an increased percentage of grass. One can conclude that there were a number of possible forces, aside from man, already present in the north that could have produced and maintained a grassland.

There are several grassland environments of limited extent in interior Alaska now. These have had a history of numerous fires and are subjected to winds far greater than average for interior Alaska. Interestingly enough, some of these are also areas where bison have been successfully reintroduced, but even after thirty-seven years, the bison have not expanded their distribution beyond the confines of these restricted grassland environments.

Rather than assuming a grassland in interior Alaska, one might postulate that the fossil animals being called grazers are not. But in the case of the horse and bison there is little room for doubt, although certainly all grazers rely on other herbaceous plants at times. The extant bison herds in the North (those reintroduced into Alaska and the indigenous herd in the Great Slave Lake area in northern Canada) and the once-existing feral horses in the Delta River, Alaska, area, utilized—and have been restricted to—limited grassland habitats. Pollen analyses of stomach contents of the frozen fossil mammoths have produced over 97 percent grass pollen (Tikhomirov 1958). That the mammoth was apparently more of a grazer than the modern elephant is indicated by the differences in tooth complexity. Studies of the food habits of modern wapiti (*Cervus elaphus*) (Murie 1951) also necessitate the classification of wapiti as primarily grazers, although they frequently shift to other plants during parts of the year. Wapiti, caribou, and musk-ox (*Ovibos*) are actually intermediate between browsers and grazers, but wapiti tend more toward the grazers and the living musk-ox more toward the browser preferences. Caribou also eat much grass, but are not generally classified as grazers. Although the saiga antelope feeds on a number of plants, grass is the major part of its diet also (Bannikow 1963). Sheep are almost strictly grazers.

Another possible explanation of the high percentage of fossil grazers is that the preservation biases favored the grazing forms. Quite to the contrary, the areas of deposition—the valley bottoms—were the habitat most likely to be occupied by one of the dominant elements of the modern fauna—the moose (*Alces*). Moose are as large boned (particularly the appendages) and would be just as likely to be preserved as either horse or bison, yet moose are one of the least common ungulates in the fossil assemblage. The woodland musk-ox, *Symbos*, is also rather rare in the collections. Apparently this genus was preferentially associated with a woodland situation (Semken et al. 1964) and, like *Alces*, could be expected to be rare in a grassland environment.

One of the chief limiting factors to grazers in the north during the winter is the condition of the snow. Flerow (1952), for example, states that snow line seems to be the most important factor influencing the northern perimeter of wapiti distribution. Depth and hardness seem to be the two main variables. If winter precipitation was less in the Alaskan refugium, as some suggest (Hopkins 1959), winter kill might not have been the obstacle to survival that it sometimes is today.

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A PALAEOENVIRONMENTAL RECONSTRUCTION OF THE "MAMMOTH EPOCH" OF SIBERIA*

Valentina V. Ukraintseva, Larry D. Agenbroad, and Jim I. Mead

The discovery and analyses of frozen carcasses of Siberian herbivores, ranging in radiocarbon ages from 9730 ± 100 to 53,170 ± 880 BP (Table 2–6), provide reconstructions of the vegetative cover and palaeoenvironment of the late Pleistocene and early Holocene "Mammoth Epoch" of Siberia. Analyses of the stomach and/or intestinal contents, as well as the enclosing sediments, serve as a contrast and comparison to the modern environments at the discovery sites. Six mammoths, one bison, and one horse (Fig. 2–31) provide the faunal basis for the botanical analyses of the ingested vegetation. The enclosing sediments provide a cross-check, and both ancient data sets are contrasted with modern environmental information.

Frozen fauna from the late Pleistocene of Siberia have been documented for more than 100 years (Chersky 1891, Pavlova 1910, Popov 1948, Sher 1971, Vereshchagin 1981, Lazarev 1982). More than fifty complete, or nearly complete, frozen speci-

*Adapted from *Vegetation Cover and Environment of the "Mammoth Epoch" in Siberia* by V. V. Ukraintseva. 1993. L. Agenbroad, J. Mead, and R. H. Hevly, eds. Published by The Mammoth Site of Hot Springs, South Dakota.

