

fauna (elephant birds, giant lemurs, and a dwarf hippo) in Madagascar is unclear. No "elephant bird hunter" sites are known to match the moa hunter sites of New Zealand. As Dewar notes, the use of the giant eggs as containers may represent quarrying or gathering of subfossil material rather than plundering of fresh nests of the giant birds by the ancient Malagasy. Unless pre-Holocene extinct faunas are found in Madagascar, the comparison with Africa cannot be synchronous. However, the prehistoric fauna was rich, especially in large primates. It is hard to envision an earlier wave of Malagasy extinctions.

While many large mammals disappeared from parts of Africa and Asia, and the range of most large species shrank in the last 100,000 years, comparatively few genera were lost. With the exception of Madagascar, the record of Afro-Asian megafaunal survival, compared with late Pleistocene disappearances in America and Australia, remains the outstanding aspect of the fossil record.

Quaternary Mammalian Extinctions in Northern Eurasia

N. K. VERESHCHAGIN AND G. F. BARYSHNIKOV

THE EXTINCTION OF PHYLOGENETIC LINES and of animal species is a complex process that depends on many biological and physical factors. Methodologically, the paleontologist concerned with extinctions works above all with the presence or absence of species at various stratigraphic levels. Additionally, he must know whether species that are linked in phylogenies are really genetically related. Finally, in reconstructing the true history of Quaternary mammalian extinctions, the investigator must be aware of taphonomic problems and must use data from collateral sciences—geology, paleogeography, and archaeology. It must be realized that the latest known record of an extinct species does not record its final extinction, but rather the continued presence of a relatively large population (Efremov 1950). Only correct interpretation of morphological, paleozoogeographical, and taphonomic data can explain extinctions.

There are four major approaches to explaining the causes and tempo of Quaternary mammalian extinctions.

1. Investigation of the influences of natural (ecological) changes—in climate, in weather conditions, in the character of the soil, in landscapes and biotopes.
2. Investigation of lost resistance, morphological plasticity, and physiological adaptation in declining or extinct species, occurring as a result of nonadaptive evolution, of evolutionary inertia, or of orthogenesis and evolutionary dead-ends.
3. Investigation of the influence of predators, epizootic diseases, and biocenotic reorganizations.
4. Study of the destructive activity of man, by direct action or by altering species habitats.

Theoretically, it seems likely that the first, second, and third groups of factors predominated in the early stages of the Quaternary, while the fourth group dominated in the later stages. It is also obvious that the most intensive extinctions occurred as a result of complex combinations of the cited causes. By necessity, we limit ourselves in this chapter to the first and fourth groups.

The colossal size of northern Eurasia and its wide variety of climates and landscapes permitted Pleistocene mammals to survive in some places after they had become extinct in others. This fact complicates the overall picture of extinction but allows a realistic evaluation of the influence of natural factors and of man on separate species and on species complexes. In other words, data on changes in the geographic ranges of Quaternary mammals are useful for establishing the causes of extinction.

Translated by R. G. Klein

The development of species ranges and their dynamics are complex phenomena, but in essence there is the original expansion (the rapid spread of a species from its place of origin), followed by temporary reduction of the range or extinction, and, finally, secondary expansions from relict areas. Flourishing relicts as a rule do not disappear if they are not affected by human activity. In the first stages, extinction is usually linked with rapid or slow shrinkage in species ranges and in overall population size. In this process, regions that were continuously occupied may be broken up into separate areas of occupation. There is a series of cases in which these facts allow a ready understanding and explanation of extinction, especially when the matter is concluded by radical or partial transformation of the environment.

Progressive reduction of a species' range under natural influences often retraces the route of its original spread. Some Central Asiatic steppe species—the yellow lemming, the corsac fox, the kulan, and the saiga—provide an example. Over the last few centuries their ranges have shrunk rapidly from west to east, first as a result of ecological factors (as yet poorly studied) and secondly as a result of human activity in the nineteenth and twentieth centuries.

In this chapter we are concerned only with mammals in the concluding stages of the Quaternary period—the late (Upper) Pleistocene and Holocene. There are too few facts to explain extinctions in the Lower and Middle Pleistocene.

The Evolution of Mammalian Communities in Northern Eurasia During the Quaternary Period

At present about 530 species of terrestrial mammals are known from the Quaternary (including the Villafranchian) of Europe and the USSR. The number of species per order is as follows:

	Number of species known
Insectivora	35
Chiroptera	30
Primates	8
Lagomorpha	30
Rodentia	220
Carnivora	75
Proboscidea	14
Perissodactyla	28
Artiodactyla	100

As many as 182 species of terrestrial mammals are known from the late Pleistocene (Würm/Wisconsin) and Holocene of the USSR. Thirty of them are extinct. The number of species per order is as follows:

	Number of species known	Number extinct
Insectivora	5	—
Chiroptera	10	—
Primates	1	1
Lagomorpha	8	2
Rodentia	82	8
Carnivora	38	5
Proboscidea	1	1
Perissodactyla	6	4
Artiodactyla	31	9
Total	182	30

We must point out that it is not clear that all the "extinct" species truly are extinct. Much of the problem is that some living species may in fact be derived from ones said to be extinct. Domestication introduces complications in this respect. Thus, for example, among the Carnivora, the Volga wolf (*Canis volgensis* M. Pavl.) is only provisionally extinct, insofar as its genes are probably present in numerous breeds of domestic dogs.

Also problematic are the cave hyena of the genus *Crocota* and the cave lion of the genus *Panthera*. It is possible that these are only cold-adapted northern subspecies of still extant African-Asiatic tropical species.

Some Pleistocene lagomorphs and rodents described as distinct species may in fact be the ancestors of present-day forms. In particular, this conjecture pertains to the Don hare (*Lepus tanaiticus* Gureev)—a probable ancestor of the present day arctic hare (or its collateral branch?)—and to some ground squirrels. In the Perissodactyla the fossil horse (*Equus ferus* Bodd. s. lato) is only provisionally extinct, since one of its subspecies undoubtedly gave rise to the flourishing breeds of domestic horses. Similarly, in the Artiodactyla the aurochs (*Bos primigenius*) is only provisionally extinct, since its genes are certainly present in modern, large-horned cattle.

