VEGETATION OF WARM LATE PLEISTOCENE INTERVALS AND THE EXTINCTION OF SOME LARGE HERBIVOROUS MAMMALS

V. V. Ukraintseva
(Botanical Institute, Leningrad)

From: *Botanicheskiy zhurnal*, 1979, No. 3, pp. 318–330.

Abstract: The results are reported of a study of plant remains from the gastrointestinal tract of large herbivorous mammals, i.e., horse, mammoth, bison, which perished, according to C^{14} data, during various periods of the Kargin interglacial in the Indigirka River basin (corresponding to the mid-Wisconsin, 45,000 to 30,000 BP). At that time, the forest reached the coast of the Arctic Ocean, and bogs spread. This led to a reduction of herbaceous communities serving as pastures. The qualitative composition of the food of the animals changed. Plants of moist and waterlogged communities, sedges, cotton-grass, grasses, and green and sphagnum mosses, began to predominate in their fodder. These communities differ considerably in their content of major nutrients (protein, albumin, fats) and mineral composition from plants of dry habitats and meadow forbs. This was the main reason for the reduction in the population of some animals and the final extinction of others.

The change of the environment toward cooling at the end of the Pliocene and in the Early Pleistocene caused the appearance of cold-loving mammals, i.e., mammoths, ovibos, yaks, reindeer, etc., which were common in the cold intervals of the Late Pleistocene in Eurasia and North America. The many bone remains and whole skeletons of these animals in the Pleistocene deposits of Siberia are well known (Cherskiy, 1891; Pavlova, 1906a, 1906b, 1910; Popov, 1947; Gromov, 1948; Vereshchagin, 1975, 1977; Lazarev, 1977a, 1977b; Lazarev and Tirskaya, 1975). About 50 almost complete skeletons of representatives of the upper Paleolithic faunistic complex have been found so far in Siberia. Nevertheless, frozen animal carcasses with well preserved entrails, including gastrointestinal tracts filled with plant remains, are extremely rare because they preserve well only under favorable burial conditions at the site at which the animals die.

Such conditions undoubtedly existed in Siberia during warm periods of the Pleistocene. These include waterlogging, a large number of lakes, very viscous soils, and permafrost. It can be assumed that permafrost thawed to a much greater depth during the warm intervals of the Pleistocene and Holocene than in cold intervals and at the present time, especially near river banks, lake shores, and along the edges of bogs. As a result, the summer mortality of large animals increased in warm intervals. The permafrost "conserved" the dead animals by preventing their decomposition. It is only because of these conditions that the frozen carcasses of animals which died in summer during the warm intervals of the Pleistocene survived to this day. We are inclined to believe that the increased summer mortality of large herbivores during the warm intervals of the Pleistocene and Holocene was one of the main reasons for the extinction of some (mammoths, woolly rhinoceros) and for the reduction of the range of others (ovibos, bison, yak, etc.) in Asia.

ISSN 0273-8457/81/0004-0189$7.50/0

The cold periods of the Pleistocene were less favorable for the burial of dead animals, the carcasses of which remained at the surface and were eaten by carnivores or decomposed. Therefore, the life of animals in the cold intervals of the Pleistocene can be described only from paleobotanical investigations of the deposits enclosing the remains of dead animals, which do not always correspond to the time of their life and death, since the redeposition of bones is possible. It is thus impossible to obtain a reliable idea of the landscapes that existed during the lifetime of the animals.

Almost wholly preserved frozen animals have been found since 1900 and are still being found in the deposits of the second and third flood-plain terraces in the basins of the Kolyma and Indigirka rivers: they include the mammoth find of 1900 on the Berezovka River, the horse find of 1968 on the El'gi River, the bison find of 1971 in the lower course of the Indigirka River, and the baby mammoth find of 1977 on the Berelekh River (Fig. 1). A complete mammoth skeleton was uncovered in 1971 on the Shandrin River, a right tributary of the lower course of the Indigirka

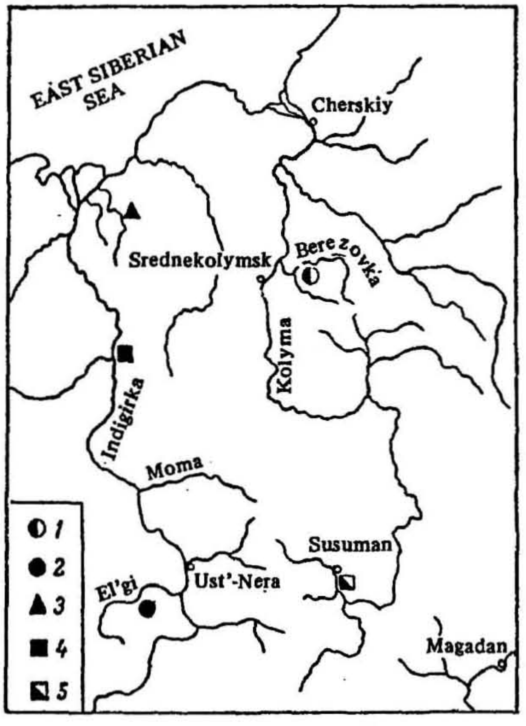

Fig. 1. Sites of the finds of whole carcasses and skeletons of Pleistocene herbivorous mammals.
Legend: 1–Mammoth, 1900, Berezovka River
2–Horse, 1968, El'gi River
3–Mammoth, 1971, Shandrin River
4–Bison, 1971, Indigirka River
5–Mammoth, 1977, Kirgilyakh creek, left tributary of Berelekh River.