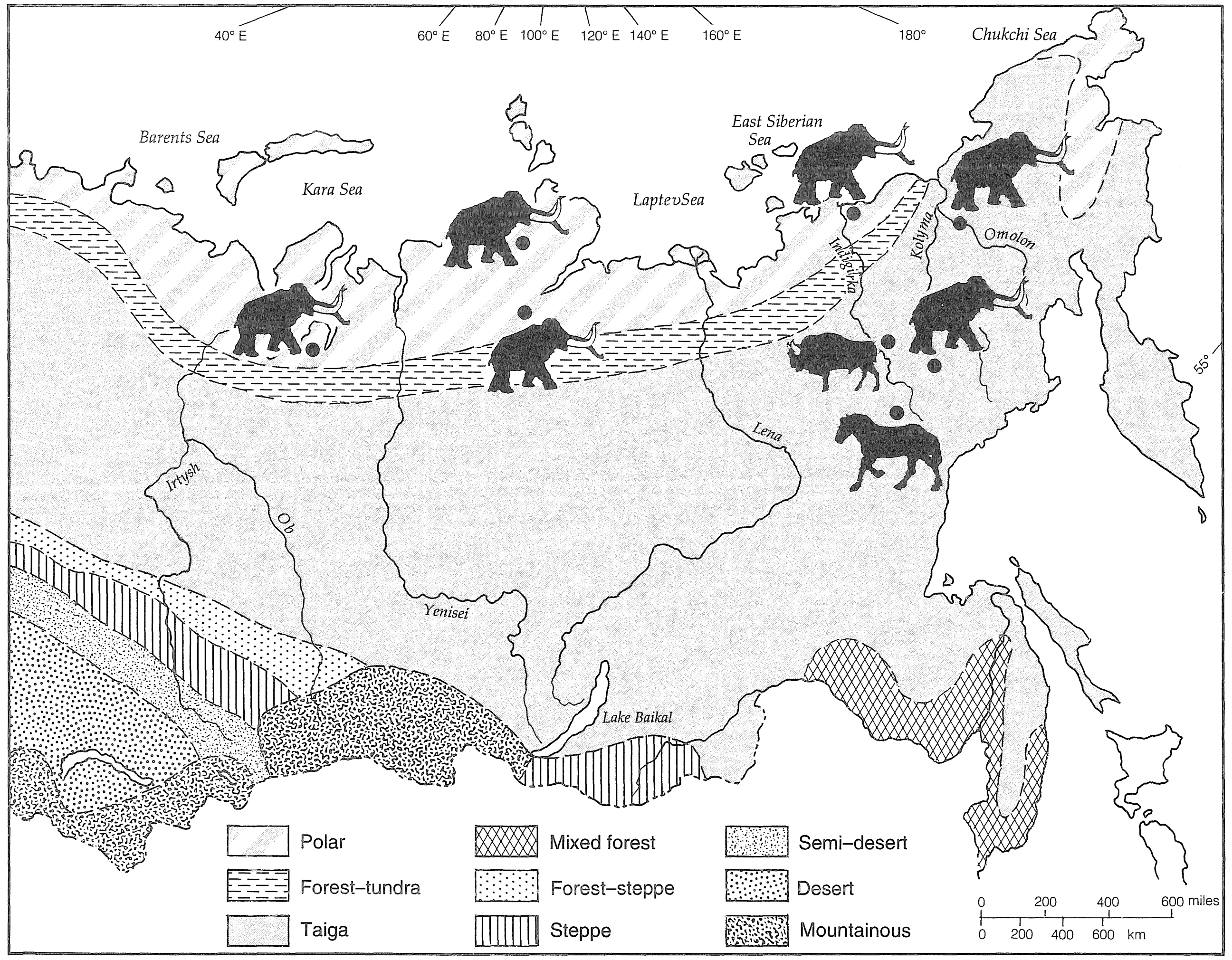


Figure 2–31 Map of Siberia, showing major vegetation zones and the locations of the fossil discoveries.

mens have been recovered. Rare instances provide frozen carcasses with well-preserved gastrointestinal tracts filled with plant matter reflecting vegetative conditions that were present in that area at the time of the animal's death.

Attempts at examination of food remains from fossil animals began as early as 1849, when investigators such as Brandt, Meyer, Marklin, and Schmalgausen analyzed plant remains stuck in the teeth of a woolly rhinoceros discovered on the Vilyuy River in Yakutia. The possibility of investigating vegetation from frozen gastrointestinal tracts began with the discovery of the Berezovka mammoth in 1900. Analyses of the plant materials from this discovery were undertaken by several investigators (Sukachev, Gerz, Szafer, Tikhomirov, Popov, Zaklinskaya, Zenkova, Savich-Lyubikkaya, Abramova, Kupriyanova, and others) between 1900 and 1960. In addition to the gastrointestinal plant remains, studies of the enclosing stratigraphic units were also undertaken. Similar studies on other specimens revealed that pollen and spores were also well preserved and recognizable.