Given the huge size of the USSR, we must use subregions to list the species of late Quaternary mammals which are known in fossil form (Table 22.1)

Table 22.1. The Species of Late Quaternary Mammals Known in Fossil Form in the USSR

Order and Species	Russian Plain and Crimea	Caucasus	Central Asia	Siberia	Far East
Insectivora					
<i>Erinaceus europaeus</i> L.	H	PH	—	H	—
<i>Erinaceus amurensis</i> Schrenk	—	—	—	—	PH
<i>Desmana moschata</i> L.	PH	—	—	—	—
<i>Talpa caucasica</i> Satunin	—	PH	—	—	—
<i>Sorex sibirica</i> Dukelsky	—	—	—	PH	—
<i>Crocidura russula</i> Gldenstaedt	—	PH	—	—	—
Chiroptera					
<i>Rhinolophus mehelyi</i> Matschie	—	PH	—	—	—
<i>Rhinolophus ferrum equinum</i> Schreber	H	PH	H	—	—
<i>Myotis blythi</i> Tomes	H	PH	H	H	—
<i>Nyctalus noctula</i> Schreber	PH	H	H	H	—
<i>Nyctalus lasiopterus</i> Schreber	PH	H	H	—	—
<i>Eptesicus serotinus</i> Schreber	PH	H	H	—	—
<i>Eptesicus nilssonii</i> Keyserling et Blasius	PH	H	H	PH	—
<i>Vespertilio murinus</i> L.	PH	PH	PH	H	H
<i>Miniopterus schreibersi</i> Kuhl	H	PH	PH	—	H
Primates					
* <i>Macaca</i> sp.	—	P	—	—	—
Lagomorpha					
* <i>Lepus tanaiticus</i> Gureev	P	—	—	P	—
<i>Lepus timidus</i> L.	?H	—	—	?H	—
<i>Lepus tolai</i> Pallas	—	—	PH	?H	—
<i>Lepus europaeus</i> Pallas	PH	PH	H	H	—
<i>Ochotona daurica</i> Pallas	—	—	—	PH	—
<i>Ochotona alpina</i> Pallas	—	—	—	PH	—
* <i>Ochotona azerica</i> Gadziev et Aliev	—	P	—	—	—
<i>Ochotona pusilla</i> Pallas	PH	—	H	—	—

NOTE: P = late Pleistocene; H = Holocene; * = extinct species

Table 22.1. The Species of Late Quaternary Mammals Known in Fossil Form in the USSR
(continued)

Order and Species	Russian Plain and Crimea	Caucasus	Central Asia	Siberia	Far East
Rodentia					
<i>Pteromys volans</i> L.	P	—	—	?H	—
<i>Sciurus vulgaris</i> L.	PH	—	—	H	H
<i>Sciurus anomalus</i> Gmelin	—	PH	—	—	—
<i>Tamias sibiricus</i> Laxmann	H	—	—	H	H
<i>Spermophilus undulatus</i> Pallas	—	—	H	PH	—
* <i>Spermophilus glacialis</i> Vinogradov	—	—	—	P	—
<i>Spermophilus relictus</i> Kashkarov	—	—	PH	—	—
* <i>Spermophilus severskensis</i> I. Gromov	P	—	—	—	—
<i>Spermophilus suslicus</i> Gldenstaedt	PH	—	—	—	—
<i>Spermophilus muscoides</i> I. Gromov	P	—	—	—	—
<i>Spermophilus musicus</i> Menetrie	—	PH	—	—	—
<i>Spermophilus pygmaeus</i> Pallas	PH	H	H	—	—
* <i>Spermophilus superciliosus</i> Kaup	P	—	?	?	—
<i>Spermophilus fulvus</i> Lichtenstein	PH	—	H	—	—
<i>Spermophilus erythrogegens</i> Brandt	—	—	H	PH	—
<i>Marmota bobac</i> Mller	PH	—	H	H	—
* <i>Marmota paleocaucaisica</i> Baryshnikov	—	PH	—	—	—
<i>Marmota marmota</i> L.	P	—	—	—	—
<i>Marmota baibacina</i> Kastschenko	—	—	H	PH	—
<i>Marmota sibirica</i> Radde	—	—	—	PH	—
<i>Marmota camtschatica</i> Pallas	—	—	—	PH	—
<i>Marmota caudata</i> Geoffroy	—	—	PH	—	—
<i>Castor fiber</i> L.	PH	PH	—	—	—
<i>Castor canadensis</i> Kuhe	—	—	—	PH	H
* <i>Hystrix vinogradovi</i> Agryropulo	P	P?	—	?	—
<i>Hystrix leucura</i> Sykes	—	PH	PH	—	—
<i>Dryomys nitidula</i> Pallas	H	PH	H	—	—
<i>Glis glis</i> J.	P	PH	—	—	—
<i>Sicista subtilis</i> Pallas	PH	—	H	H	—
<i>Sicista caucasica</i> Vinogradov	—	?H	—	—	—
<i>Allactaga jaculus</i> Pallas	PH	—	H	H	—
<i>Allactaga elater</i> Lichtenstein	PH	H	H	—	—
<i>Allactaga williamsi</i> Thomas	—	PH	—	—	—
<i>Pygerethmus platyurus</i> Lichtenstein	P	—	H	—	—
<i>Alactagulus pygmaeus</i> Pallas	PH	H	H	—	—
<i>Dipus sagitta</i> Pallas	PH	H	H	H	—
<i>Sciropoda telum</i> Lichtenstein	PH	H	H	H	—
<i>Paradipus ctenodactylus</i> Vinogradov	—	—	—	PH	—
<i>Nannospalax leucodon</i> Nordmann	?H	—	—	—	—
<i>Spalax microphthalmus</i> Gldenstaedt	?H	PH	—	—	—
<i>Apodemus sylvaticus</i> L.	PH	PH	H	H	—
<i>Apodemus flavicollis</i> Melchior	?H	H	—	—	—
<i>Mus musculus</i> L.	PH	H	H	H	H
<i>Rattus rattoides</i> Hodgson	—	—	PH	—	—
<i>Nesokia indica</i> Gray	—	—	PH	—	—
<i>Ellobius lutescens</i> Thomas	—	PH	—	—	—
<i>Ellobius talpinus</i> Pallas	PH	—	—	—	—
<i>Ellobius tancrei</i> Blasius	—	—	H	—	—
<i>Allocricetulus eversmanni</i> Brandt	PH	—	PH	—	—
<i>Tscherskia albipes</i> Ugnev	—	—	H	H	—
* <i>Cricetulus argyropuloi</i> I. Gromov	—	P	—	—	PH
<i>Cricetulus migratorius</i> Pallas	PH	PH	H	H	—
<i>Mesocricetus raddei</i> Nehring	—	PH	—	—	—
<i>Cricetus cricetus</i> L.	PH	PH	H	PH	—
<i>Merionus erythourus</i> Gray	—	H	PH	—	—
<i>Merionus meridianus</i> Pallas	PH	H	H	—	—

Table 22.1. The Species of Late Quaternary Mammals Known in Fossil Form in the USSR
(continued)