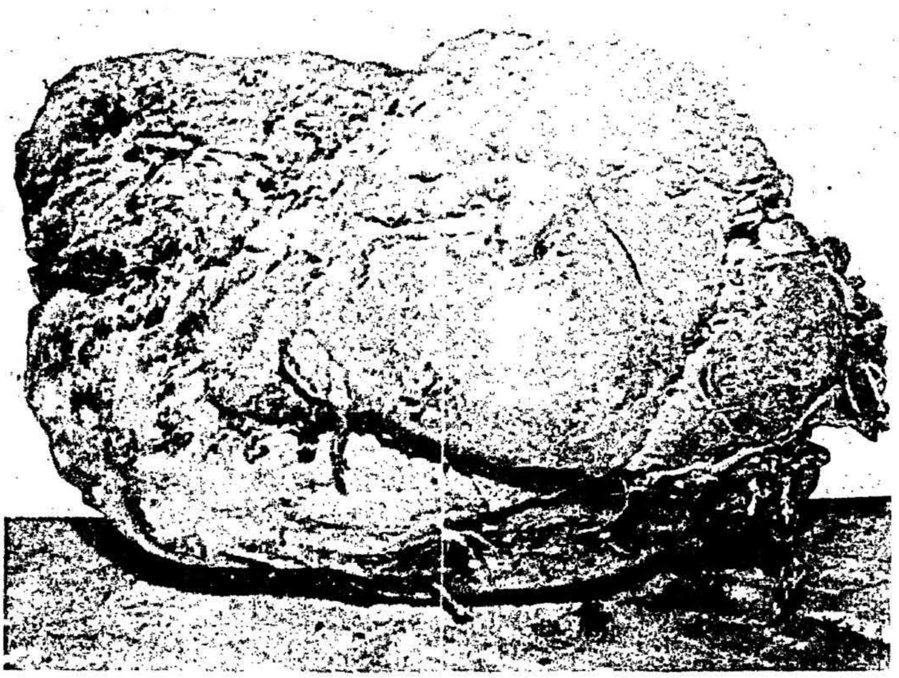

Fig. 2. Gastrointestinal tract of the Shandrin mammoth, filled with plant residues (frozen). General view. Photographed by N. V. Lovelius.

River (Vereshchagin, 1975). The frozen gastrointestinal tract of this animal, filled with more or less digested plants, was well preserved under the ribs (Figs. 2 and 3). It weighed 290 kg. About 15 kg of the plant remains in it were sent for study to the Botanical Institute in Leningrad. This unique find made it possible for the first time to study the structure of the gastrointestinal tract of a mammoth. All the aforelisted finds are extremely important for paleozoological, paleobotanical, and paleogeographic reconstructions.

The plant cover is one of the main factors characterizing the living conditions of large hervibores. Therefore, study of the content of the gastrointestinal tracts of fossil animals buried *in situ* makes it possible to: (i) determine the composition of the plants the animals ate shortly before they died and, consequently, directly in the area in which they died; (ii) reconstruct the flora and the character of the vegetation in the areas of their death; (iii) obtain an idea of the landscapes and climate during the lifetime of these animals; and (iv) establish the living conditions and understand the reasons for the extinction of mammoths and some of their "satellites".

As early as in 1861, when no such findings were known, A. F. Middendorf wrote: "What complete idea would we obtain of their (mammoths–V.U.) living conditions and reasons for their extinction if the stomach contents of the best preserved carcasses were to be subjected to microscopic analysis" (p. 855). M. S. Voronin, V. N. Sukachev,

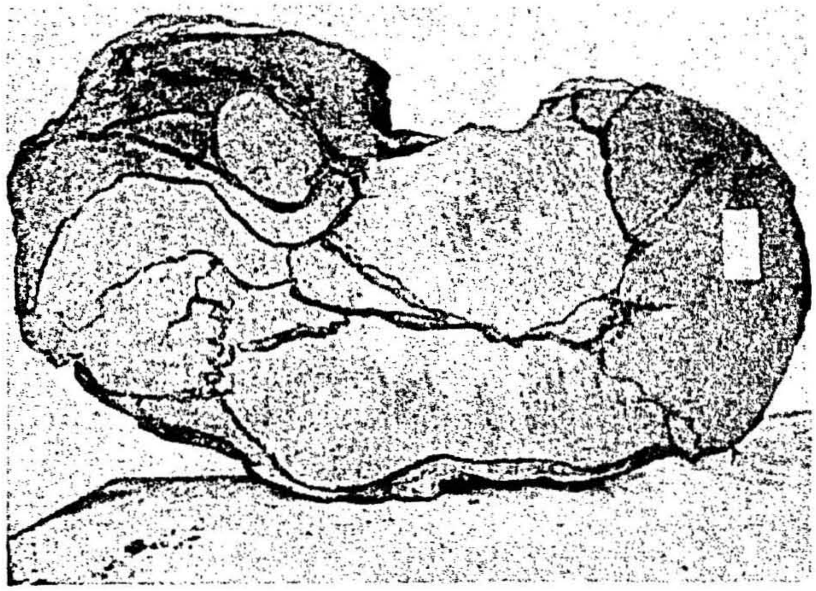

Fig. 3. Gastrointestinal tract of the Shandrin mammoth in cross section. Photographed by N. V. Lovelius.

A. I. Tolmachev, B. A. Tikhomirov, Ye. D. Zaklinskaya, and L. A. Kupriyanova gave great importance to the study of the plant remains from the stomachs of fossil animals.