In the period 1968–1973, several well-preserved specimens of horse, bison, and mammoth were discovered. The gastrointestinal contents, as well as

Table 2–6 Radiometric Chronology of the Mammoth Fauna from Siberia, Some of Which Provided Associated Gastrointestinal Remains

	Indigirka River Basin (Eastern Siberia)	
Shandrin Mammoth (5)	Shandrin River, tributary to lower Indigirka River	40,350 ± 880
Mammoth	Berelekh River, left tributary of the Indigirka River	39,590 ± 870 13,700 ± 400 12,240 ± 160 11,830 ± 110
Selerikhan Horse (3)	Selerikhan gold mine, upper Indigirka River (on Balkhan Creek)	38,590 ± 1120
Mylakhchin Bison (4)	Middle Indigirka River	29,500 ± 1000
	Kolyma River Basin (Eastern Siberia)	
"Dima" Mammoth (6)	Kirgilyakh Creek, left tributary of the Kolyma River	41,000 ± 1100
Mammoth (1)	Berezovka River	44,000 ± 3500
	Khatanga River Basin (Western Siberia)	
Vereshchagin's Mammoth (7)	Bolshaya Lesnaya Rassokha, right tributary of the Novaya River	53,170
*Mammoth	Terekhtiyk River	44,540 ± 1840 44,170 ± 1870
*Taimyr Mammoth (2)	Mamontovaya River	11,450 ± 450
*Yuribey Mammoth (8)	Yuribey River, Gydan Peninsula	10,000 ± 70 9730 ± 100

*No plant remains within the gastrointestinal tract.

the enclosing sediments, were examined for palaeovegetational clues. In 1973 a program of botanical studies of fossil fauna was initiated by B. A. Tikhomirov and V. V. Ukraintseva. This program included the following steps: (1) macrovegetation analysis of the gastrointestinal tract; (2) carpological analyses of the material; (3) palynological analyses of various portions of the tract; and (4) radiocarbon dating of the remains. Geological and botanical investigations of the burial sites were also taken, where feasible, making the investigations multidisciplinary in nature. These combined data allowed a vegetational reconstruction for the period in which the animal lived (and died). This also provided a data base for the characteristics necessary for a palaeoclimatic reconstruction of the burial site.

The results of many of these investigations were issued in Russian in many publications of limited distribution. Little of these data were available to a non-Russian audience. Dr. Ukraintseva undertook the task of summarizing earlier reports, as well as her own research, in an English-language version of these investigations. In addition to synthesizing the ecological information amassed in the period 1900–1979, Dr. Ukraintseva used these data in an attempt to explain the cause of extinction of some members of the fauna of the late Pleistocene "Mammoth Epoch" of Siberia.

Of the late Pleistocene fossil animals depicted in Figure 2–31 and Table 2–6, analyses of the gastrointestinal contents of six of these animals (four mammoths, one horse, and one bison) was possible. The gastrointestinal contents are interpreted as vegetation taken in by the animals shortly prior to their

