

Figure 6. Digestible energy content of bromegrass plants, stems, and leaves at different stages of development (adapted from Kilcher and Toreisen, 1973, with permission)

toxic levels of specific nutrients have importance as evolutionary plant defense mechanisms, they likely have little effect on an herbivore's daily choice of food. There is very little evidence that herbivores discriminate against "secondary compounds." Freeland and Janzen (1974) stated that: "Herbivores should prefer to feed on plants or plant parts containing small amounts of 'secondary compounds'". Similarly, humans should discriminate against potatoes, spinach, carrots, radishes, bananas and tea which contain solanine, nitrates, carotatoxin, goitrogens, pressoramines and tannins, respectively (Gibson, 1980): but there is no evidence of such discrimination.

### SPECULATIONS AND OBSERVATIONS

1) Bell's model of successive grazers suggests that during the growing season, horses and mammoths utilized the tall portions of the grass which were highest in fiber while bison and smaller mammals may have followed them and used the higher-quality portions of the plants.

2) During the winter, little opportunity existed for selective grazing: the mature grass was low in protein, high in cell-wall constituents and, hence,

low in digestible energy. Mammoths and horses would have required large quantities of this low-quality forage daily, whereas bison most likely would have lowered their feed intake to a maintenance level and used nitrogen recycling in order to cope with the low-protein level.

3) Selection favored animals which could grow very rapidly and reach maturity quickly. While mature ruminants and monogastrics can apparently utilize low-quality forage to meet maintenance requirements, growing animals require higher quantities and qualities of food. However, animals can, to some extent, cease growing for a period of time without affecting ultimate body size. Under such conditions, they exhibit "compensatory" growth when feed supplies increase.

4) Large animals had some advantages in terms of survival in cold weather, due to a low surface area to mass ratio. The large animal has more resistance to cold and can survive periods of intense cold more easily than a smaller animal.

5) Animals which gained rapidly deposited a great deal of fat during the growing season and had an advantage. Fat is not just a source of energy for the winter; it is also a very efficient insulator. Also, a heavy hair coat would have provided a great deal of insulation.

6) Mammoths and horses, which ate large amounts of feed and digested it less efficiently than ruminants, converted a lot of mature plant material to forms which could be utilized by the vegetation for future growth. For example, plant protein was converted to urea which was used by the vegetation as a source of nitrogen. Perhaps heavy use by mammoths and horses provided for new growth of high-quality material for ruminants which might have followed in the grazing succession.

7) The demise of the arctic steppe was likely caused by a change in vegetation and, hence, a decrease in the supply of food. Cold per se would not affect these animals although a very heavy snow cover could have hampered their movements and feeding ability.

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## PALEOECOLOGY OF THE MAMMOTH FAUNA IN THE EURASIAN ARCTIC

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An analysis of the morphology and ecology of the late Pleistocene mammoth fauna of arctic Eurasia indicates that they lived in a cold, dry climate in steppe and steppe-tundra biotopes and landscapes characterized by hard, frozen ground. The decimation of the mammoth fauna came as a result of temperature increases during interstades within the Valdai (i.e., Würmian of Europe, Wisconsin of North America) cold interval and the establishment of taiga and tundra vegetation at the end of this interval. The animals surviving the ecological catastrophe at the end of the Pleistocene (e.g., reindeer, arctic fox, marmot, souslik ground squirrel, and lemming) were able to persist in the severe conditions of present-day tundra as a result, in some cases, of their capacity for long migrations and, in others, of physiological adaptations that enabled them to cope with deep snow and occasional winter thaws. (Abstract by V.C.S.)

Key words: Pleistocene mammoth fauna, ecology and morphology of; reindeer; arctic fox; marmot, souslik; ground squirrel; lemming

### INTRODUCTION

Siberian deposits of late Pleistocene (Zyrian, Kargin, and Sartan<sup>1</sup>) age contain a remarkable abundance of large mammal fossil remains. Since large animals are extremely scarce in the recent mammal faunas of the tundra and forest-tundra, conditions during the late Pleistocene must have been quite different. A consideration of the paleoecology of the late Pleistocene theriofauna is of particular interest because of the current rapid industrialization of arctic areas, the ongoing attempts to regulate utilization of the gene pool of such remaining animals as wild reindeer, polar

fox, aquatic birds, and fish, and the recent attempts to enrich Siberian arctic faunas by introducing exotic species such as muskrat and reintroducing regionally extinct species such as musk ox.

The present paper is concerned only with zoological materials, including former geographic ranges, morphological characteristics, biology, and the probable ecological requirements of the extinct species. We also compare these data with similar information about species that have survived the Pleistocene. Special attention is devoted to the results of research on frozen fossil carcasses of Quaternary mammals, which have enabled us to revise earlier concepts of the adaptations and modes of life of the animals comprising the mammoth fauna.<sup>2</sup>

<sup>2</sup>We intend to devote a future paper to the similarities and differences between the landscapes and faunas of the Pleistocene steppe-tundra of Eurasia and those of the present African savanna.

<sup>1</sup>The Zyrian, Kargin, and Sartan intervals of Siberia correspond to Würm I, II, and III of the Alpine climatic sequence widely used in Europe and to the Happy, Bouthellier, and Duvanny Yar intervals of Hopkins (this volume).—Eds.

## ORIGIN AND COMPOSITION OF THE MAMMOTH FAUNA

Many aspects of the history of arctic theriofaunas remain obscure because of the lack of Tertiary fossils. Nevertheless, if we take into consideration the morphological conservatism of fossil mammals such as zebrine horses, the broad-fronted elk or moose, musk oxen, and trogontherian beavers found in early Pleistocene deposits in northeastern Siberia (Sher, 1971), we can say that a significant part of the arctic theriofauna must have developed locally within the boundaries of Beringia and the subarctic zone. The origin of arctic and subarctic theriofaunas has also been discussed recently by Pidoplichko (1954), Shvarts (1963), Sher (1971), and Kuzmina (1977). Like earlier zoogeographers, these authors have concluded that the recent fauna of the Arctic is a heterogeneous aggregation consisting partly of endemics and partly of relatively late steppe colonists. This "steppe appearance" is especially well developed, as we shall see, in the late Pleistocene mammoth fauna.

