bergh & de Vos describe fossils from northwestern Europe collected by fishermen and paleontologists in and around the Netherlands, providing a view of evolutionary trends based on abundant finds of proboscideans such as Pliocene *Anancus*, through the later forms such as *Elephas antiquus* and *Mammuthus primigenius*.

Forsten's paper on horses from the Steinheim site describes how the middle Pleistocene taxon *Equus steinheimensis* relates morphometrically to other caballoid horses from Europe, preparing the way for further evolutionary studies. Baryshnikov's paper is a careful analysis

of variability through time and space in the taxon *Crocota spelaea*, through the immense span of the Pleistocene and across the huge expanse of Russia. Garutt's paper is a stimulating reconstruction of woolly rhinoceros social behavior, based on a study of healed skull injuries in the taxon, and supplemented by references to live rhino behavior and Upper Paleolithic cave paintings (recently discovered).

The paper by Vereshchagin & Tomirdiaro reviews the main taphonomic research projects carried out in the former Soviet Union, underscoring the critical importance of such studies not only for helping to understand Pleistocene animal behavior, but also for aiding in the reconstruction of the evolution of past environmental systems such as landscapes underlain by permanent ice. Kozhevnikov & Ukraintseva remind us in their paper that the idea of a 'tundra-steppe' (also sometimes equated with mammoth-steppe or arctic steppe) during the Pleistocene is not a fully thought-out concept, and in fact is an unfortunate shorthand term adopted to name an ecosystem that was not so much 'steppe' as something entirely distinct.

The paper by Hauf, Joger, Zimmermann, Lazarev & Vartanyan is one of a growing number of pioneering contributions that address an old problem - the phylogenetic position of mammoths - in a thoroughly new way, through comparative genetic analyses of elephants and well-preserved mammoth tissue. The concluding paper by Haynes is a final reflection on the First International Mammoth Conference, the papers that came out of it, and the future series of more Mammoth Conferences to come.

Out of the 60 presentations at the First Conference, this collection of 14 papers should be seen as only scratching the surface of all the interesting and valuable knowledge and suggestions that emerged. It is our hope that readers of this collection will sense the excitement of

discovery and insight about mammoths and their associated species throughout the Pleistocene, and that the untapped wealth of information about mammoths and the mammoth fauna can be presented

in future collections and continued International Conferences that bring together experts and students in an atmosphere of learning, exchange, and cooperation.