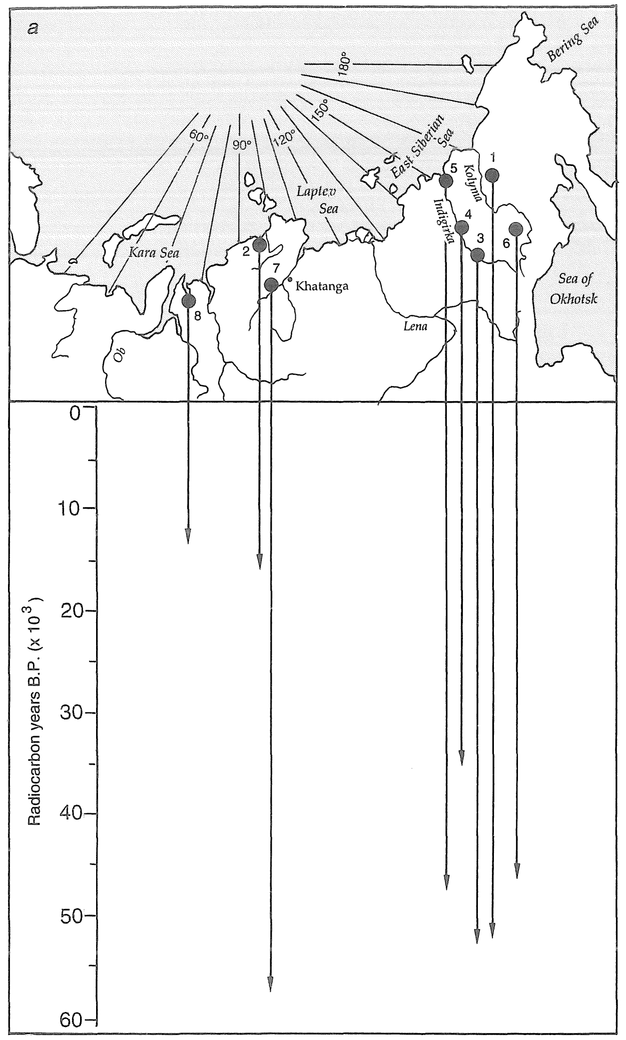


Figure 2–32a Locations of frozen carcasses and skeletons of animals which perished in Siberia in the Pleistocene and early Holocene. Arrows designate their radiocarbon dates; date of discovery in parentheses. *(1)* Mammoth, Berezovka River (1900); *(2)* Taimyr Mammoth, Mamontovaya River (1948); *(3)* Horse, Elga River (Selerikhan Creek) (1968); *(4)* Bison, middle Indigirka River (1971); *(5)* Mammoth, Shandrin River (1971); *(6)* Mammoth ("Dima"), Kirgilyakh Creek (1977); *(7)* Vereshchagin's Mammoth, Bolshaya Lesnaya Rassokha River (1978); *(8)* Yuribey Mammoth, Yuribey River Valley (1979).

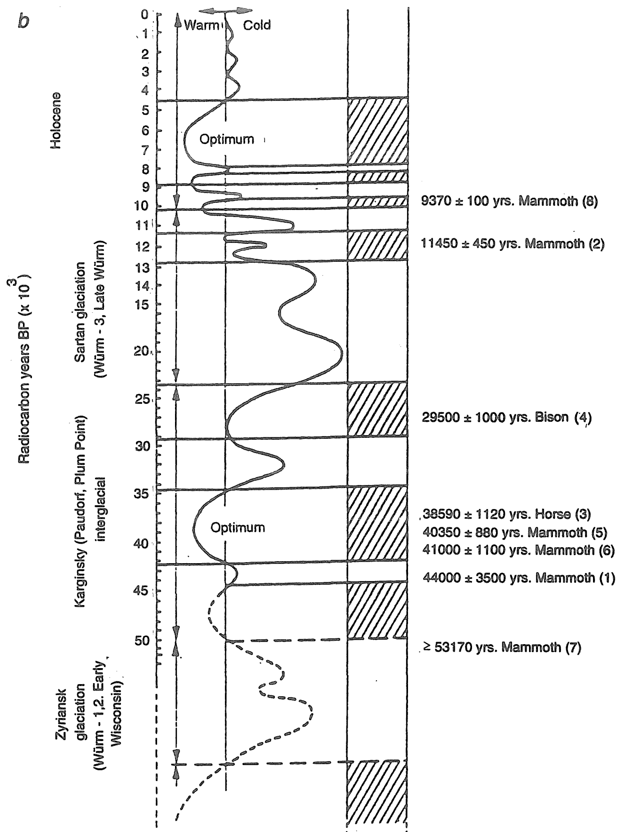
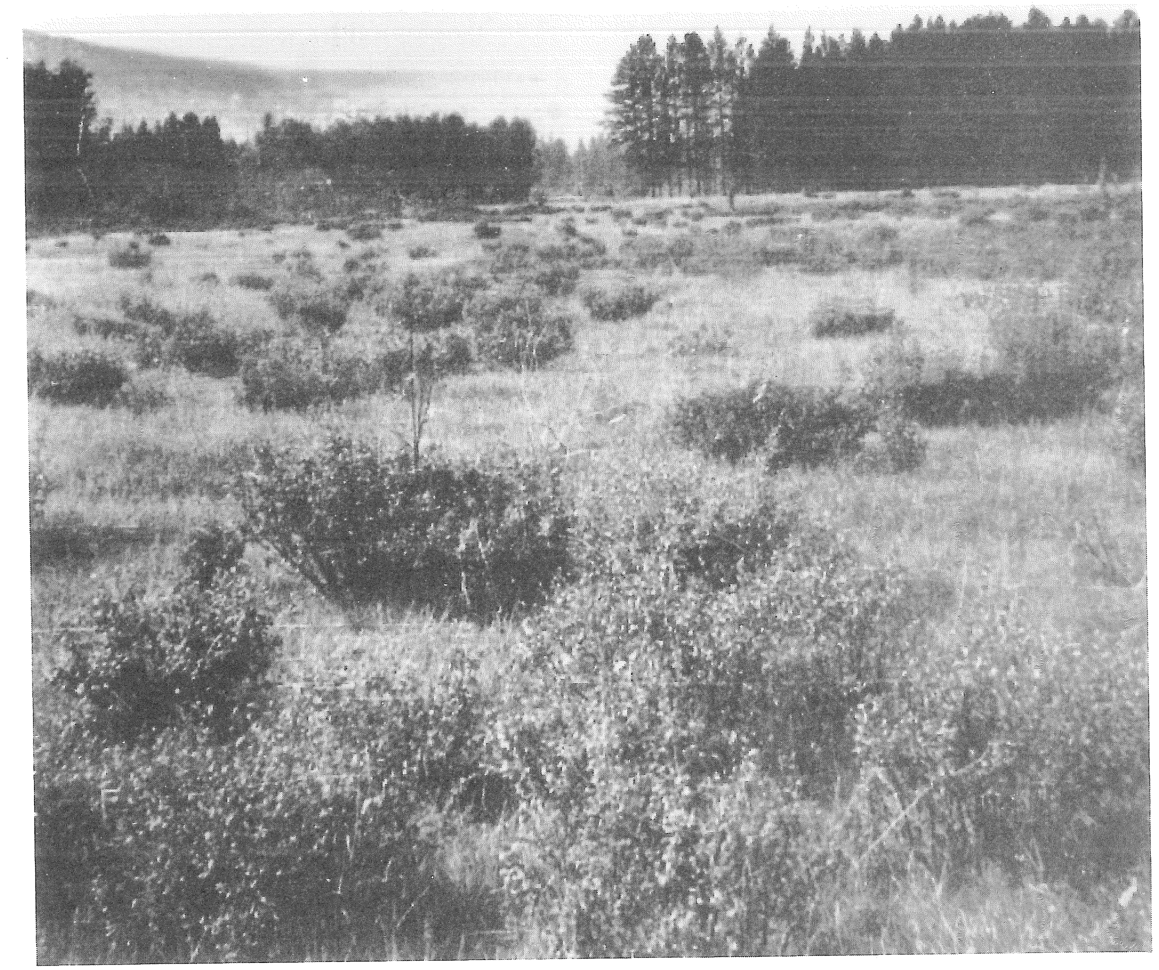