Order and Species	Russian Plain and Crimea	Caucasus	Central Asia	Siberia	Far East
<i>Rombomys opimus</i> Lichtenstein	—	H	PH	—	—
<i>Myospalax myospalax</i> Laxmann	—	—	—	PH	—
<i>Myospalax aspalax</i> Pallas	—	—	—	PH	—
<i>Prometheomys schaposchnikovi</i> Satunin	—	PH	—	—	—
<i>Clethrionomys rufocanus</i> Sundeval	H	—	—	PH	H
<i>Clethrionomys glareolus</i> Schreber	PH	H	—	PH	—
<i>Clethrionomys rutilus</i> Pallas	H	—	—	PH	H
<i>Lagurus lagurus</i> Pallas	PH	—	—	PH	—
<i>Eolagurus luteus</i> Eversmann	P	—	H	PH	—
* <i>Dicrostonyx quillielmi</i> Sanford	P	—	—	P	—
<i>Dicrostonyx torquatus</i> Pallas	?H	—	—	?H	—
<i>Lemmus sibiricus</i> Kerr	PH	—	—	PH	—
<i>Myopus schisticolor</i> Lilljeborg	H	—	—	H	—
<i>Arvicola terrestris</i> L.	PH	PH	H	—	—
<i>Pitymys subterraneus</i> Selus-Longchamps	PH	—	—	—	—
<i>Pitymys majori</i> Thomas	—	PH	—	—	—
<i>Pitymys daghestanicus</i> Schidlovskii	—	PH	—	—	—
<i>Microtus gregalis</i> Pallas	PH	—	H	PH	—
<i>Microtus socialis</i> Pallas	?H	PH	H	—	—
<i>Microtus fortis</i> Buchner	—	—	—	PH	H
<i>Microtus maximowiczii</i> Schrenk	—	—	—	H	P
<i>Microtus oeconomus</i> Pallas	PH	—	H	PH	—
<i>Microtus agrestis</i> L.	PH	—	—	PH	—
<i>Microtus arvalis</i> Pallas	PH	PH	—	PH	—
<i>Microtus transcaspicus</i> Satunin	—	—	PH	—	—
<i>Lasiopodomys brandti</i> Radde	—	—	—	PH	—
<i>Chionomys gud</i> Satunin	—	PH	—	—	—
Carnivora					
<i>Nyctereutes procyonides</i> Gray	—	—	—	—	PH
<i>Canis lupus</i> L.	PH	PH	PH	PH	PH
<i>Canis aureus</i> L.	H	PH	PH	—	—
* <i>Canis volgensis</i> M. Pavlova	PH	—	—	—	—
<i>Alopex lagopus</i> L.	PH	—	—	PH	—
<i>Vulpes vulpes</i> L.	PH	PH	PH	PH	PH
<i>Vulpes corsac</i> L.	PH	H	H	H	—
<i>Cuon alpinus</i> Pallas	H	PH	H	PH	PH
<i>Selenarctos thibetanus</i> G. Cuvier	—	?	—	—	?H
<i>Ursus arctos</i> L.	PH	PH	H	—	PH
* <i>Ursus spelaeus</i> Rosenmller et Heinroth	P	PH	—	—	—
* <i>Ursus rossicus</i> Borissiak	P	P	—	P	—
<i>Thalarcos maritimus</i> Phipps	—	—	—	PH	—
<i>Martes zibellina</i> L.	?H	—	—	PH	PH
<i>Martes martes</i> L.	PH	PH	—	—	—
<i>Martes foina</i> Erxleben	H	PH	H	—	—
<i>Martes flavigula</i> Boddaert	—	—	—	—	PH
<i>Gulo gulo</i> L.	PH	P	—	PH	PH
<i>Mustela erminea</i> L.	H	H	H	PH	?H
<i>Mustela nivalis</i> L.	PH	PH	H	PH	H
<i>Mustela sibirica</i> Pallas	H	—	—	PH	PH
<i>Mustela altaica</i> Pallas	—	—	H	?H	H
<i>Putorius eversmanni</i> Lesson	PH	H	H	PH	—
<i>Vormela peregusna</i> Gldenstaedt	H	PH	H	—	—
<i>Meles meles</i> L.	PH	PH	H	PH	PH
<i>Lutra lutra</i> L.	PH	H	H	PH	PH

Table 22.1. The Species of Late Quaternary Mammals Known in Fossil Form in the USSR
(continued)

Order and Species	Russian Plain and Crimea	Caucasus	Central Asia	Siberia	Far East
* <i>Crocota spelaea</i> Goldfuss	P	P	?	P	P
<i>Hyaena hyaena</i> L.	—	H	PH	—	—
<i>Panthera leo</i> L.	H	H	—	—	—
* <i>Panthera spelaea</i> Goldfuss	P	P	P	P	?
<i>Panthera tigris</i> L.	—	H	H	—	PH
<i>Panthera pardus</i> L.	?	PH	PH	—	PH
<i>Uncia uncia</i> Schreber	—	—	PH	H	—
<i>Felis silvestris</i> Schreber	PH	PH	—	—	—
<i>Felis libyca</i> Forster	H	H	PH	—	—
<i>Felis euptilura</i> Elliot	—	—	—	—	?H
<i>Felis chaus</i> Gldenstaedt	PH	PH	H	—	—
<i>Lynx lynx</i> L.	PH	PH	H	H	PH
Proboscidea					
* <i>Mammuthus primigenius</i> Blumenbach	P	P	?	P?	P
Perissodactyla					
* <i>Equus ferus</i> Boddaert	PH	PH	PH	PH	PH
<i>Equus przewalskii</i> Poliakov	—	—	?H	?	—
* <i>Equus hydruntinus</i> Regalia	P	P	?	—	—
<i>Equus hemionus</i> Pallas	H	H	PH	PH	—
* <i>Dicerorhinus kirchbergensis</i> Jaeger	—	P	—	—	—
* <i>Coelodonta antiquitatis</i> Blumenbach	PH	?	P	P	P
Artiodactyla					
<i>Sus scrofa</i>	PH	PH	PH	H	PH
* <i>Camelus knoblochi</i> Nehring	PH	?	PH	—	—
<i>Moschus moschiferus</i> L.	—	—	—	H	PH

A Review of Some Extinct Pleistocene Mammals

The Mammoth—*Mammuthus primigenius* Blumenbach, 1799

We can now trace the evolution of north Eurasian mammoths from the Lower Pleistocene, when thin-enameled teeth of large elephants appear for the first time. It is possible, however, that they derive from archidiskodons (genus *Archidiskodon*), which convergently developed "mammoth features" as an adaptation to the severe conditions of early glaciations in northeast Siberia.