The combined Pleistocene and Holocene mammal faunas of the Eurasian Arctic contain approximately 40 species, excluding the Pinnipedia and Cetacea (Table 1). The indicator species for the late Pleistocene mammoth fauna in arctic Siberia

include the mammoth (*Mammuthus primigenius*), Chersky horse (*Equus lenensis*), woolly rhinoceros (*Coelodonta antiquitatis*), reindeer (*Rangifer tarandus*), steppe bison (*Bison priscus*), Baikal yak (*Poepbagus mutus*), musk ox (*Ovibos moschatus*), saiga antelope (*Saiga tatarica*), bighorn sheep (*Ovis nivicola*), Pleistocene hare (*Lepus tanaiticus*), Kamchatka marmot (*Marmota camtschatica*), long-tailed souslik or ground squirrel (*Citellus parryi*), true lemmings (*Lemmus* spp.), hooped lemmings (*Dicrostonyx* spp.), narrow-skulled vole (*Microtus gregalis*), polar bear (*Thalarcos maritimus*), wolf (*Canis lupus*), arctic fox (*Alopex lagopus*), cave lion (*Panthera spelaea*), and wolverine (*Gulo gulo*). Most of these animals prefer open, treeless landscapes. Details of the morphological and ecological adaptations of most of these species are discussed below.

## EXTINCT SPECIES IN THE SIBERIAN ARCTIC

### Mammoth (*Mammuthus primigenius* Blumenbach, 1799)

*Geologic age and history of range.*—Tusks, teeth, bones, and skulls of mammoth are known from many hundreds of localities in all of the land-

scape zones of northern Eurasia. Occurrences range in age from middle Pleistocene (Riss) to Würm III and the beginning of the Holocene.

*Morphology.*—In body proportions and tooth structure, mammoths were closer to the Indian than to the African elephant. They were characterized by a cervical sinus, high withers, and a strongly sloping posterior. The ears were small, one-tenth to one-twelfth the size of those of the African elephant and one-fifth to one-sixth the size of those of the Indian elephant.

The woolly coat was thick, consisting of a fine underfur 15 or 16 cm long and guard hairs up to a meter in length. Hair hung in a long skirt-like mane from the dewlap and the abdomen. The trunk, ears, tail, and feet above the soles were completely covered with hair.

The tusks of old males were overdeveloped and weighed as much as 100 to 120 kg. They were 3.5 to 4.5 m long and curved upward and inward, ultimately crossing. The tusks of females were weaker, thinner, shorter, and straighter. The ends of the tusks began to wear down at the outer side when the animal was two or three years old. We have come across tusks that had been broken during the life of the animal and that eventually were abraded smooth again at the broken end. We have also seen tusks with what must have been very abnormal growths.

*Ecology.*—Only the summer feeding habits are known thus far (Ukrainitseva, 1979). The Beresovka mammoth from the Kolyma River basin (Hertz, 1902; Pfitzenmaier, 1939) (Fig. 1) fed on sedges, grasses, and mosses. The Shandrin mammoth (Vereshchagin, 1975) fed on cottongrass, sedges, and mosses, as well as willow, alder, and dwarf-birch twigs. Winter food probably consisted of dry grasses, supplemented with willow, birch, alder, and larch twigs. The report by the engineer Beckendorf (1900) that a mammoth stomach from the Indigirka River contained spruce needles is quite a mystery, because there has never been any spruce along the Indigirka. Very large individuals of mammoth would have required 200 to 300 kg of succulent feed daily, and they must have caused considerable damage to floodplain vegetation.

The pervasive grinding down of the ends of even the smallest tusks suggests that they may have been used for stripping bark from trees and for scraping ice off vertical surfaces. The broken and subsequently smoothed ends of some tusks

may be evidence that tusks were also used to break ice so that the animals could quench their thirst during dry and snowless winters.

No detailed fertility data are available, but the reproduction rate was probably lower than that of present-day elephants. Among the remains of some 140 mammoths excavated from the Berelekh "mammoth cemetery", 30% are juveniles 10 years old or less, and 2% are fetuses (Vereshchagin, 1977; Baryshnikov, et al., 1977).

Mammoths may have undertaken long seasonal migrations similar to those of African elephants. They probably made their way northward along the river valleys in spring, perhaps reaching the coast of the Arctic Ocean only in summer, and then probably moved southward for the winter.

*Landscapes and biotopes.*—Morphoecological data indicate that mammoths inhabited open landscapes of meadows and steppes with shrub thickets in the river valleys. Winters were probably extremely severe and cold with little snow and no watering places.

*Taphonomy.*—The largest concentrations of bone remains are observed in the ancient alluvium of broad river valleys. The carcasses of dead animals were carried by spring floods into the quiet water of larger rivers, where they became macerated. Some of the carcasses were deposited directly on the floodplains. Some mammoths died in landslides on hills and river banks, others became mired in mud, and still others fell into pits thawed into ground ice in the permafrost. Secondary anthropogenic burials of bones and skulls are characteristic of some Late Paleolithic encampments in European Russia and southern Siberia.

Whole carcasses and skeletons and partial skeletons with soft tissue attached have been preserved in permafrost in the tundra and forest zones of Siberia, especially in northern Yakutia. Most finds are between 11,000 and 45,000 years old. The latest find comes from the sharply cut valley of Kirgilyakh Creek near Susuman in the upper reaches of the Kolyma River basin (Shilo, et al., 1977). There, in 1977, a yearling mammoth that had starved to death some 40,000 years earlier was found buried in mud and rocky slope debris at the intersection of three ice wedges. An important discovery outside of our area was a skeleton with attached oil-soaked tissues and ligaments from the Staruni tar seeps in the eastern Carpathian Mountains of Poland (Niezabitowski, 1914a).