Figure 2–32b Schematic displaying the causes of relatively fast extinction of mammoth and some of its associates. Warm intervals are shown by hachures; ^{14}C dates of death of some representatives of the faunal complex are designated by numbers.

death and burial. Therefore, they represent unique samples of the vegetation existing at a time and place just before the animal's death. Each of the fossil floras represented has a "core" flora of plant species which still grow in the area of the fossil locality. They also contain a "zonal" component which is comprised of flora peculiar to, and distinct to, the discovery area at the time of sampling.

Synopsis of Fossil Localities and Their Analyses

Vereshchagin (Khatanga) Mammoth The head with trunk and tusks, a femur, crus, and foot, plus hide, ligaments, and two ribs were found on the west bank of the Bolshaya Lesnaya Rassokha River in 1977 (Vereshchagin and Nikolaev 1981) (Fig.



Vicinity of Bolshoi Selerikhan River. Larch taiga association. (*Photo courtesy of N. V. Lovelius.*)

2–32*a* [7]). The remains were found in permafrost sand 105 cm above a peat bed. The locality is presently in a shrub tundra.

At the time of death (±53,000 BP), the area was a meadow-like grass-forb community with sedge-grass communities near the river. Pollen gives evidence of cold conditions resulting in a polar-desert flora prior to the animal's death. Postmortem conditions created polygonal bogs and peat with invasion of larch forests.

Kirgilyakh Mammoth ("Dima") Gold miners found the remains of the baby mammoth, "Dima," on a tributary of the Berelekh River in 1977 (Shilo et al. 1983) (Fig. 2–32*a* [6]). The remains were unusually complete and well preserved and allowed anatomical and biochemical studies.