For stratigraphic purposes, many Soviet paleontologists and geologists accept the hypothesis that mammoths (genus *Mammuthus*) originated from archidiskodon elephants: Gromov's archidiskodon (*Archidiskodon gromovi* Garutt et Alexeeva), southern archidiskodon (*A. meridionalis* Nesti), and Taman archidiskodon (*A. tamanensis* Dubrovo), from the Upper Villafranchian (Khapry and Taman faunal complexes), through the intermediate form of the trogontherii elephant (*A. trogontherii* Phlig), characteristic of the early Pleistocene (Tiraspol complex) (Gromov 1948, Dubrovo 1964, Gromova 1965, Alekseeva 1977, Garutt 1981).

Vereshchagin believes, however, that it is more likely that the archidiskodons and mammoths split in the latest Pliocene, while the mammoths and the closely related Asiatic elephant *Elephas maximum* L.) separated in the Lower Pleistocene. Thenius (1980) holds a similar opinion.

Table 22.1. The Species of Late Quaternary Mammals Known in Fossil Form in the USSR
(continued)

Order and Species	Russian Plain and Crimea	Caucasus	Central Asia	Siberia	Far East
<i>Dama mesopotamica</i> Brooke	—	P?	—	—	—
<i>Cervus nippon</i> Temminck	—	—	—	—	PH
<i>Cervus elaphus</i> L.	PH	PH	PH	PH	PH
<i>Capreolus capreolus</i> L.	PH	PH	—	—	—
<i>Capreolus pygargus</i> L.	P	H	PH	PH	PH
* <i>Megaloceros giganteus</i> Blumenbach	P	P	P	P	—
<i>Alces alces</i> L.	PH	PH	—	PH	PH
<i>Rangifer tarandus</i> L.	PH	—	—	PH	?
* <i>Bos primigenius</i> Bojanus	PH	P	PH	P	?
* <i>Poepphagus baikalensis</i> N. Vereshchagin	—	—	—	P	?
* <i>Bison priscus</i> Bojanus	P	P	P	PH	P
<i>Bison bonasus</i> L.	H	?H	—	—	—
* <i>Spirocerus kiakhtensis</i> M. Pavlova	—	—	—	P	—
<i>Gazella subgutturosa</i> Gldenstaedt	H	H	PH	—	—
<i>Procapra gutturosa</i> Pallas	—	—	—	PH	—
* <i>Parabubalis capricornis</i> V. Gromova	—	—	—	?	—
<i>Saiga tatarica</i> L.	PH	PH	PH	P	—
<i>Ovibos moschatus</i> Zimmermann	P	—	—	PH	—
<i>Naemorhedus caudatus</i> Milne-Edwards	—	—	—	—	PH
<i>Rupicapra rupicapra</i> L.	—	PH	—	—	—
<i>Capra aegagrus</i> Erxleben	—	PH	H	—	—
<i>Capra sibirica</i> Pallas	—	—	PH	PH	—
<i>Capra caucasica</i> Gldenstaedt et Pallas	—	PH	—	—	—
* <i>Capra prisca</i> Woldrich	—	P	—	—	—
<i>Ovis orientalis</i> Gmelin	—	PH	—	—	—
<i>Ovis vignei</i> Blyth	—	—	PH	—	—
<i>Ovis ammon</i> L.	?	P	H	PH	—
<i>Ovis nivicola</i> Eschscholz	—	—	—	PH	—

The cold-adapted species of mammoth apparently evolved in northeast Asia. It was already widely distributed throughout the Eurasian periglacial zone in the Middle Pleistocene (Mindel/Riss and Riss). However, the large mammoths of the Khazar fauna of eastern Europe are sometimes regarded as a distinct species, *Mammuthus chosariensis* Dubrovo.

M. primigenius was most widely distributed in the Riss/Wrm and especially in the Wrm (Valdaj), when mammoths occurred across Eurasia from the Atlantic to the Pacific, and through Alaska into North America. They lived north of the Arctic Circle and the margins of the Arctic basin and spread south to the edges of the Central Asiatic and Mongolian deserts. In Europe they reached Spain, the southern tip of Italy, and the Transcaucasus.

The remains of mammoths are common in Mousterian sites in the Crimea (Chokurcha) and northern Caucasus (Il'skaya, Dakhovskaya), but they do not occur in Upper Paleolithic sites there. By this time the southern limit of mammoth distribution had apparently retreated northward.

Research by Soviet biologists, paleogeographers, and geologists has now produced firm ideas on the biology and ecology of the mammoths. In the north these elephants were well adapted to a dry, cold, and sharply continental climate. The thick cover of hair, the wool on the trunk, and the abundant fat deposits under the skin bear witness to this adaptation. The investigation of stomach contents has provided data on diet.

In summer mammoths fed primarily on herbage—prairie grasses, sedges, cotton grass, and the terminal shoots of shrubs (willow, birch, and alder). They tore the bark off willow and larch with their tusks. In winter, when water bodies froze and snow was absent, mammoths could apparently obtain water by using their tusks to scrape ground ice from the vertical walls of cliffs or from subsurface cracks. This hypothesis seems to be confirmed by lateral wear commonly found on the ends of tusks even in young individuals, and by the frequency of fractured tusks, probably broken in such activity. As yet, there are no data on the winter diet of mammoths, but it probably consisted of dried grass and shoots of leaf-bearing shrubs and conifers (larch, pine, and fir).

Mammoths apparently undertook long southerly treks along the river valleys, especially in the event of heavy snowfalls and droughts. They very often died during flash floods in the valleys and floodplains of the rivers or when they tried to cross the ice of lakes and rivers that was insufficiently solid and masked by early snowfalls.

The bodies of mammoths were buried in earth slides at the base of slopes, in soil flows thawed by the sun, in fluvial silts and sands, and in deltas. Freezing in the sediments, the bodies were preserved for millenia. Rare but excellent burials of carcasses occurred when animals fell into insidious cracks eroded in ground ice by small streams. Soft tissues and even whole bodies were preserved to the present because the mammoths lived in a permafrost environment, with winter temperatures of minus 60–80 degrees centigrade.

In northeast Siberia (Yakutia) frozen mammoth carcasses were buried in windborne loessic silts that form the covering (Sartan) loam deposits. This phenomenon is shown by the presence of thick ice seams that pass to a depth of 30–40 m and press up columns of powdery soil with bones and, in places, disarticulated carcasses of mammoths. These facts, confirming the cold adaptation of the mammoths, are vital for explaining their life, death, and extinction.