According to K. K. Flerov (1965), herbivorous mammals are of great importance to the determination of past landscapes. He writes: "The great diversity of biological types and ecological niches they occupy make mammals excellent indicators of landscapes. The close relation between herbivorous mammals and the flora makes it possible to judge even more soundly the conditions under which a given species lived. It must not be foregotten that the smallest deviation in the composition of the vegetation serving as food to the mammals, in their mode of gathering it, and in their migration reflects sharply on their structure. All this makes mammals one of the best objects for paleogeographic reconstructions compared to other animals" (p. 121).

The first opportunity to study the composition of plants in the gastrointestinal tract of a fossil animal appeared in 1900 when an almost completely preserved frozen mammoth carcass was found on the Berezovka River, a right tributary of the Kolyma River, about 320 km to the northeast of Srednekolymsk (Gertz, 1902). V. N. Sukachev (1914), who studied the stomach content of this mammoth, came to the conclusion that it fed mainly on meadow grasses. These data are supported by the morphology of mammoths, which are true grass eaters, having special structures for grabbing

Fig. 4. Baby mammoth, Dima, 1977, Kirgilyakh creek. Photographed by S. Steshenko.

(Flerov, 1931) and crushing hard grasses (Gromov, 1948). Flerov showed that the "bilobate" structure of the end of the mammoth trunk is associated with the feeding mode. The end of the trunk, consisting of a strongly developed lower lobe and of an upper digitiform process, was an excellent organ for gathering grasses. According to Gromov (1948), as the jaws evolved from primitive *Elephans merionalis* to the mammoth, the tooth crown became higher, the number of dental plates increased, folded enamel appeared and its thickness decreased. Gromov, like most other researchers, believes that such a transformation of the jaw was produced by a change in food composition from more succulent and soft to coarser. This was probably caused by the migration of the ancestors of the mammoths from the forests to open areas, where hard to chew and poorly digestible grasses predominate.

The plant remains from the stomachs of another three fossil animals, i.e., the horse found on the Selerikan River, the mammoth from the Shandrin River, and the bison discovered in the middle reach of the Indigirka River (Fig. 1), have now been investigated. The stomach content of the baby mammoth found June 23, 1977, on Kirgilyakh Creek in the upper course of the Kolyma River (Fig. 4) is under investigation. The composition of the plants eaten by the animals shortly before they died (Table 1) has been established from pollen, spores, plant tissues (Tikhomirov, Kul'tina (Ukraintseva), 1973; Solonevich, Vikhireva-Vasil'kova, 1977; Solonevich et al., 1977; Ukraintseva, 1977; Ukraintseva et al., 1978), fruits and seeds (Yegorova, 1977).

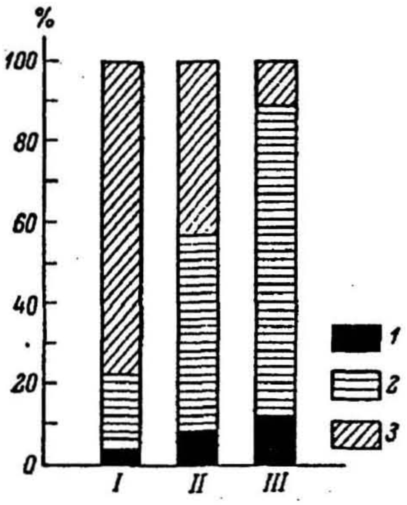

Fig. 5. Composition of plants, identified from pollen and spores, in the contents of gastrointestinal tracts.
Legend: I. Mammoth, Shandrin River
II. Bison, Indigirka River
III. Horse, El'gi River
1. Tree, shrub, and undershrub pollen
2. Grass pollen
3. *Bryophyta* and *Pteridophyta* spores.

The difference in the composition of plants eaten by the animals is shown in Fig. 5, according to palynological data. The pollens of herbaceous plants account for 80.3% of the content of the gastrointestinal tract of the horse that died on Bol'shoy Selerikan Creek (El'gi River), tree, shrub, and undershrub pollen for 8.4%, and the spores of various mosses and ferns for 11.3% (Ukraintseva, 1977). Grass pollen and spores were found almost in equal amounts in the contents of the gastrointestinal tract of the bison from the Indigirka River (Ukraintseva et al., 1978), 49.7 and 43.4%, respectively. Tree, shrub, and undershrub pollen accounted for 6.9%. Moss spores predominated in the gastrointestinal tract of the mammoth found on the Shandrin River, amounting to 77%, grass pollen amounted to 19.4%, and tree, shrub, and undershrub pollen only to 3.6%.

It is important to note that the percentage ratio of pollen and spores of various plant groups, i.e., grasses, mosses, trees, shrubs, and undershrubs, is fairly close to that of the same groups determined from macroremains. According to N. G. Solonevich and V. V. Vikhireva-Vasil'kova (1977), the remains of herbaceous plants predominated in the gastrointestinal tract of the horse, amounting to 90% of the entire plant mass; wood remains amounted to 5-7%, and the remains of various mosses to 1-2%.