The site is in the Upper Kolyma highlands, which currently have a sparse larch forest with a birch-alder-mountain pine understory. At the time of the animal's death (±41,000 to 40,000 BP), the environment was very similar to the present one, with sparse larch forests in river valleys and moist to dry tundra upland communities. Sedge marshes and meadows occupied the floodplain.

Pollen analyses suggest a warming period at about 38,000 BP in which tundras and herb communities decreased and larch forests spread.

Shandrin Mammoth A mammoth skull and tusks were found on the east bank of the Shandrin River in 1972 (Fig. 2–32*a* [5]). Excavation revealed a skeleton at the base of the second terrace (Vereshchagin 1975). Internal organs were well preserved by permafrost and the entire gastrointestinal tract was transported in a frozen state to the Novosibirsk Biological Institute. Radiocarbon dating of the forage mass from the gastrointestinal tract provided an age of 40,350 ± 880 BP. Botanical analyses indicate the mammoth lived in larch forests and open woodlands with low shrub breaks. The Shandrin River valley was occupied by grass communities with herb-moss bogs and shrubby moss meadows. The fodder within the gastrointestinal tract indicated sedges, cotton grass, other grasses, plus sprigs and leaves of shrubs such as alder, willow, low birch, and larch shoots; mosses were also included in the diet.

At present the Shandrin River valley is treeless, an area of subarctic tundra. Modern plant communities, which would be similar to those at the time the mammoth died, occur 100–250 km south of the burial site.

Selerikhan Fossil Horse Found in a gold mine, 8 to 9 m below the surface, this Chersky horse died with its stomach full around 38,590 ± 1120 BP (Fig. 2–32*a* [3]). It died in an ancient valley corresponding to a 110–120-m-high terrace of the Bolshoi Selerikhan River. Modern vegetation is comprised of floodplain forests of larch and poplar, with a thick willow and alder understory; hillsides are covered with arid larch forests and steep hillsides by steppe vegetation. There are also sedge marshes and sedge-cotton grass bogs.

The plants in the horse's stomach indicate it died suddenly after having eaten (Vereshchagin 1977). Residence time of food in a horse's gastrointestinal tract is usually less than ten hours; therefore, the plants in the stomach represent the vegetation of the burial site area at the time of the horse's death.

Dating of the horse and its fodder indicates it died during the Karginsky interglacial, possibly by having fallen in a thermokarst scour. That its death occurred in late July or early August is suggested by ripened fruits of sedges but unripened grasses. The food indicates the animal grazed on a variety of habitats such as dry steppe, moist meadows, riparian aquatic vegetation, plus minor amounts of forest habitat plants. The conclusions reached were that the present vegetation is less rich than that of the time of the horse's death. The Lena–Aldan forests are regarded as modern equivalents.

Mylakhchin Bison In 1971 a hunter found a fossil bison on the middle Indigirka River (Fig. 2–32*a* [4]). It was buried in a loess-loam at the base of the loess-ice terrace, about 40 m above the modern river. The bison died 29,500 ± 1000 BP in an area currently known as the Aluyi lowland. The modern Indigirka River is forested but contains many swamps and lakes. Larch forests alternate with dwarf birch communities and bogs. It is a relatively poor modern flora. Sedges and grasses dominated the bison's food plants with some low birch, willow, alder, and mosses. It is believed the animal died in early summer in the late Pleistocene (middle Würm/middle Wisconsin). The landscape at the time of the animal's death was interpreted as consisting of open, treeless plant communities such as tundra and forest-steppe.

Yuribey Mammoth The youngest representative of the studied fauna, this mammoth died 10,000 ± 70 BP (Arslanov et al. 1980) (Fig. 2–32*a* [8]). The tightly filled gastrointestinal tract was preserved.

The modern vegetation community is comprised of dwarf willow and birch tundra. The animal died in an early Boreal period with stable vegetative cover being expanded due to a warming climate. The Yuribey River valley was occupied by sedge-grass communities and some sedge bogs. Bushy tundra may have been sparsely present. It appears the climatic conditions at the time of death were similar to modern. The mammoth apparently drowned in the river, or a lake.

Berelekh Mammoth Population A large "cemetery" of mammoths was discovered on the Berelekh River (Vereshchagin 1977; Mochanov and Fedoseeva, this volume). The bone bed formed between 11,870 ± 60 and 10,260 ± 150 BP (Lozhkin 1977). A

Dyuktai culture archaeological site was found 200 m downstream. The "cemetery" contained an estimated 140 mammoths, 4 wolverines, 1 cave lion, 1 woolly rhinoceros, 3 Chersky horses, 4 reindeer, and 2 bison.