One very puzzling aspect of mammoth history is the fact that so few remains are known from the period beyond 50–60,000 years ago, that is, from before the last glacial epoch (Würm, Wisconsin), and also from the period beyond the range of radiocarbon dating. At the same time, taphonomic theory suggests that conditions appropriate for the burial of mammoth skeletons must have been abundant in the preceding Riss/Würm (Dnepr/Valdai) interglacial, when there was extensive ground thawing, erosion, and reconstitution of the draining system (fig. 22.1).

Whenever Pleistocene extinctions are considered, mammoths always receive the most attention. For almost two centuries now, when solid facts and ecological and taphonomic observations were lacking, scholastic discussions or fantastic musings have dominated logical deductions. From the time of Peter the Great and the first printed articles about the mammoth by the state councilor and scholar Tatishchev (Tatishchev and Gmelin 1730), it became popular to think that the mammoth lived in a warmer climate, similar to the African and Asiatic elephants, and that it perished when the climate got colder. This idea has survived right to the present among both scholars and laymen.

In order to explain the massive death and preservation of skeletons and of frozen mammoth carcasses, it has been common to resort to the Deluge hypothesis in its various forms. Usually, the idea is that Siberian rivers transported the carcasses of mammoths from south to north (Middendorf 1860). More rarely, transport is ascribed to a giant wave that was driven through the Himalayas following volcanic eruptions (Pallas 1773) or by the force of a meteor striking the Pacific Ocean. People who are not acquainted with the nature of the buried carcasses and bones believe it is quite possible that the animals perished when an asteroid captured a portion of the atmosphere, leading to rapid deterioration in the climate of Siberia. Howorth (1887) presented a detailed version of the Deluge hypothesis in a broad review of how animals get buried. For its abundant examples of various types of burial in Quaternary deposits, Howorth's century-old account has no equal.



Figure 22.1. Head of the Katanga mammoth (Tajmyr Peninsula), dated to 53,000 years ago. (Photo by N. K. Vereshchagin, 1978)

The first rational ideas on the life of mammoths and on the relationship between the frozen carcasses and the ground ice of the Arctic appeared in the works of the Russian Polar Expedition under the leadership of Toll'. These ideas created the basis for understanding the extinction of our northern elephants. Toll' (1897) himself linked the extinction to the breaking up of a former Arctic continent between Asia and America, which led to a less continental, but colder, climate. As a result, rich pastures disappeared. The geologist and paleontologist Cherskij (1891) thought that greater cold and the development of the taiga zone explained the disappearance of the mammoth fauna in northeast Siberia.

Later reviews of the causes of mammoth extinction were published at the beginning of the twentieth century by the paleontologist Pavlova (1924); the journalist Digby (1926), who visited Yakutia at the beginning of the century; the preparator Pfizenmayer (1926), who excavated the Berezovka mammoth; the geographer Tolmachoff (1929); and others. Basically, they considered the possibility that extinction was a result of human activity, of physical changes in the mammoth's habitat, or of excessive development of the tusks.

Captain Gernet (1930, 2nd ed. 1981) used the glacial theory itself to support the vague and muddle-headed explanation of mammoth extinction from the cold. The geologist Gromov (1948) ascribed mammoth extinctions to climatic deterioration during the Würm. The geophysicist Budyko (1967) saw the same cause and supported it mathematically by hypothesizing small numbers of northern elephants and significant destructive power to primitive hunters.

The paleontologist Pidoplichko (1969) believed that Paleolithic hunters were unquestionably responsible for destruction of the mammoths that lived in the Ukraine and the southern part of the Russian Plain. He drew parallels to the hunts of African aborigines, and pointed out that if there were half a million mammoths in eastern Europe, Paleolithic hunters could have destroyed them in a single millenium.

The ichthyologist Lindberg (1972) naively attempted to explain the extinction of the mammoth by a rise in the level of the Pacific Ocean. The resulting overflow of the Baltic into the Black Sea wiped out the animals on the Russian Plain, while individuals living on the New Siberian Islands were cut off from the mainland and died from the cold.

The paleogeographer Velichko (1973) drew a convincing and detailed picture of a hyperzone of productive tundra-steppe, inhabited by the mammoth fauna, and ascribed the destruction of the mammoth complex and the extinction of the mammoths themselves to landscape changes—thawing of the ground, development of bogs over great expanses, and development of forests at the boundary between the Pleistocene and the Holocene.

The zoologist Vereshchagin (1971b, 1979) believed that the mammoth became extinct primarily as a result of the radical reconstitution of climates and landscapes in northern Eurasia at the end of the last glacial epoch. However, in the southern regions of eastern Europe and Siberia the destructive influence of primitive man could have predominated.

In the opinion of the paleogeographer and frozen-ground specialist Tomirdiario (1977), the extinction of the mammoth and of the mammoth fauna in northeast Siberia came about at the end of the Würm (Valdaj), when an "ecological catastrophe," linked to climatic amelioration, led to the thawing of the Arctic basin and the melting of ground ice. The fodder-rich tundra-steppe was transformed into a moist, boggy, mossy tundra. There would be no place for mammoths in the present arctic tundra of Eurasia with its dense snow driven by the winds.

The geographer Kvasov (1977) also thinks that one of the reasons for the extinction of the mammoths and the mammoth fauna was the postglacial rise in temperature and humidity, connected with the development of extensive water bodies, the periglacial lakes.

Finally, there is the curious notion of the graphic artist Krause (1977), who compared some of the morphological features of the mammoths (woolly coat, ear structure, fat deposits, etc.) to the same features in other northern animals. As a result, with the direct logic of a person not acquainted with the paleogeographic facts, he declares that the cold adaptation of the mammoths is only a "scientific fiction" and that these beasts, having been adapted to a warm climate, perished from the cold. Such ideas, however, are not new and only confirm the tenacity of naive notions formulated in the eighteenth and nineteenth centuries.

Paleobiologists have repeatedly called attention to human influences on the mammoth population of Eurasia, especially in connection with the investigation of Paleolithic sites. In eastern Europe and in Siberia, massive "cemeteries" of mammoth bones and puzzling constructions made of their skulls and bones have been found (fig. 22.2). Usually, these constructions have been regarded as the foundations of ruined dwellings (Pidoplichko 1969), but some of them could have had ritual meaning or could have been used for musical purposes (Bibikov 1981). With regard to the extinction question, the principal significance of these bone heaps is that they could indicate the existence of intensive hunting. However, there are still no direct data to support the existence of such hunts. For example, traces of blows from tools have not been found on the bones.

At the same time there are numerous actualistic observations showing that primary animal "cemeteries" can form without human help when the carcasses of trampled creatures are concentrated in river meanders and oxbows (Vereshchagin 1972).