Table 1  
Composition of the Late Pleistocene and Recent  
Theriofaunas of the Eurasian Arctic

Orders	Number of Species			
	Known from their Fossil Remains			Known in Modern Fauna
	Total	Became Region- ally extinct	Survived the Pleistocene	
Insectivores	?	?	?	4
Duplicidentata (Lagomorpha)	2	1	1	2
Rodentia	7	2	5	12
Carnivora	7	1	6	7
Proboscidea	1	1	—	—
Perissodactyla	3	3	—	—
Arctiodactyla	7	5	2	3
TOTAL	27	13	14	28

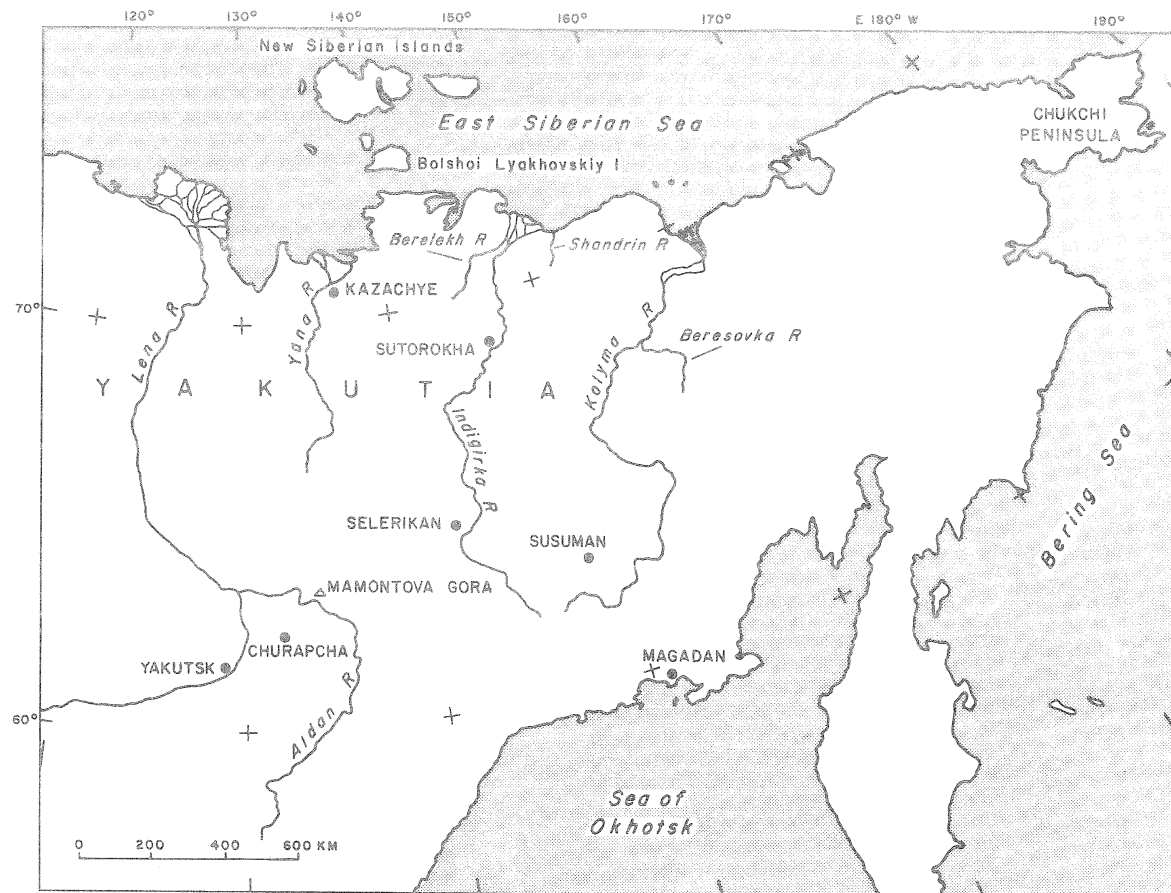


Figure 1. Northeastern Siberia showing places mentioned in the text

### Chersky Horse (*Equus lenensis* Rusanov, 1968)

**Geologic age and history of range.**—The Anthropogene (late Cenozoic) deposits of Arctic Eurasia have yielded three or four species of horses. The Chersky horse was present during the late Pleistocene and ranged over all of northeastern Siberia from the Taimyr to the Chukchi Peninsula. Extinction probably occurred at the beginning of the Holocene, although it has been suggested that a small population of wild horses may have survived in northern Yakutia until the historical epoch (Vereshchagin and Lazarev, 1977).

**Morphology.**—Judging from the 37,000-year-old frozen carcass of a stallion found at Selerikan in the Indigirka River basin, the Chersky horses were low (134 to 136 cm at the withers) but heavy (Lazarev, 1977a, b). The hooves were massive,

especially the front ones. The edges of the horny shoe-like ridge rimming the front hooves of the Selerikan stallion were noticeably worn down. Functionally, the Chersky horse occupied an intermediate position between draught animals and race horses.

The Selerikan stallion was a bay—i.e., coffee-brown with a dark streak running down the spine and a black mane and tail. The coat was thick and as much as 50 or 60 mm long on the sides.

The mummified remains of a pregnant mare have been found in frozen sediments in the Indigirka River basin (Garutt and Yurijev, 1966).

**Ecology.**—The stomach and intestines of the Selerikan horse contained herbaceous plants (90%), woody plants (5% to 7%), and mosses (1% or 2%). *Festuca*, a grass, and *Kobresia*, a sedge, predominated among the herbaceous plants; *Salix* (willow) and *Betula nana* (dwarf birch) twigs were

the principal woody plant materials; and remains of green *Polytrichum* and *Sphagnum* predominated among the mosses (Ukraitseva, 1979).

**Landscapes and biotopes.**—Judging from the habitat preferences of domestic Yakutian horses and the wild Przewalski horse, late Pleistocene Chersky horses must have preferred open country but could have entered sparse, light coniferous forests of larch and pine if the snow in winter were loose and not more than 50 or 60 cm deep.

**Tapponomy.**—Remains of Chersky horses are abundant in the alluvium of Siberian rivers and in redeposited lacustrine loess-like loams, as well as in loess of Sartan age. Frozen carcasses occur in silty rock detritus in small intermontane valleys, where the animals evidently perished in mudflows.

### Woolly Rhinoceros (*Coelodonta antiquitatis* Blumenbach, 1807)

**Geologic age and history of range.**—Bone remains, primarily of skull fragments of woolly rhinoceros are known from all of the landscape zones of northern Eurasia excepting the desert (Vereshchagin and Baryshnikov, 1980). Woolly rhinos first appear at the end of the middle Pleistocene in deposits of Riss age. No bone remains are known younger than the end of the Paleolithic.

**Morphology.**—The appearance and body proportions of the woolly rhinoceros were similar to those of the African white rhinoceros (*Diceros simus* Burchell, 1817), but differed, of course, in having a hairy coat. Short legs and hypertrophy of the horns were characteristic features, especially in the female. The front horn reached a length of 135 cm, and the posterior one, 50 cm. The woolly coat was soft and thick, dingy yellow and reddish-brown, and 10 or 15 cm long on the trunk. The ears were about three-quarters the size of those of the living species. The hooves had a small bearing surface, evidently an adaptation to firm, solid substrates.