The data obtained made it possible to establish qualitative differences between the floras in the areas where the fossil animals were found and confirmed the existence

TABLE 1

Composition of Plants Identified in the Contents of the Gastrointestinal Tracts of Herbivorous Pleistocene Mammals of Siberia*

Состав растений, определенных в содержимом желудочно-кишечных трактов растительноядных плейстоценовых млекопитающих Сибири *

Plant	Animal, date of its death, according to C^{14}							
	Berezovka mammoth 44,000 years ago		Shandrin mammoth 41,740 ± 1920 years ago		Selerikan horse 38,590 ± 1180 years ago		Malykhchin bison, 29,500 ± 1000 years ago	
	macro-remains	pollen, spores	macro-remains	pollen, spores	macro-remains	pollen, spores	macro-remains	pollen, spores
Larix dahurica Turcz.			+	+				+
Larix sp.	+					+		
Picea obovata Ledeb.						+		
P. cf. *ajanensis* Fisch.						+		
Picea sp.				+				
Pinus sibirica (Rupr.) Mayr		+						+
P. pumila (Pall.) Regel				+		+		+
P. sylvestris L.						+		
Pinus sp. sp.						+		
Juniperus sp.						+		
Salix sp.$_1$—sp.$_3$						+		
Salix sp.$_2$						+		
Salix sp.$_3$						+		
Salix sp. sp.		+	+	+	+	+		+
Populus suaveolens Fisch.						+		
Betula sp. ex sect. *Costatae*						+		
B. alba L. s. l.	+					+		
B. fruticosa Pall.						+		
B. platyphylla Sukacz.						+		+
B. exilis Sukacz.				+		+		+
Betula sp. ex sect. *Nanae*			+					+
Betula sp. sp.				+	+	+		
Alnus hirsuta (Spach) Rupr.		+				+		+
A. fruticosa Rupr.				+	+	+		+
Alnus sp.	+	+	+?					
Corylus cf. *cornuta* Marsh.						+		
Ulmus pumila L.						+		
U. cf. *propinqua* Koidz.						+		
Ulmus sp.								+
Caragana jubata (Pall.) Poir.		+						
Typha sp.								+
Potamogeton sp.						+		
Agropyron cristatum (L.) Gaertn.	+	+				+		
Agropyron sp.		+				+		
Alopecurus alpinus s. l.	+	+						
Beckmania eruciformis L. s. l.	+	+						
Bromus sibiricus Drob.		+						
Calamagrostis sp.			+					
Helictotrichon krylovii (N. Pavlov) Henrard.			+					
Hordeum violaceum Boiss. et Huet	+							
Phragmites communis Trin.		+						
Elymus sp.		+						
Festuca sp. sp.			+					
Poa arctica R. Br.						+		
Poaceae gen.	+	+	+	+		+	+	+
Carex lagopina Wahlenb.	+							
Carex sp. sp.	+					+		
Eriophorum sp.								
Kobresia cf. *capilliformis* Ivanova				+				
Kobresia sp.							+	
Cyperaceae gen.		+	+	+		+	+	+
Juncus sp.						+		
Allium shoenoprasum L.						+		
A. strictum Shrad.						+		
Oxyria digina (L.) Hill (?)		+						+

*Sukachev, 1914; Kupriyanova, 1957; Tikhomirov, Kul'tina-Ukraintseva, 1973; Solonevich, Vikhireva-Vasil'kova, 1977; Solonevich et al., 1977; Ukraintseva, 1977; Ukraintseva et al., 1978.

324

TABLE 1 (cont'd)

Продолжение

Plant	Animal, date of its death, according to C^{14}							
	Berezovka mammoth 44,000 years ago		*Shandrin mammoth 41,740 ± 1920 years ago*		*Selerikan horse 38,590 ± 1180 years ago*		*Malykhchin bison, 29,500 ± 1000 years ago*	
	macro-remains	*pollen, spores*	*macro remains*	*pollen, spores*	*macro-remains*	*pollen, spores*	*macro-remains*	*pollen, spores*
Polygonum bistorta L.								+
P. foliosum H. Lindberg						+		
P. scabrum Moench						+		
Rumex acetosella L.		+						
Rumex sp.						+		
Atriplex sp.		+						
Chenopodium sp.						+		
Chenopodiaceae gen.								+
Cerastium sp.		+						
Dianthus sp.		+				+		
Lychnis sibirica L.						+		
Minuartia arctica (Stev.) Asch.						+		
M. macrocarpa (Pursh.) Ostenf.						+		
Melandrium sp.		+						
Sagina sp.		+				+		
Silene sp.						+		
Stellaria jacutica Schischk.						+		+
Stellaria sp.								+
Caryophyllaceae gen.				+		+		+
Nuphar pumilum (Hoffm.) DC.						+		
Nymphaea sp.						+		
Caltha palustris L.		+				+		
Ranunculus acris L.	+							
Ranunculus sp.						+		
Thalictrum foetidum L.						+		
Ranunculaceae gen.								+
Papaver sp.						+		+
Polygala sp.								
Brassicaceae		+				+		+
Sedum purpureum (L.) Schult.						+		
Saxifraga sp. sp.				+		+		+
Dryas punctata Juz.				+				
Potentilla emarginata Pursh.						+		
P. multifida L.						+		
Potentilla sp.		+				+		+
Rubus arcticus L.						+		
Sanguisorba officinalis L.		+				+		
Rosa sp.		+						
Rosaceae gen.		+				+		+
Astragalus sp.						+		
Hedysarum sp.						+		
Oxytropis sordida (Willd.) Pers.	+	+						
Lathyrus pilosus Cham.						+		+
Fabaceae gen. (*Leguminosae*)						+		+
Epilobium sp.						+		
Aegopodium podagraria (L.) (?)		+						
Angelica dahurica (Fisch.) Benth.		+				+		
Apiaceae (*Umbelliferae* gen.)						+		+
Vaccinium vitis-idaea L.			+	+				
Ericaceae gen.			+	+		+	+	+
Gentiana sp.		+						+
Phlox sibirica L.								+
Polemonium boreale Adams								+
Labiatae gen.				+		+		
Pedicularis sp.				+		+		+
Valeriana capitata Pall.				+		+		
Artemisia borealis L.								
A. dracunculus s. l.								
A. sacrorum Ledeb. s. l.						+		
A. vulgaris L.				+		+		