Figure 22.2. Ruins of a mammoth bone dwelling. Village of Mezhirich in the Ukraine. (Photo by N. K. Vereshchagin, 1971)

Paleolithic hunters could have transported fully mascerated mammoth bones from such now-dry natural accumulations to the high terraces of rivers for use as construction material. While we do not deny the probable existence of active mammoth hunts conducted with spears, poisoned javelin points, and arrows, or involving drives into natural traps and artificial pits, onto thin ice or even into a marshy bog, we must point out that there is still no undisputed evidence that this happened.

Massive, primary, natural burials of mammoth bones—in situ "mammoth cemeteries"—occur in subaqueous deposits in river valleys and lake basins. Secondary burials, which owe their existence to primitive people, also occur in river valleys and along the edges of lake basins, but they are found most often in the loesses and loesslike loams of the high terraces, both in eastern Europe and in Siberia (fig. 22.3).

Considering the immensity of the mammoth's range, encompassing a wide variety of natural conditions, it is impossible to assert that only one natural factor caused its extinction, for example, climatic amelioration leading to an ecological catastrophe in which boggy tundra and taiga replaced cold tundra. The proponents of this position must then use Upper Paleolithic people and their more abundant Neolithic successors to explain the disappearance of the mammoth in southern Siberia, where steppe dominated.

The same insufficiencies are hidden in explanations that speak of an "evolutionary blind alley," for we still do not know what negative morphological and physiological features could serve to explain mammoth extinction.

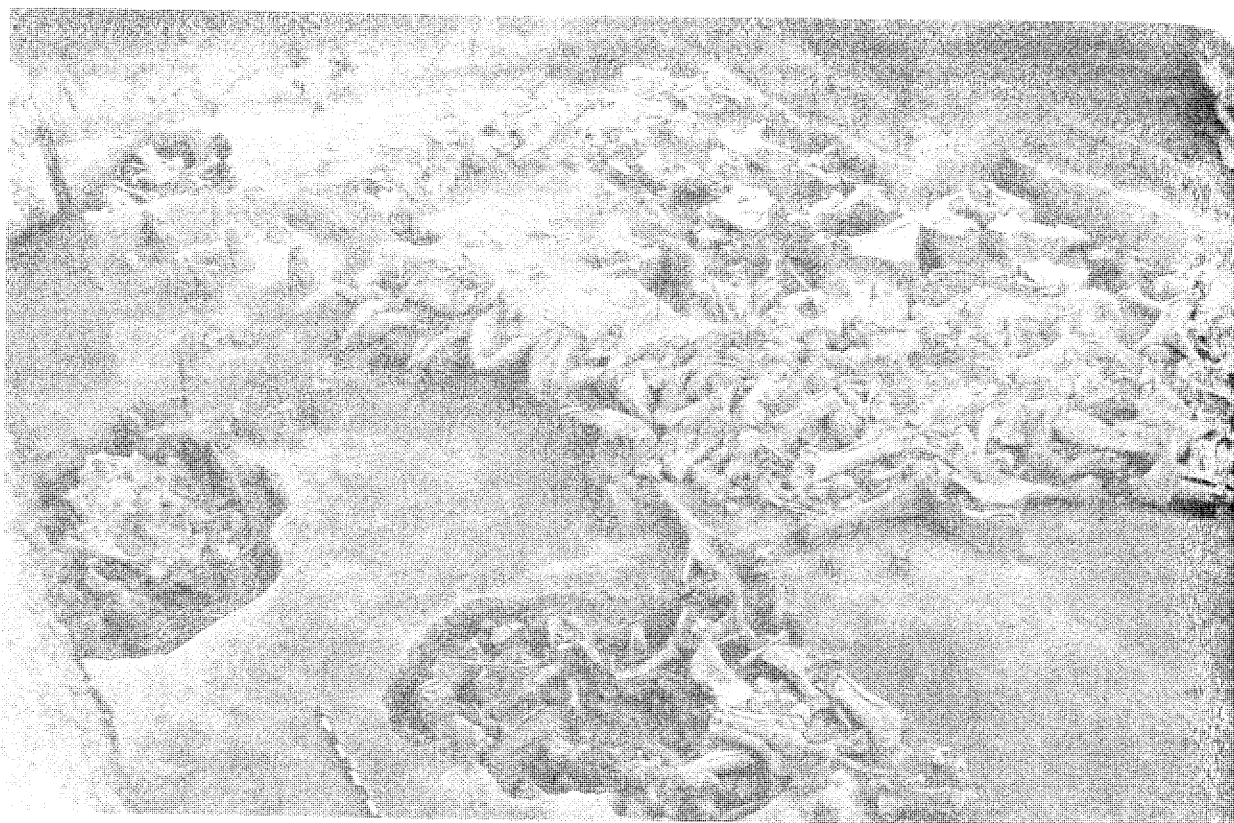


Figure 22.3. Ruins of a mammoth bone dwelling. Village of Kostenki on the Don. Paleolithic site of Kostenki XI. (Photo by N. K. Vereshchagin, 1960)

Meanwhile, any reasonable explanation must take into account the latest chronological dates. Table 22.2 shows them for Europe and the U.S.S.R. Together with other similar dates for the extinction of Pleistocene species in Eurasia and North America (Kurtén and Anderson 1979), these dates can help in the search for the cause of extinction of the woolly elephant.

When the mammoth became extinct, its distinctive stomach botfly *Cobboldia rusanovi* Grunin 1973 also disappeared. This was one of three species of botflies known for these proboscideans.

The Great Cave Bear *Ursus spelaeus* Rosenmüller et Heinroth, 1794

Cave bear history may be traced from the early Pleistocene, when speleoid features began to appear in European *Ursus etruscus* Cuvier. From the intermediate form *U. deningeri* Reich., *U. spelaeus* evolved in the Middle Pleistocene (the Riss) (Erdbrink 1953, Gromova 1965). The karst regions of central Europe and the Mediterranean littoral were the homeland of the great cave bear. In the north the species' range extended to southern England, Belgium, and southern Poland, and it included the Urals, the Crimea, and the Caucasus. Each karst region contained its own cave bear population, with little or no movement between regions. For example, isolated by flat