**Ecology.**—Compressed woody remains of broadleaf species such as willow and alder and also mineral particles have been found in the deep alveoles of the upper teeth of the woolly rhinoceros. Lumps of excrement found in the area of the large intestine within the skeleton of a rhinoceros at Churapcha settlement in central Yakutia contained shoots of grasses, cottongrass, and sedges (Lazarev, 1977b). Pollen found in the

foeces consisted of Gramineae (89%), Compositae (4.5%), and *Artemisia* (2.5%). No data are available on their winter feeding habits, but it is quite clear that the woolly rhinoceros was predominantly a grazer (Garutt, et al., 1970).

Nothing is known of reproductive patterns.

**Landscapes and biotopes.**—The woolly rhinoceros probably inhabited open areas in the cold and snowless steppe-tundra. In valleys and river floodplains it probably kept to shrub thickets.

**Tapponomy.**—Floods killed many rhinos and buried some complete carcasses in river valleys. Carcasses and other remains were also buried in the petroleum seeps of Staruni in the Carpathian region (Niezabitowski, 1914b). Skin fragments have been found in the Nizhneudinsk Cave in the Sayan Mountains (Chersky, 1879). Rhinos are only a minor component of the faunal material found in Paleolithic camp sites and never exceed 3% of either the total number of bones or the minimum number of individual animals in the well-studied Paleolithic encampments of the Russian lowland.

### Steppe Bison (*Bison priscus* Bojanus, 1807)

**Geologic age and history of range.**—*Bison priscus* ranged over all of northern Eurasia and North America during middle and late Pleistocene time. Bison disappeared from the arctic zone of Eurasia at the end of the Pleistocene but persisted in the steppe zone until the Middle Ages.

**Morphology.**—*Bison priscus* was heavily built. The head was large and protected by massive horns. The animal stood high at the withers, but its posterior was relatively gracile. The hooves were small and adapted to a firm substrate.

The hairy coat was heavy and as long as 75 cm at the front of the trunk, furnishing protection against steppe winds (distribution of hair on the trunk of the recent European forest bison, *Bison bonasus*, is more uniform). The tail was short and covered with short hair. The coat on the carcass of a female *B. priscus* preserved in frozen ground at Sutorokha settlement on the Indigirka River was similar in color to that of a modern female Canadian forest bison (*Bison bison atabascae* Rhoads, 1897) (Flerow, 1977, 1979).

**Ecology.**—Recent bison are predominantly grazers. The hypsodont molars and the wide cochleariform incisors of *B. priscus* are similar to those

of modern bison and suggest that, like modern plains bison, *B. priscus* fed on coarse, dusty, steppe grasses. Modern bison migrate in herds numbering several hundreds or even thousands under pressure of summer droughts or snowy winters. This may also have been true of *B. priscus*.

Reproductive rates are low in the living American and European bison; the first calf is generally born only when the female reaches an age of two or three years. Interrupted growth bands on horn sheaths recovered from permafrost in north-eastern Siberia suggest that *B. priscus* females typically brought forth 11 or 12 calves during a lifetime.

*Landscapes and biotopes.*—*B. priscus* inhabited open steppes and arctic steppe-tundra landscapes characterized by thin winter snow cover. Present-day American bison inhabit prairies and also mixed prairie and taiga in southern Canada.

*Taphonomy.*—Recent European bison have been known to die because of excessive snow cover in the Beloyezhe Sanctuary and in the Caucasus, and bison in North America have perished during winter blizzards and periods of icy, crusted snow. Pleistocene *B. priscus* in the Arctic also died during snowstorms, during floods in river valleys, and by falling through thin ice. Carcasses and skeletons were then buried in oxbow lakes under layers of silt.

In the lowlands of Eurasia, bison remains are commonly found in loess and loess-like loam. The female carcass from Sutorokha settlement was buried in frozen loess-like loam. Articulated legs with skin and hair have also been found in water-laid loess and rock detritus at Kazachye village on the Yana River and Struyka Creek on the Indigirka (Flerow, 1977).

#### Yak (*Poepbagus mutus* Przewalski, 1883)

*Geologic age and history of range.*—The present-day range of yak is confined to Tibet. However, a related and probably ancestral species (*P. bunnelli* Frick, 1937; *P. baicalensis* N. Vereshchagin, 1955) has been encountered in the Pleistocene of the Kuznetsk Basin, the Altai, Transbaikalia, and central Yakutia in Siberia, and in the Fairbanks district of Alaska.

*Morphology.*—The wild Tibetan yak is the largest of the present-day wild cattle. Tibetan yaks have massive bodies, high withers, and relatively

short legs. They are covered with shaggy black hair and an abundance of underfur. Fluffy hair hangs almost to the ground from the legs, sides, and abdomen, enabling the animals to sleep on cold stones or snow. The tail, like that of a horse, is completely covered with long, coarse hair.

*Ecology.*—Recent yaks feed on herbaceous vegetation. In winter, they are capable of obtaining dry grass from beneath thin snow. Yaks forage alone or in groups of two or three. They visit watering places regularly in winter but can get along on snow if necessary.

Mating takes place in October and calving in June and July. The female gives birth to a single calf.

*Landscapes and biotopes.*—Yaks presently inhabit the rocky, treeless, semiarid, high-altitude landscapes of Tibet. Yaks reached Alaska during the Pleistocene by way of the treeless plateaus of northeastern Siberia.

*Taphonomy.*—Fossil yak remains have been discovered in cave deposits in the Altai Mountains. Yak bones are also sometimes encountered in lowland river alluvium. Yak remains in the Kuznetsk basin, and in Transbaikalia, come from colluvial slope debris.

#### Musk Ox (*Ovibos moschatus* Zimmermann, 1780)

*Geologic age and history of range.*—During middle and late Pleistocene time, musk oxen ranged throughout the Arctic, reaching England in the west, France and Moldavia in the south, and Alaska, Canada, and the northern conterminous United States in the east. Musk oxen probably survived until the historical period in northern Siberia and were present until the 19th century in Alaska. They are presently native to northern Greenland, part of northern mainland Canada, and the Canadian Arctic Archipelago. They were reintroduced to Nunivak Island, Alaska, during the 1930s, to several other places on the Alaskan mainland during the late 1960s, and to Taimyr Peninsula and Wrangel Island in Siberia during the 1970s.