The cemetery thus began to develop in late Sartan. The locality was one of grass and low bush-grass tundra, with sedge-grass low areas. Study of the deposits suggests an interval of fluctuating wet-cold to dry-warm episodes.

Summary and Conclusions

Based on the data amassed from the gastrointestinal tracts, the enclosing sediments, and the radiocarbon dates, Ukraintseva proposes the following model of extinction of members of the mammoth fauna of Siberia.

1. In the past 75,000 years (equivalent to the Wisconsinan of North America) there were cycles of relatively cold (glacial) conditions and relatively warm (interstadial) intervals. The cold cycles favored the shrinkage of forest habitats with an increase in favorable mammoth fauna habitat, i.e., steppes and tundra. During the interstadials, forests advanced rapidly and swampy areas and boggy regions increased, causing segregation and breakup of favorable habitats, as well as increasing opportunity for fatal accidents and burials of representatives of mammoth fauna (Fig. 2–32*b*).

2. More than 221 taxa of plants are known from the analyses of gastrointestinal contents of large herbivores which died within the interval of 53,000–10,000 years ago. The plants represented in various specimens change due to selectiveness by the animal, and to minor differences in vegetational patterns of the areas of death. Dr. Ukraintseva concludes that wet ground fodder was of less nutritional value than cold, dry ground fodder. This supports a concept of greater mortality in interstadial intervals.

The duration of warm and cold intervals had an important effect on animal populations. Fluctuation toward cooling caused the emergence of cold-adapted organisms. A study of rates of loess accumulation led to the conclusion that separate cold, glacial epochs did not exceed 50,000 years, and that even in those epochs, warming or warm intervals totaled up to half of a given interval. This led to the conclusion that cold-adapted fauna necessarily had to exist in unfavorable climatic intervals.

Population size was governed by these oscillations. In cold (glacial) intervals, vast areas of treeless landscapes led to large interbreeding herbivore populations. Warm (interglacial) periods accompanied by forest and swamp/bog expansion were dominated by small and medium herbivore populations. These warm periods caused reductions of suitable habitat and food reserves, as well as causing deterioration of food nutrients. These combined factors led to lower birthrates and higher mortalities. Large interbreeding populations with high birthrates were divided into medium- and small-sized intrabreeding groups.

Certain elements of the mammoth fauna were adapted to cold, dry climates. Their food sources were also more nutritious. As rates of climatic change increased, small segments of formerly large animal populations were unable to adapt and became extinct.

Some members of the mammoth fauna such as bison, reindeer, musk-oxen, etc., were less specialized to cold environments than were mammoths, woolly rhinoceros, and others, and they, therefore, survived to the present. The Siberian model presents no crucial role for human predation in the extinction of mammoths and woolly rhinoceros. Human involvement at the Berelekh "cemetery" is suggested. Climate change is seen as sufficient explanation for the extinction of cold-adapted members of the mammoth epoch fauna.

The Siberian climate-change model viewed from a temperate North American perspective finds important differences. First, considering only the mammoths, the Siberian model is concerned solely with arctic and subarctic *Mammuthus primigenius*. In North America, by contrast, there were contemporary temperate zone species of mammoths (*M. imperator* and *M. columbi*), which were probably more numerous and widespread than *M. primigenius*. The environmental change depicted in the model driving the extinction of Siberian woolly mammoths would have had no effect on New World temperate zone mammoths—in fact, warming should have enhanced their environment, by expansion of suitable habitat.

Whereas human predation is not considered to be an effective element of extinction in Siberia, it has a more visible aspect in temperate North America.

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PALAEOECOLOGY OF THE PALAEOLITHIC OF THE RUSSIAN FAR EAST

*Yaroslav V. Kuzmin**

In Siberia and the Russian Far East, voluminous chronological, palaeogeographical, and faunal data were collected from the 1960s to the 1980s (Ravsky 1972; Tseitlin 1979; Tseitlin and Aseev 1982; Bazarova 1985; and others). The new archaeological discoveries introduced data on the ages and environments of sites. They also permitted palaeoecological reconstructions in which all components of the human environment could be appraised as they relate to the possibility of human existence in the vast and cold territory of Siberia (Arkhipov 1991).