TABLE 1 (cont'd)

Продолжение

Plant	Animal, date of its death, according to C^{14}							
	Berezovka mammoth 44,000 years ago		*Shandrin mammoth 41,740 ± 1920 years ago*		*Selerikan horse 38,590 ± 1180 years ago*		*Malykhchin bison, 29,500 ± 1000 years ago*	
	macro-remains	*pollen, spores*	*macro-remains*	*pollen, spores*	*macro-remains*	*pollen, spores*	*marco-remains*	*pollen, spores*
Artemisia sp.				+		+		+
Aster sp.						+		+
Centaurea sp.								+
Cirsium sp.						+		
Gnaphalium uliginosum L. s. l.								
Mulgedium sibiricum (L.) Less.						+		
Saussurea sp.						+		
Asteraceae gen.				+		+		+
Indet. dicotyledoneae				+		+		+
Indet. monocotyledoneae						+		+
Hepaticae								+
Sphagnum angustifolium C. Jens.			+					
S. girgensohnii Russ.			+					
S. sp. ex sect. *Subsecunda*			+					
S. sp. ex sect. *Palustria*			+					
Sphagnum sp. sp.			+	+	+	+	+	+
Polytrichum commune Hedw.			+					
P. strictum Sm.			+		+			
Polytrichum sp.₁₋₃					+		+	+
Dicranum sp.				+				+
Pottia sp. (*Pottiaceae*)								+
Distichium capillaceum (Hedw.) B. S. G.					+			
Tortula ruralis (Hedw.) Crome					+			
Bryum sp. sp.					+		+	
Aulacomnium turgidum (Wahlenb.) Schwaegr.	+		+					
Thuidium abietinum (Hedw.) B. S. G.					+			
Thuidium sp.					+			
Drepanocladus fluitans (Hedw.) Warnst. (=*Hypnum fluitans* (Dill.) L.)	+							
Drepanocladus sp.					+			
Calliergon sp.					+			
Tomenthypnum nitens (Hedw.) Loeske								
Rhytidium rugosum (Hedw.) Kindb.					+			
Bryales sp.₁₋₄		+		+		+		+
Equisetum sp.				+		+		+
Botrychium lunaria Sw.						+		+
Lycopodium alpinum L.						+		
Lycopodium sp.								
Selaginella sibirica (Milde) Heiron.		+				+		+
S. pleistocenica sp. nov.						+		
Selaginella sp.								+
Dryopteris sp.						+		+
Polypodiaceae gen.								+
Indet. sporites						+		+

The mosses were identified by A. L. Abramova (Botanical Institute, Leningrad).

в теплые периоды плейстоцена кардинально менялся состав растений, которыми питались крупные растительноядные млекопитающие. В составе кормов этих животных начинали доминировать растения влажных и заболоченных местообитаний — осоки, пушицы, злаки, зеленые и сфагновые мхи (рис. 5, *I* и *II*), которые по содержанию основных питательных of plant zonation during the warm periods of the Pleistocene. According to C^{14} data (see Table 1), these animals died during various stages of the Kargin interstadial (Hettweigian, according to the European scale; Port-Talbot 1, 2; Plum-Point, according to the American scale) (Geynts, Garutt, 1964; Arslanov, Chernov, 1977), which covered the time interval between the Zyryan (more than 50,000 years ago) and the Sartan (which began 25,000 years ago) glaciations. The optimum of the Kargin interglacial occurred in the middle of this interval, i.e., Melokhetskoye warming, which occurred approximately 42,000-32,000 years ago (with an optimum about 40,000 years ago–Kind, 1972).

Climatic conditions in Siberia were milder than now during the Kargin interglacial, especially during its optimum phase. This is attested by the existence in that period of a forest vegetation in the now treeless regions of the Indigirka basin. It has been established from investigations of the content of the gastrointestinal tract of the mammoth from the Shandrin River (Solonevich et al., 1977) that there were *Larix gmelinii* forests in the region of the mammoth find about 42,000 years ago, the bark, needles, seed scale remains, and pollen of which were found in its stomach. At the present time, marshy and hummocky tundras and sedge-hypnum and sphagnum bogs are common in the Shandrin River basin. The waterlogged larch forests and open woodlands of the basin of the Ercha River, a right tributary in the lower course of the Indigirka River, can serve as an analog of the vegetation of the Proto-Shandrin River during the lifetime and death of the mammoth. The northern limit of these larch forests is 200 km south of the site of the mammoth find.