*Morphology.*—Musk oxen have a thick-set body. Ears, neck, legs, and tail are very short. Hooves on the lateral second and fifth digits are small and high above the ground. Blood circulation in the legs is relatively sluggish, an adaptation to extremely cold winter temperatures.

Musk-ox fur is very thick; downy underfur 10 to 15 cm long comprises 60 to 80% of the coat. Guard hair on the chest and sides hangs almost to the ground, reaching a length of 60 to 90 cm. The fur is dark grayish-brown in winter and dark brown in summer.

*Ecology.*—Summer diet consists of meager shoots of grasses, sedges, cottongrass, willow, and dwarf birch. In winter, musk oxen feed on lichens, dry grass, and the twigs of shrubs. They are capable of securing food from beneath snow 15 or 20 cm deep, and remain quite fat at the end of winter. Because of their exceptional ability to utilize pasture economically, musk oxen do not migrate long distances.

Musk oxen can easily endure temperatures of  $-50^{\circ}$  to  $-60^{\circ}$ C. Their greatest threat is from deep snow, especially with an icy crust. A heavy snowfall can result in the death of all the young animals and of many adults.

Musk oxen live in small herds. Females calve once every two years. Yearling calves typically constitute 8% to 12% of Arctic herds.

*Landscapes and biotopes.*—Living musk oxen spend their winters in tundra areas on plateaus, among coastal dunes, and on rocky coastal slopes—places where snow is blown away by the winds. During the late Pleistocene, musk oxen inhabited lowland steppe-tundra landscapes.

*Taphonomy.*—In northeastern Siberia musk-ox remains are encountered in alluvial deposits of large rivers and in loess-like blanket loams. *Ovibos* is common in Late Paleolithic archaeological sites along the tributaries of the Dnieper and upper Don Rivers in the European part of the Soviet Union.

#### Saiga Antelope (*Saiga tatarica* Linnaeus, 1766)

*Geologic age and history of range.*—Fossil *Saiga tatarica* first appears in middle Pleistocene beds. The Pleistocene range of saiga extended westward to England and France, northward to the upper reaches of the Pechora River and the New Siberian Islands, northeastward to Alaska and coastal northwestern Canada, and southward to northern China and the Crimea. Northeastern Siberia and Alaska were inhabited by a northern subspecies, *Saiga tatarica borealis* Chersky, 1876 (= *S. ricei* Frick, 1937). *S. tatarica* is presently confined to the steppes and semiarid regions of the Kalmyk SSR, Kazakhstan, and Mongolia.

*Morphology.*—The saiga is a small, thin-legged antelope with a large head. It has a probosciform and gibbous snout with a large nasal cavity which is thought to function to remove dust from inhaled air and perhaps to warm this air during winter. The hooves are narrow, with small bearing surfaces, making them suitable only for very firm ground. The front hooves are considerably larger than the hind ones; this is evidently an adaptation for winter foraging beneath thin snow.

The color of its short summer fur is pale sandy yellow. Its winter fur is almost white and very thick, the staple up to 70 mm in length.

*Ecology.*—Saiga feed on steppe vegetation, predominantly on grasses and chenopods. They live in large herds, migrating seasonally in search of fresh forage or snow to quench thirst in winter. They are capable of running 60 or 70 km/hour.

Mating takes place in December. The female gives birth in May to two or, very rarely, three young.

Deep snow poses the greatest danger to saiga, and they die in large numbers during exceptionally snowy winters. Mass deaths also occur occasionally while saiga are crossing thin ice on rivers and lakes.

*Landscapes and biotopes.*—Recent saiga inhabit dry steppe lowlands and semiarid regions. They keep to flat country with firm, solid substrate, resolutely avoiding even slightly broken terrain. During the late Pleistocene, saiga inhabited the open expanses of steppe-tundra and steppe landscapes.

*Taphonomy.*—Fossil bones of *Saiga tatarica* are commonly found in the alluvium of lowland rivers. In Europe and the Crimea, they have been recovered from tar seeps and are commonly encountered in Pleistocene loam and in Paleolithic archaeological sites in river valleys and caves.

#### Cave Lion (*Panthera spelaea* Goldfuss, 1810)

*Geologic age and history of range.*—Bone remains of these lions have been found in much of northern Eurasia and North America. In Eurasia, they appear in Eopleistocene beds and disappear at the end of the late Pleistocene during Würm III, but small populations may have persisted into Holocene time in the Caucasus and in Tibet. Cave lion remains are known in North America only from deposits of Illinoian and Wisconsin age.

*Morphology.*—Cave lions were large, relatively long-legged cats similar in form to hybrids of tiger and lion. The opening of the internal nares is wider than in tigers, indicating a potential for powerful respiration and an ability to run short distances at high speeds (Vereshchagin, 1971).

Its winter fur was probably quite fluffy. It is unlikely that the cave lion had either a lion-like mane or a distinct tuft on its tail.

*Ecology.*—The cave lion was a eurytopic, cold-tolerant species which, like other members of the mammoth fauna, was poorly adapted to movement in deep snow. Prey, judging from the associated fauna, probably consisted of horses, donkeys, giant deer, red deer, reindeer, bison, aurochs, yak, musk oxen, sheep, goats, and saiga. Young mammoths and rhinoceroses were probably also attacked.

Reproductive patterns are unknown but probably were similar to those of other large cats, which produce two to four young per litter.

*Landscapes and biotopes.*—The cold steppe-tundra, forest-steppe, and gallery forests of river valleys would have been the usual habitat of cave lions. They ascended to altitudes of more than 2000 m and used caves as shelters.

*Tapponomy.*—Bones of *Panthera spelaea* are commonly found in caves and less commonly in alluvium, colluvium, and loess. They are also common in Paleolithic cave and valley occupation sites. Remains of cave lions are especially numerous in the tar seeps of southern California, where they are third in abundance after dire wolf and machairodont.

## SPECIES IN THE SIBERIAN ARCTIC THAT SURVIVED THE PLEISTOCENE

### Reindeer (*Rangifer tarandus* Linnaeus, 1758)

*Geologic age and history of range.*—The reindeer's fossil record begins in the early Pleistocene of Europe. During late Pleistocene time, its range extended westward to the British Isles and the Pyrenees, southward to the Alps and the Crimea, and eastward across Beringia to northeastern North America.