Archaeological and palaeogeographical investigations in the Russian Far East have been summarized in several monographs (Krasnov 1984; Krushanov 1989). Using these data as a base and adding the results of the writer's own geoarchaeological investigations, the concern here will be with

*I thank Ruslan S. Vasilievsky, Natalia B. Verkhovskaya, Sergei S. Ganzei, Sergei A. Gladyshev, Valery A. Lynsha, and Valery P. Stepanov for fruitful discussions during preparation of this manuscript. I also thank John F. Hoffecker for correction of style and grammar. Research was supported in part by a grant from the International Research and Exchange Board with funds provided by the U.S. Department of State (Title VIII). Neither of these organizations is responsible for the views expressed.

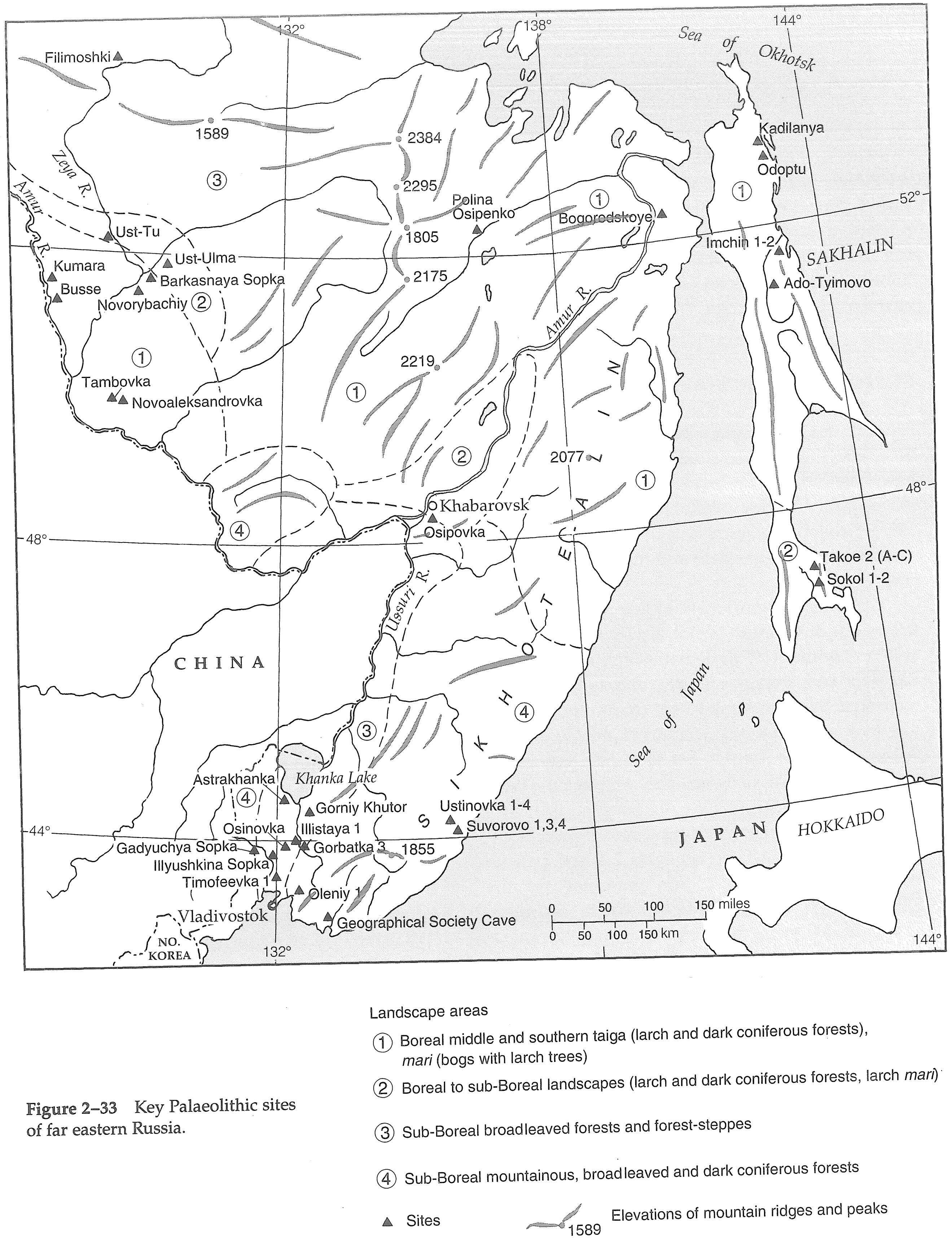

Figure 2–33 Key Palaeolithic sites of far eastern Russia.