Table 22.2. Latest Chronological Dates for Mammoth in Europe and the USSR

Country	Site	Date (yr B.P.)
Europe		
Sweden	Lockarp	13,360 ± 95 (Lu-796)
		13,090 ± 120 (Lu-796.2)
		13,260 ± 110 (Lu-865)
France	La Colombière	13,390 ± 300 (Ly-433)
Switzerland	Praz Rodet	12,270 ± 210 (Ly-877)
USSR		
European part	Kunda, Estonian SSR	9,780 ± 260 (TA-12)
	Kostenki 2, Voronezh Oblast'	11,000 ± 200 (GIN-93)
	Timonovka I, Bryansk Oblast'	12,200 ± 300 (IGAN-82)
	Yudinovka, Bryansk Oblast'	13,650 ± 200 (LU-153)
		13,830 ± 850 (LU-103)
Siberia	Avdeevo, Kursk Oblast'	13,900 ± 200 (IGAN-78)
	Yuribej, Gydansk Peninsula	10,000 ± 70 (LU-1153)
	Mamontovaya, Tajmir	11,450 ± 250 (T-297)
	Berelekh, Yakutsk ASSR	10,370 ± 90 (SOAN-327)
		12,240 ± 160 (LU-149)
		13,700 ± 80 (MAG-114)
	Yar Berezovskij, Irtysh R.	12,860 ± 90 (SOAN-1283)

SOURCE: Berglund et al. 1976, Orlova 1979, Vereshchagin 1982a

steppes, a small colony of these animals lived on the Zhigulevsk Highland (Samarsk Dome) in the central Povolzh'e. The cave bears of the Caucasus were also isolated and evolved at a slow rate. Until the very end of the Pleistocene they maintained archaic features of *U. deningeri* (Baryshnikov and Dedkova 1978).

The morphological features of *U. spelaeus* were enormous size and weight (up to 1,000 kg); flat, bunodont molars; a bulging frontal; a powerful sagittal crest; a narrow nasal foramen; and a shortened tibia. These features suggest that the cave bear was less mobile and more vegetarian than the contemporary *Ursus arctos* L. Ecologically the cave bear was closely tied to caves, in which it lived and bore its young. This behavior turned out to be fatal for the species at the end of the Würm (Wisconsin). Practically all of its remains have been found in caves; remains are virtually unknown from alluvium, loess, or covering loams.

Paleolithic tribes regularly hunted the cave bear, and in western Europe there was a strong link between this animal and the life and evolution of man. Similarly, remains of at least 200 individual bears were found in the Acheulean levels of Kudaro I in the Caucasus.

The cave bear probably became extinct at the same time as the mammoth and the rhinoceros in the late Würm (Magdalenian), since cave bear bones have not been found in Mesolithic sites on the Russian Plain or in the Urals.

Kurtén (1968, 1976) and Gabuniya (1969) review the many hypotheses that have been advanced to explain the extinction of the cave bear. The most popular hypotheses are degeneration as a consequence of inbreeding in isolated populations, imperfect morphological adaptations to a vegetarian diet via nonadaptive evolution, and Paleolithic destruction of the bears in their caves. Like Davitashvili (1969), Gabuniya thinks that cave bears were outcompeted and displaced by brown bears, but this is confusing cause and effect. The omnivorous brown bear may have competed with the herbivorous bear but could not have caused its destruction. In any case, brown bears were rare in the Pleistocene.

We note the fatal attraction of caves to the cave bears. At the end of the glacial epoch, some of the caves that the bears regularly occupied became insidious traps when water levels rose in rivers and streams during the thaw. For example, a succession of caves in the upper reaches of the Kama and Pechora rivers in the Urals became death traps over a period of several centuries (Vereshchagin 1982b).

The bears survived somewhat longer in the western Caucasus and in the upper reaches of the tributaries of the Rion (Kudaro II) than in other regions. Cave bear bones with well-preserved collagen have been found in local caves.

A basic factor in the extinction of this species was the change from a dry, continental climate to a moist one, which made for damp and uncomfortable microclimates in cave refuges.

A closely related species was the small cave bear *Ursus rossicus* Borissiak, which was morphologically even more specialized. It lived in eastern Europe and western Siberia outside karst regions, that is, it was less tied to caves. Nonetheless, like its giant colleague, it became extinct, a fact which seems to point to some evolutionary dead end in the morphology of the cave bear.

The Cave Hyena *Crocota spelaea* Goldfuss, 1823

Pliocene and Quaternary deposits in the Old World have produced remains of various species of hyenas belonging to two basic phylogenetic branches, represented today by the genera *Crocota* and *Hyaena*. Representatives of both genera occurred in the Pleistocene of Europe. The striped hyena (*Hyaena hyaena* L.) disappeared in Europe sometime during the Pleistocene, while the cave hyena survived to the end of it (Thenius 1980).

In cranial and skeletal features the cave hyena is very similar to the spotted hyena (*Crocota crocuta* Erxl.) of Africa. Therefore European paleontologists frequently consider the cave hyena to be a northern subspecies of typical African *Crocota*. However, this conclusion is debatable.

In Europe, *C. spelaea* appeared in the Cromerian Interglacial, and in the USSR in the Tiraspol' fauna. At the same time, in a series of features, the early forms—for example, the small hyena from Süssenborn—resembled the modern spotted hyena more than the cave hyena (Soergel 1936).

The cave hyena was highly specialized with extremely massive bone-crushing molars and weak canines. Its progressive and regressive features were more highly developed than in modern *Crocota*. It possessed the awkward construction and elevation of the forepart of the body found also in the cave bear.

The range of the cave hyena covered all of Europe and the subtropical and middle latitudes of northern Asia, reaching to about 56 degrees N in Siberia. It apparently did not penetrate the arctic zone, nor did it occupy high mountains, since its remains have not been found in alpine sites in the Caucasus (Kudaro, Tsona). If the concept of a single African-Eurasian species is correct, then it did not become extinct, but merely suffered a catastrophic shrinkage of the northern, Eurasiatic portion of its range. The cave lion presents a potentially analogous case (see below).

Massive accumulations of cave hyena bones, together with coprolites and bones of prey animals, have been found in many European caves. For example, Kirkdale Cave in England provided abundant remains of hyenas of all ages, from newborn to old, while Tornewton Cave supplied more than 20,000 cave hyena teeth (Kurtén 1968). In the USSR hyena bones are common in caves in the Altaj (Hyena Den Cave) and the Far East (Geographic Society Cave) (Ovodov 1980). The species denned in caves and sometimes died there, vanishing into karst wells (Ageeva et al. 1978).

Like the African spotted hyena, the cave hyena fed primarily on carcasses of large ungulates and thus completed the stage of "secondary biomass" utilization, prior to final destruction by larval insects and bacteria. It is also possible that it hunted rodents, young ungulates, and mammoths.

Reduction in the numbers and range of the cave hyena coincided with the disappearance of herds of steppe and forest-steppe ungulates at the boundary between the Pleistocene and the Holocene, when the plains became boggy and the taiga developed. Like the modern aborigines of Africa, Paleolithic hunters only rarely captured hyenas; fragments of hyena bones, skulls, and teeth are rare in Paleolithic sites, especially in ones dated to the Solutrean-Magdalenian Culture. In the USSR no cave hyena bones have been found in any Mesolithic or Neolithic site.