*Morphology.*—The reindeer is a medium-sized deer of moderately heavy build. Its eyes are large and vision is excellent. Reduction of the lower incisors is a distinctive dental feature.

Its feet are adapted for movement across compact snow and boggy surfaces. The phalanges are set wide apart, the lateral digits move apart freely, and the hooves are saucer-shaped. These adaptations enable reindeer to crater snow up to 80 cm deep to gain access to food (Formozov, 1946; Flerow, 1950).

Both males and females bear antlers through the winter. It is possible that antlers are used to keep competing individuals away from winter food.

The winter coat is very thick and impermeable to wind and snow during blizzards. Guard hairs are thick and brittle, with hollow medullary cells. The animals are light-colored in winter.

The antlers of taiga and forest reindeer are more weakly developed than those of tundra populations. Like moose, forest reindeer have relatively long legs, possibly as an adaptation to the loose, deep snow of the forest environment. Pleistocene antlers from Denmark and the Angara region of Siberia are similar to those of modern tundra reindeer (Yermolova, 1978). The late Pleistocene reindeer of Eurasia have, compared with modern reindeer, relatively short legs with digits set wider apart, and more flattened and widened hooves (Kuzmina, 1971).

*Ecology.*—A number of adaptations (the large eyes and excellent vision, the structure of the metatarsus, the ability to feed on lichens, and the strong herd instinct) have made reindeer well adapted to life in open, treeless spaces where the snow is not too deep. The great mobility and endurance of these animals enables them to undertake long seasonal cross-country migrations.

Reindeer feed on grass and semishrubs in summer and on reindeer lichen which they dig from under the snow in winter. Occasionally they feed on lemmings, voles, and birds' eggs. Forest reindeer also consume tree lichens. C. C. Flerow (1935) postulated that Pleistocene reindeer also fed on steppe grasses, and that the partial reduction of the lower incisors occurred during Holocene time in response to a softer diet.

The reproductive cycle is similar to that of other subarctic deer. Mating takes place in September, and single or twin calves are born in June.

*Landscapes and biotopes.*—Reindeer now prefer sparse coniferous forests and moss bogs in the taiga zone and moss-lichen vegetation in the tundra zone. In June, they migrate to the shores of the Arctic Ocean for relief from mosquitoes and flies. At the end of August, they begin the migration to the forest-tundra for winter feeding on reindeer-lichen pasture. During the Pleistocene, reindeer evidently inhabited open, tundra-like landscapes.

*Tapponomy.*—The largest concentrations of reindeer remains are found in loess and loess-like loam associated with Late Paleolithic encampments. Bones and antlers of *Rangifer tarandus* are constantly encountered in northern Eurasia (though never abundantly), in alluvium, hillside colluvium, peat, and other perennially frozen sediments.

### Long-tailed Souslik or Ground Squirrel (*Citellus parryi* Richardson, 1827)

*Geologic age and history of range.*—The present-day range of the souslik covers the tundra, forest-tundra, and northern forest zones of northeastern Siberia, Alaska, and Canada. Three mummified carcasses of *Citellus glacialis*, a related species which inhabited Beringia probably during late Pleistocene time, have been found at a depth of 12.5 m in permafrost in the Dirin-Yuryakh River valley (not shown on Fig. 1) in the Indigirka basin (Vinogradov, 1948). Skeletal remains of late Pleistocene sousliks are also known from the northern part of the maritime lowland of Yakutia and from Bolshoi Lyakhovsky Island.

*Morphology.*—The long-tailed is the largest of the Paleoarctic sousliks. Summer pelage is a distinctly spotted brownish-ocher on the body; the head is darker, and the winter coat is lighter. Pleistocene sousliks were larger, and their tails were shorter.

*Ecology.*—Present-day sousliks feed on grass, berries, mushrooms, green mosses, insects, and the flesh of vertebrates. Mating takes place in spring, and 10 or 12 young are born in each litter.

*Landscapes and biotopes.*—In the lowland tundra and forest-tundra of Yakutia, sousliks are found in areas where the soil thaws deeply in the dry meadow and steppe segments of south-facing hill slopes and river valleys. Here they excavate their holes and go into winter hibernation.

Some behavioral traits of long-tailed sousliks are unique among tundra mammals. That they burrow deeply, hibernate in winter, and restrict themselves to a few local biotopes are indications of the relict nature of this species in the Arctic and Subarctic.

*Tapponomy.*—Bones of sousliks are encountered in loess and washed silts. The frozen carcasses found by Vinogradov (1948) bore winter fur, and their pose was typical of hibernating animals, indicating that they must have died in their nesting chambers.

### True Lemmings (Genus *Lemmus* Link, 1795)

*Geologic age and history of range.*—Two recent species, *Lemmus* Linnaeus, 1758 and *L. sibiricus* Kerr, 1792 (= *L. obensis* Grants, 1827) inhabit the lowland and mountain tundra and forest-tundra of the Holarctic. A third, *L. amurensis* Vinogradov, 1924, lives in open spaces in the forest zone of eastern Siberia. Lemming remains are found in Pleistocene deposits in central France, Czechoslovakia, the Ukraine, and the Altai Mountains, far south of their present-day range.

*Morphology.*—Lemmings are medium-sized voles with very short tails and small ears concealed by fur. The winter coat is fluffy and up to 22 mm in length. The soles of the feet are covered with hair. Siberian lemmings turn a lighter color as winter approaches, but only the lemmings of the New Siberian Islands turn pure white (Ognev, 1948).

*Ecology.*—Siberian lemmings live in colonies and excavate shallow tunnels. They feed on the common species of sedges and cottongrasses. In summer, they also consume berries, mushrooms, mosses, and the bark of shrubs. They are active during winter, burrowing under the snow in search of food. They may even reproduce during winter.

Abrupt population fluctuations characterize Siberian lemmings. Spontaneous mass migrations of the young are a characteristic phenomenon in stress situations (e.g., flooding or freezing of their tunnels).

*Landscapes and biotopes.*—Lemmings are typical rodents of the present-day tundra. They prefer swampy areas with herbaceous vegetation and a moss cover or hummocky moss and sedge marshes along lakeshores. Arctic lemmings have adapted to

life in the moss and turf stratum of the tundra where air and soil temperatures are low, permafrost is shallow, and snow is present during winter. Their ancestors probably inhabited forest swamps, shrubby sphagnum bogs, and sparse taiga, as does the present-day Amur lemming (*L. amurensis*). With the disappearance of the forests and the formation of open tundra landscapes, lemmings began to inhabit marshy tundra biotopes in periglacial regions.