Study of the stomach content of the horse from the Selerikan River and of its enclosing deposits (Ukraintseva, 1977; Belorusova et al., 1977) showed that mountain larch forests with *Picea obovata* and, possibly, *P. ajanensis* were common in the upper course of the Indigirka River about 40,000 years ago and that large birch from sect. *Costatae* and *Alnus hirsuta* probably grew in valley forests. Meadow and meadow-steppe communities, serving as pastures, played an important part in the landscapes. At that time, *Kobresia capilliformis*, which is now a typical plant of the high mountains of Soviet Central Asia, the Middle East, and Mongolia, where it is sometimes found in the middle and upper part of the forest belt, formed a noticeable part of the herbaceous communities of the study area. The horse stomach contained 800 fruits of this species. T. V. Yegorova (1977) ascribes the extinction of *Kobresia capilliformis*, a species once abundant in the range of habitat of the horse, to the increase in the continentality of the climate of Eastern Siberia in post-Kargin time, particularly to the sharp decrease in snow cover depth. To the south and southwest of the area in which the horse was found, the forests consisted not only of coniferous but also of broadleaf species, i.e., elm, filbert, etc., the pollens of which were well preserved in the horse's stomach.[1]

V. N. Sukachev has identified the wood samples from under the carcass of the Berezovka mammoth and in the enclosing deposits. He found *Alnus* sp., *Larix* sp., and *Betula alba* s. l., which grow even now in the Kolyma River basin and in the

[1] The good preservation of the pollen precludes its interpretation as "redeposited".

area of the mammoth find. He came to the conclusion that the climate at the time of the death of the mammoth was no more severe than now. Sukachev gave no indication of whether it was warmer or the same as now. At any rate, there is no doubt of the existence of forest communities consisting of the mentioned species.

Later determinations from pollen and spores led L. A. Kupriyanova (1957) to conclude that the climate during the lifetime and at the death of the Berezovka mammoth was warmer than now, since some plants, encountered at that time on the Berezovka River, i.e., *Pinus sibirica, Caragana jubata*, etc., are now found much farther south and southwest. The Berezovka mammoth died in the beginning phases of the Kargin interglacial, when herbaceous communities were still more widely represented and valley type forests predominated.

The paleobotanical data obtained thus testify to the prevalence of forest landscapes in the Indigirka basin down to its lower course during the optimum phases of the Kargin interglacial. The increase in forests and bogs in the warm intervals of the Pleistocene led to a sharp reduction of herbaceous communities, which were widespread during the cold (glacial) intervals of the Pleistocene in Eurasia and North America. As a result, the composition of the plants eaten by large herbivorous mammals changed drastically in warm periods. Plants of moist and waterlogged habitats, i.e., sedge, cotton grass, grasses, and green and sphagnum mosses, began to predominate in the food of these animals (Fig. 5I and 5II). These plants differ considerably in their content of major nutrients (protein, albumins, fats) and mineral composition (especially calcium, potassium, phosphorus) from plants of dry habitats and from meadow forbs (Larin, 1958). Green mosses are an abundant but inferior food (Koshkina, 1961).

The protein content in fodder is one of the most important indicators of its nutritional value (*Tebenevochnyye* . . . , 1971). Sedges and grasses, the remains of which predominate in the stomachs of the mammoth and bison, have almost the same nutritional value and content of mineral elements. The sedges of moist habitats are inferior in nutritional value and in mineral composition, particularly in the content of calcium, to the sedges of desert and mountain habitats (Larin, 1958). *Eriphorum vaginatum*, one of the common and important spring foods of the reindeer, contains only 0.33% calcium and 2.70% of raw ash, while its main winter food, *Cladonia alpestris*, has 0.13% calcium and 0.54% raw ash (Yegorov, Kuvayev, 1959). The importance of calcium, potassium, phosphorus, and other nutrients to large herbivores is indisputable. Their low intake reduces the birth rate and increases winter mortality.

We believe that the seasonal variation in nutrients and mineral substances played an important part in the life of extinct animals (mammoths, woolly rhinoceros), as it does in the life of present animals. It has been established that the content of protein and albumin decreases sharply in pastures in the winter-spring period (*Tebenevochnyye* . . . , 1971). The protein deficiency is aggravated by a sharp decrease of individual, irreplaceable amino acids. The protein content in major species of fodder the species: by a factor of 3.5–6.3 in grasses and of 2.6–6.4 in sedges. The content of protein and albumin in plants in the Srednekolymsk region decreases to a lesser degree in winter, by a factor of 2.4-3.5 in grasses and of 2.4-5.2 in sedges. As the content of protein changes so does its qualitative composition. For example, the total content of nine irreplaceable amino acids (excluding tryptophan) in the investigated fodder grasses of the Verkhoyansk and Srednekolymsk regions varies from 19 to 37 g/kg of air-dry substance in summer, equals 7-11 g in winter, and decreases to 4-3 g by spring. The sharp decrease of the protein-albumin value of winter fodder has a negative effect on the albumin metabolism and productivity of animals and particularly horses.

It must be emphasized that the calcium content in fodder plants is frequently low in summer (0.08-0.50%) and in some cases does not meet the requirement of horses in it, while it is high and often excessive (0.2-1.7%) in winter. An elevated calcium content was probably a vital necessity for such large animals as the mammoth, ovibos, bison, yak, woolly rhinoceros, etc., which have a massive skeleton.

It must be assumed that the variation in nutrients and mineral substances was probably different in the cold intervals of the Pleistocene but favorable to such large herbivores as the mammoth, requiring not only a large amount of fodder but also full-valued fodder for their normal vital activity.

Thus, the change in the environment during the warm intervals of the Pleistocene in the direction of improved ecological conditions from the human point of view was harmful to mammoths, ovibos, yaks, saigas, and other animals adapted to life in a "dry" cold climate (Garutt, 1965; Formozov, 1969; Flerov, 1978). However, the mammoth and its satellites continued to exist in these warm periods pessimal to their life. Such animals as the Saiga and Poephagus, adapted to life under arid conditions (Flerov, 1978, 1979), left the Siberian Northeast, remaining only in arid zones in the Holocene.

The shortage of fodder and its low quality, the increase in humidity, severe waterlogging and thermal settling of soils, and a deep snow cover had the result that animal mortality increased strongly in summer and winter during the warm intervals of the Pleistocene. The number of animals of the "mammoth" faunistic complex probably decreased strongly during the Kargin interglacial, particularly in the phase of the climatic optimum. During the Sartan ice age, when herbaceous communities increased again, conditions were more favorable for the mammoth and its satellites, but their number had probably become so small by that time that the mammoths became extinct during the next, Holocene, warming in the entire paleo-Arctic and in North America, not being able to adapt to the ecological conditions of warm intervals. The ovibos became extinct in Europe and Asia, remaining only in Canada, the islands of the Canadian Archipelago, and in Greenland, where existing climatic and landscape conditions are associated with the presence of glaciers or their proximity.

Analysis of plant remains from the stomachs of fossil herbivorous mammals of Siberia and of the dates of their death leads to the following conclusions:

1. The dates of the death of the known well-preserved carcasses of large extinct herbivorous mammals belong to various stages of the Kargin interglacial.

2. At that time, conditions in Siberia were favorable for the burial of such large animals as the mammoth, the woolly rhinoceros, bison, etc.

3. The increase in forests and bogs in warm periods led to a sharp reduction of pastures.

4. The quality of the fodder deteriorated and this resulted in a decrease in birth rate and greater winter mortality.

5. The summer and winter mortality of the animals increased in warm periods and ultimately led to their extinction.

6. Many animals adapted to life in a "dry" cold climate with extensive herbaceous communities could not survive the Holocene warming and became extinct or reduced their range.

7. The extinction of mammoths and of their "satellites" had many reasons. However, these reasons were determined by the fluctuating character of the Pleistocene environment (Velichko, 1973), the succession of cold (glacial) and warm (interglacial) epochs, and a sharp change of ecological conditions to which these animals were unable to adapt.

Bibliography

Arslanov, Kh. A., and S. V. Chernov. "Absolute age of the fossil Selerikan horse." In: *Fauna i flora antropogena Severo-Vostoka Sibiri* [Anthropogene Fauna and Flora of the Siberian Northeast]. Leningrad, 1977.

Belorusova, Zh. M.; N. V. Lovelius, and V. V. Ukraintseva. "Paleogeography of the Late Pleistocene and Holocene in the region of the find of the Selerikan horse." In: *Fauna i flora antropogena Severo-Vostoka Sibiri* [Anthropogene Fauna and Flora of the Siberian Northeast]. Leningrad, 1977.

Cherskiy, I. D. "Description of the collection of post-Tertiary mammals gathered by the Novosibirsk expedition." Appendix 1 to: *Zap. Akad. nauk*, SPb., Vol. 65, 1891.

Flerov, K. K. "Trunk of mammoth (*Elephas primigenius* Blum.) found in the Kolyma district (Siberia)." *Izv. Akad. nauk SSSR*, ser. 7, 1965.

______. "Origin of the Canadian fauna in relation to the history of the Bering region." In: *Chetvertichnyy period i yego istoriya* [Quaternary Period and its History]. Moscow, 1965.

______. "Mammals and Pleistocene environment," *Priroda*, 1970, No. 11.

______. "Bisons of the Siberian Northeast." In: *Mamontovaya fauna i sreda yeye obitaniya v antropogene v SSSR* [Mammoth Fauna and Its Habitat During the Anthropogene in the USSR]. *Tr. Zoolog. inst. Akad. nauk SSSR*, 73, 1978.

______. "Geographische Verbreitung des Poephagus." *Quartärpaläontologie*, III. Weimar, 1979.

Formozov, A. N. "Fauna of Paleolithic camps of the European USSR." In: *Priroda i* *razvitiye pervobytnogo obshchestva na territorii yevropeyskoy chasti SSSR* [Nature and the Development of Primitive Society in the European USSR]. Moscow, 1969.

Garutt, V. Ye. "Fossil elephants of Siberia." *Trudy n.-i. inst. geologii Arktiki*, 143, 1965 (Anthropogene Period in the Arctic and Subarctic).

______ and K. V. Yur'yev. "Mummified remains of a wild horse from the permafrost of the Indigirka River basin." *Byull. komissii po izucheniyu chetvertichnogo perioda*, 31, 1966.

Gerts, O. F. "Report of the leader of the expedition of the Imperial Academy of Sciences to the Berezovka to dig up a mammoth carcass." *Izv. Imp. Akad. nauk*, Vol. 16, 4, 1902.

Geynts, A. Ye., and V. Ye. Garutt. "Radiocarbon determination of the absolute age of the fossil remains of a mammoth and a woolly rhinoceros from the permafrost of Siberia." *Dokl. Akad. nauk SSSR*, 154, 6, 1964.

Gromov, V. I. *Paleontologicheskoye i arkheologicheskoye obosnovaniye stratigrafii kontinental'nykh otlozheniy chetvertichnogo perioda na territorii SSSR* [Paleontological and Archeological Evidence for the Stratigraphy of Continental Quarternary Deposits in the USSR]. 1948.

Kind, N. V. "Late Quaternary changes in the climate and glaciation in the Old and New World (radiocarbon chronology)." In: *Stratigrafiya, sedimentologiya i geologiya chetvertichnogo perioda. Mezhd. geol. kongr., XXIV sessiya. Dokl. sov. geologov* [Stratigraphy, sedimentology, and geology of the Quaternary. International Geological Congress, Session 14. Reports of Soviet geologists.] Moscow, 1972.

Koshkina, T. V. "New data on the nutrition of the Norwegian lemming (*Lemmus lemmus*)." *Byull. MOIP, otd. biol.*, 66(6), 1961.