*Taphonomy.*—Lemming remains are preserved in caves and in river alluvium.

### Hoofed or Collared Lemming (Genus *Dicrostonyx* Gloger, 1841)

*Geologic age and history of range.*—The hoofed lemming lineage has been characterized by rapid evolution during late Cenozoic time. *Praedicrostonyx* (Guthrie and Matthews, 1971), the early Pleistocene ancestral genus, is known from western Europe, northeastern Siberia, and Alaska, and evidently dispersed throughout circumpolar regions during periods of cooling (Gromov and Polyakov, 1977). *Dicrostonyx* remains are found in late Pleistocene deposits in the foothill and lowland areas of Eurasia as far south as France, the Ukraine, the Altai foothills, and central Yakutia. Recent *Dicrostonyx* species have a Holarctic distribution in tundra and forest-tundra, extending even to islands in the Arctic Ocean.

*Morphology.*—Hoofed lemmings are medium-sized voles characterized by a short, hairy tail and small external ears in the form of skin folds. The summer fur of the Siberian hoofed lemming (*D. torquatus* Pallas, 1779) is brownish-gray. The winter fur is snow-white and clearly differentiated into underfur and guard hair that may be as long as 20 mm. The soles of the feet are thickly covered with hair. As winter approaches, the claws on the front feet enlarge rapidly, acquiring the form of small, sharp hooves which enable the animal to dig runways at the soil surface in dense snow.

*Ecology.*—Siberian hoofed lemmings feed predominantly on the shoots, leaves, and bark of dwarf birch and willow shrubs, as well as cloud-berry and crowberry. They bring forth several litters of four to six young each year. Population fluctuations and the consequent migrations are not as pronounced in *Dicrostonyx* as in *Lemmus*.

*Landscapes and biotopes.*—Hoofed lemmings

prefer the dry, elevated, well-drained parts of the tundra. They excavate their tunnels under stones, in crevices, and in hummocks.

Their morphophysiological adaptations indicate that they evolved in cold, dry, open, tundra-like landscapes in which permafrost was present and winter snow was dense and long-lasting.

*Taphonomy.*—Remains of *Dicrostonyx* are commonly encountered in owl scats in Pleistocene caves and in ancient river alluvium.

### Narrow-Skulled Vole (*Microtus gregalis* Pallas, 1778)

*Geologic age and history of range.*—Fossil remains of this species are known from deposits as old as middle Pleistocene. During the late Pleistocene, its southern range extended to France and to the upper reaches of the Don River. Five frozen mummified carcasses were found in late Pleistocene deposits approximately 37,000 years old in the Dirin-Yuryakh River valley in the Indigirka basin (not shown on Fig. 1).

*Morphology.*—Narrow-skulled voles show clearly defined adaptations for burrowing, i.e., a narrow skull and shortened limbs. Their winter fur is thick and up to 22 mm in length. The coats of recent narrow-skulled voles vary from light ocher to dark grayish-brown in summer, turning white as winter approaches. The coats of the frozen fossil *M. g. egorovi* Fejgin from the Dirin-Yuryakh River valley (Gromov and Polyakov, 1977) were brownish-rust colored as a result of melanin pigment breakdown after death.

*Ecology.*—*Microtus gregalis* prefers legumes and grasses but in the Arctic feeds mainly on sedges, cottongrass, and prostrate willows. Grass fodder is stored for winter. These animals excavate complex runways under the snow at the ground surface. In the northern part of their range, they begin to reproduce at the end of June, giving birth to as many as three litters of nine offspring each year.

*Landscapes and biotopes.*—Narrow-skulled voles inhabit open landscapes ranging in character from semiarid steppes to lowland and mountain tundra and alpine meadows. They also inhabit meadow glades in the forest zone and in the alpine forest belt and are found in river valleys and along the shores of lakes in the tundra.

*Taphonomy.*—The bones of these animals are commonly encountered in the Pleistocene alluvi-

um of Siberian rivers. They have also been recovered from bituminous loam near Karmalka in the Tatar SSR.

### Arctic Fox (*Alopex lagopus* Linnaeus, 1758)

*Geologic age and history of range.*—Fossil remains of this animal are common in Quaternary deposits as old as late Riss. During late Pleistocene time, the Eurasian range of the arctic fox extended southward to France, Rumania, and the Crimea, Altai, and Baikal regions. They presently inhabit the tundra and forest-tundra of the Holarctic.

*External form.*—These small foxes have short legs and small ears. Pelage is grayish in summer and turns white in winter. The winter fur has long, soft guard hairs and a very dense underfur. The soles of the feet are covered with long, thick hair.

*Ecology.*—The arctic fox is ecologically similar to the steppe fox (*Vulpes corsac* Linnaeus). It is omnivorous, but its basic diet generally consists of lemmings and voles. Shelter is a hole in a gully slope. At the end of May or in June, the females bring forth 8 to 12 and sometimes as many as 20 pups; these develop more rapidly than do red-fox pups. Populations vary greatly from one year to another.

*Landscapes and biotopes.*—Arctic foxes presently inhabit open tundra areas. In winter, some follow the polar bears far northward over the ice of the Polar Basin. Others move southward to the forest zone, especially when lemmings are scarce. Arctic fox are poorly adapted for movement over loose forest snow, however. Those reaching the southern part of the forest zone are unable to return and die of hunger.

*Taphonomy.*—Fossil remains of Pleistocene arctic fox are common in alluvium. They are especially common in Paleolithic caves and occupation sites.

## HABITAT OF THE MAMMOTH FAUNA

Having examined the species composition, functional morphology, and ecological requirements of the species comprising the mammoth faunal complex, we can now reconstruct with considerable confidence the ecological situation in the Arctic during the Wurmian-Sartanian-Wisconsin

cold period. A comparison of the Pleistocene with the living arctic fauna leads to the following conclusions:

A climate colder and drier than that of the present is indicated by the density and form of the thick woolly coats of the mammoth, rhinoceros, horse, bison, musk ox, and yak. The pelts of all these animals had skirt-like fringes that would have been susceptible to a lethal wetting and freezing in cold, damp, maritime climates with frequent cycles of freezing and thawing. The fur of those mammals that have persisted in the Arctic to the present time—the lemmings, the arctic foxes, the reindeer and the bighorn sheep—is quite different in structure. Further proof of the severity of the late Pleistocene arctic climate is to be seen in the greater stature but smaller ears and tails of many late Pleistocene species compared with those of their living descendants.

That soils were generally firm and dry is indicated by the prevalence of fast-moving cursorial species such as horse, bison, and saiga antelope, by the relatively small hooves of many of the ungulates, and by the wide distribution of deep burrowers among the smaller animals. At present the soil thaws only to depths of 28 to 30 cm beneath the moss cover of lowland tundra at 70°N latitude in Yakutia. It could hardly have thawed more deeply under a grass cover during late Pleistocene time, but the ground must have remained firm and dry and swampy areas must have been at a minimum<sup>3</sup>. Areas of deeper thaw must have been present, however: sousliks, marmots, arctic foxes, and wolves now den either on south-facing slopes where the ground thaws and dries to depths of 60 or 70 cm or in the sandy alluvium of floodplains where the soil thaws to depths of 100 to 120 cm.

The snow cover was generally thin, and flat areas were probably blown bare by winter winds, making dried vegetation available to mammoths and ungulates during winter. A complete absence of snow during some severe winters seems to have

<sup>3</sup>If soils were drier, as they seem to have been, depths of seasonal thaw may have been much greater during late Wisconsin time than during the Holocene. Because of the greater heat capacity of wet soils and because large amounts of heat are required to thaw segregated ice, the depth of thaw in a given summer temperature regime is much greater in dry than in wet frozen soils.—*Eids*.

forced the large mammals to obtain ice from rock crevices and from vertical ice walls or else to migrate to other regions in search of snow and unfrozen springs.

The vegetation inhabited by the mammoth fauna can be shown to have consisted of open steppe on the watersheds and gallery forest and shrub thickets in the valleys. Most of the species comprising the mammoth fauna, including the mammoth itself, horse, rhinoceros, northern saiga, Baikal yak, bison, bighorn sheep, musk ox, long-tailed souslik, marmot, and cave lion, are or were inhabitants of open landscapes. Grasses predominated in the diet of the mammoths and of most of the ungulates. The patchy modern distribution of some of the small mammals, notably the long-tailed souslik and the Kamchatka marmot, and their occurrence in relict areas of steppe vegetation is further evidence that Arctic landscapes were once extensive steppe lands.

There seems to be a strong case for high biological productivity in the unglaciated Arctic during late Pleistocene time. The abundance of bone remains of mammoths, ungulates, rodents, and carnivores in the Quaternary deposits of northern Siberia seems in itself to indicate a high level of productivity for the plant associations of the late Pleistocene. Admittedly, an alternate explanation might be that bones as well as soft tissues are simply preserved better and occur more commonly in permafrost than in places where the ground has long remained unfrozen. However, high productivity for a possible modern analog of the Pleistocene steppe-tundra has been established by Tomirdiario (1972), who reports hay yields of 4000 to 5000 kg per hectare in the grass and mixed-herb vegetation of the *alas* meadows which occupy drained Siberian tundra lakes for 15 or 20 years until superseded by mosses and sedges.

#### FACTORS IN THE EXTINCTION OR SURVIVAL OF ELEMENTS OF THE MAMMOTH FAUNA

Deaths due to old age or accidents associated with unfavorable weather conditions such as storms, glazed frost, snowless winters, floods, and other stress situations should not be confused with extinction. Extinction, as a rule, is a lengthy process associated with a low reproductive rate and a

death rate that exceeds the natural increase of the population. Lacking statistics, we must limit ourselves to an analysis of environmental factors that were detrimental to some species but had little effect on others.

Bone remains of the large mammals comprising the mammoth fauna are scattered diffusely in loess, loess-like clayey loam, marine and lacustrine mud, and fluvial sand in the vast tundra regions of Siberia. Mass "burial grounds" containing thousands of bones representing hundreds of individual animals are rare and generally represent fluvial reconcentrations in oxbow lakes in river valleys and deltas (Vereshchagin, 1974, 1977, 1979).

Radiocarbon dates on bones and soft tissue point to the occurrence of two intervals of intensive animal destruction, 45,000 to 38,000 and 12,000 to 10,000 years ago (Vereshchagin, 1972; Orlova, 1979); these intervals coincide with the warmest phase of the Kargin Interstade, 42,000 to 37,000 years ago, and the end of the Sartan Glaciation, 11,000 to 10,000 years ago (Kind, 1973). The warm intervals of the Pleistocene saw an increase in winter precipitation, depth and looseness of snow cover, frequency of winter thaw, depth to permafrost, and abundance of lakes and swampy areas in the Arctic. Forests spread to the shores of the Arctic Ocean, and the extent of areas of herbaceous vegetation diminished drastically (Ukrainitseva, 1979). This habitat deterioration led to an increase in mortality among the large mammals. A change in the quality of the diet is indicated by study of stomach contents of frozen carcasses: the food consumed by mammoths and ungulates began to consist predominantly of wet-ground plants such as sedges, cottongrass, sphagnum, and green mosses—plants that are nutritionally inferior to the plants of dry habitats and the mixed herb cover of meadows (Ukrainitseva, 1979).

Climatic warming and humidification were detrimental to the mammoth and to several other species, and their populations evidently diminished drastically in northern Siberia during the Kargin Interstade. The increase in the role of herbaceous communities during the Sartanian cooling created better conditions for the mammoth and its associated species, but their numbers were already so diminished that mammoth and rhinoceros became extinct; horse, bison, saiga, yak, and lion disappeared from Arctic regions, and musk ox disappeared from Eurasia.

Reindeer, bighorn sheep, lemmings, narrow-skulled voles, arctic fox, polar bear, and a number of other species successfully survived the shocks of late Pleistocene environmental changes and have survived into the Holocene Arctic, either because of their capacity to undertake long seasonal migrations or because high reproductive rates and morphofunctional adaptations enabled them to cope successfully with deep snow. Finally, the sousliks and marmots have been preserved as Pleistocene

relicts on small, persisting patches of steppe-tundra.

It is natural to ask whether the former productivity of the Eurasian Arctic could be restored and an abundance of ungulates once more maintained through the aid of artificial cultivation of the primary biomass and reintroduction of horse, bison, and musk ox. The answer probably must be no as long as the present climate persists and until a new glacial epoch sets in.