Kupriyanova, L. A. "Analysis of the pollen of the plant remains from the stomach of the Berezovka mammoth (contribution to the problem of the character of vegetation in the epoch of the Berezovka mammoth)." In: *Sb. pamyati Afrikana Nikolayevicha Krishtofovicha* [Collection in Honor of Afrikan Nikolayevich Krishtofovich]. IV. 1957.

Lazarev, P. A. "History of the find of the Selerikan horse carcass and of its study." In: *Fauna i flora antropogena Severo-Vostoka Sibiri* [Anthropogene Fauna and Flora of the Siberian Northeast]. Leningrad, 1977a.

______. "New find of a woolly rhinoceros skeleton in Siberia." Ibid., 1977b.

______ and N. F. Tirskaya. "Concerning the remains of a woolly rhinoceros in Churapcha village (central Yakutia) and the spore-pollen spectra of enclosing deposits." In: *Palinologicheskiye materialy k stratigrafii osadochnykh otlozheniy Yakutii* [Palynological Data for the Stratigraphy of the Sedimentary Deposits of Yakutia]. Yakutsk, 1975.

Larin, I. V. "Food value of sedges." *Dokl. VASKhNIL*, 8, 1958.

Middendorf, A. F. *Puteshestviye na sever i vostok Sibiri* [Travel to Northern and Eastern Siberia]. IV, 1861.

Pavlova, M. V. "Description of fossil mammals collected by the Russian Polar Expedition in 1900-1903, Part 1." *Zap. imp. Akad. nauk. Ser. VIII. Fiz.-matem otd.*, 21, 1, 1906a.

______. "Etudes sur l'histoire paléontologique des ongulés. IX. Sélénodontes posttertiaires de la Russie." *Mémoires de l'Académie Impériale des Sciences de St.-Petersbourg.* VIII Série. Classe physico-mathématique, 22, 1, 1906b.

______. "Description of the fossil remains of mammals in the Troitskosavsk-Kyakhta Museum." *Tr. Troitskosavsko-Kyakht. otd. Priamurskogo otdela Russk. geograf. obshchest.*, 13, 1, 1910.

Popov, Yu. N. "Find of fossil mammal carcasses in the Pleistocene permafrost layers of the Siberian Northeast." *Byull. komissii po izucheniyu chetvertichnogo perioda*, 13, 1948.

Solonevich, N. G., and V. V. Vikhireva-Vasil'kova. "Preliminary results of a study of plant remains from the gastrointestinal tract of the Shandrin mammoth (Yakutia)." In: *Fauna i flora antropogena Severo-Vostoka Sibiri* [Anthropogene Fauna and Flora of the Siberian Northeast]. Leningrad, 1977.

Sukachev, V. N. "Investigation of the plant remains in the food of the mammoth found on the Berezovka River in the Yakutsk region." In: *Nauchnyye resul'taty ekspeditsii, snaryazhennoy Akademiyey nauk dlya raskopki mamonta, naydennogo na r. Berezovke v 1901 godu* [Scientific Results of the Expedition Mounted by the Academy of Sciences to Dig Up the Mammoth Found on the Berezovka River in 1901]. 3. St. Petersburg, 1914.

Tebenevochnyye pastbishcha i kormovyye rasteniya tabunnogo konevodstva severo-vostochnykh rayonov Yakutskoy ASSR [Winter Pastures and Fodder Plants for Horse Breeding in the Northeastern Rayons of the Yakut ASSR]. Yakutsk, 1971.

Tikhomirov, B. A. "Environmental conditions and vegetation in the epoch of the mammoth in northern Siberia," *Problemy Severa*, Vol. 1, 1958.

______ and V. V. Kul'tina (Ukraintseva). "Investigation of the pollen and spores from the stomach of the fossil Selerikan horse." *Dokl. Akad. nauk SSSR*, 209, 6, 1973.

Ukraintseva, V. V. "Reconstruction of the flora and vegetation during the lifetime and death of the fossil Selerikan horse from palynological data." In: *Fauna i flora antropogena Severo-Vostoka Sibiri* [Anthropogene Fauna and Flora of the Siberian Northeast]. Leningrad, 1977.

______, K. K. Flerov, and N. G. Solonevich. "Botanical analysis of the plant remains from the gastrointestinal tract of the bison found in Yakutia," *Botan. zh.*, 63, 7, 1978.

Velichko, A. A. *Prirodnyy protsess v pleystotsene* [Natural Process in the Pleistocene]. 1973.

Vereshchagin, N. K. "Concerning the mammoth from the Shandrin River." *Vestnik zoologii*, 2, 1977.

______. "Description of parts of the carcass and skeletal remains of the Selerikan horse." In: *Fauna i flora antropogena Severo-Vostoka Sibiri* [Anthropogene Fauna and Flora of the Siberian Northeast]. Leningrad, 1977.

Yegorov, A. D. *Khimicheskiy sostav kormovykh rasteniy Yakutii (lugov i pastbishch)* [Chemical Composition of the Fodder Plants of Yakutia (Meadows and Pastures)]. Moscow, 1960.

______ and V. B. Kuvayev. "Two interesting deer fodder plants in the Northeast of Yakutia." *Priroda*, 1959, No. 4.

Yegorova, T. B. "Carpolite analysis of the plant remains of the food of the fossil Selerikan horse." In: *Fauna i flora antropogena Severo-Vostoka Sibiri* [Anthropogene Fauna and Flora of the Siberian Northeast]. Leningrad, 1977.