The cave hyena's extinction is seen by some paleozoologists as a result of excessive specialization and of the anthropological factor—a sharp decline in the number of wild ungulates combined with the growth of agriculture and stock-breeding (Pidoplichko 1951a).

The Cave Lion *Panthera spelaea* Goldfuss, 1810

The history of this gigantic cat is both uncertain and puzzling. Its earliest record in Europe is from the Cromerian Interglacial in the Mosbach fauna. Some European paleontologists (Ryabinin 1919, Hemmer 1967, Kurtén 1968) think that the cave lion was only a subspecies of the modern African *Panthera leo* L. Although these animals are far apart in time and space, they are very similar in cranial and skeletal features. However, there are some differences. The cave lion exhibited even greater specialization of the feline type than the modern lion (Vereshchagin 1971a).

The concept of a single species implies the existence of a single range from the Cape of Good Hope in southern Africa through Scandinavia, Tajmyr (Taymyr), and Beringia in Eurasia, and into North America, to California and Mexico. No other species of mammal has a comparable range (Kurtén and Anderson 1980).

Other scholars (Goldfuss 1821, Leidy 1853, Gromova 1932) believe that the cave lion was a separate species. Besides its adaptation to cold conditions and its typically large size, it possessed cranial and skeletal features reminiscent of both the lion and the tiger (*P. tigris* L.). Its distribution was limited to the northern half of Eurasia, including Europe, from the British Isles through the Crimea, the Caucasus, Siberia, the Far East, Beringia, and even Alaska and the whole southern half of North America, where there was a closely related subspecies, *P. spelaea atrox* Leidy.

In habits and morphology the cave lion was closer to the lion than to the tiger. In the mountains it used caves as refuges, but on the plains it survived without them. It fed on horses, deer, bison, musk ox, and saiga, and in America on horses, bison, camels, and giant sloths. Its existence depended on the abundance of these herbivores.

The cave lion apparently became extinct when populations of ungulates declined sharply at the end of the Würm (Valdaj, Wisconsin). It is interesting that this extinction apparently occurred at the same time in Eurasia and North America, around 10,000 years ago.

Naturally, the proponents of a single African-Holarctic species of lion recognize the extinction of only the north Eurasiatic and North American Pleistocene populations of this remarkable animal. In Europe paleontological finds indicate that a lion of African type survived longest on the northern Black Sea littoral (until 3000 B.C.; Bibikova 1973). On the Balkan Peninsula, lion was still present at the beginning of the Christian era, if we believe Herodotus that lions preyed on the camel caravans of Xerxes.

The Woolly Rhinoceros *Coelodonta antiquitatis* Blumenbach, 1799

A characteristic "fellow traveler" of the mammoth, the woolly rhinoceros apparently evolved in the early Pleistocene in the steppes of Mongolia, Transbaikal, and north China. Here the ancestral, early Quaternary form, *C. tologoiensis* Beljaeva, has been found at Tologoi on the River Selenga. Here is also the greatest concentration of woolly rhinoceros fossil remains, dating mainly from the Middle and Upper Pleistocene.

In western Europe the woolly rhinoceros is known from the Mindel (Frankenhausen, Bornhausen), where the molars are less specialized than in later forms (Sickenberg 1962). The woolly rhino became very numerous in the Riss. On the Russian Plain woolly rhinoceros skulls and rarer ones from Merck's rhinoceros (*Dicerorhinus kirchbergensis* Jaeger) occur in the alluvium of the Don and Volga, dated to the second half of the Middle Pleistocene.

The woolly rhinoceros achieved its maximum distribution in the Würm (Valdaj), when it was widespread throughout northern Eurasia, reaching the shores of the North Sea on the west and Italy, the northern Caucasus, and Kirgizia on the south. In north-east Siberia it reached the Kolyma and Anadyr basins and the shores of the Sea of Okhotsk. It is unclear why it was unable to cross the Bering Land Bridge into the New World during the Würm (Wisconsin) continental phase.

A series of morphological and biological features—the low position and inclination of the head, the thick woolly coat, the grassy diet (judging by the stomach contents of the Churapcha specimen from Yakutia)—indicates that this rhinoceros inhabited cold tundra-steppe. There is a paradoxical ecological similarity between the Eurasian tundra-steppe rhinoceros and the white rhinoceros of the African savannas.

It is usually believed that this species became extinct at the same time or earlier than the mammoth, and earlier in Siberia than in western Europe. However, from the collagen* still found in woolly rhinoceros bones in the covering loams of the Ukraine, Pidoplichko (1951b) sometimes established very late dates, on the order of 800–1000 years B.C. "Fresh" examples of rhinoceros bones with the distinct odor of collagen also occur in the Kazan University collections. Other materials from various places, dated by radiocarbon, provide dates on the order of 12–14,000 years B.C. (figs. 22.4, 22.5).

Upper Paleolithic people energetically hunted the woolly rhinoceros. In Upper Paleolithic sites on the Russian Plain rhinoceros bones comprise 1.5–3 percent of all the bones from animals that people exploited (Vereshchagin 1979), while the figure reaches 3–4 percent in sites in Cisbaikal (Ermolova 1978). In the Transbaikal steppes rhinoceros remains are remarkably abundant both in natural burials and in Paleolithic sites. We know little about Paleolithic methods for hunting the rhinoceros or about the impact these hunts may have had on the species. Active hunting with javelins and arrows is shown in the wall art of La Colombière Cave (France). It is probable that the animals were also caught in pits dug across their habitual trails.

Neither depictions of the woolly rhinoceros nor its bones have been found in Mesolithic or Neolithic sites. Thus, the best explanation for its extinction at the end of the Pleistocene and beginning of the Holocene is its morphological inability to adapt to the changing environment. There is a notable analogy to the mammoth in this respect.

The Giant Deer *Megaloceros giganteus* Blumenbach, 1803

Large-antlered deer of the tribe Megalocerini are known in Europe from the Villafranchian and in the USSR from the time of the Khapry fossil mammal complex (Baryshnikov 1981). Through time they increased in body size, while their antlers became more complex and more palmate.

Giant deer apparently first appeared in Europe. An early representative—*Megaloceros giganteus antecedens* Berck. from the Mindel-Riss of Germany (Steinheim)—had broadly palmate antlers. However, these were directed posteriorly, permitting the animals to occupy forest. In the Middle Pleistocene (Riss) *M. giganteus*, with broadly splayed antlers, became abundant (Gromova 1965). Its remains are common

*No positive ¹⁴C dates on collagen. —EDS.

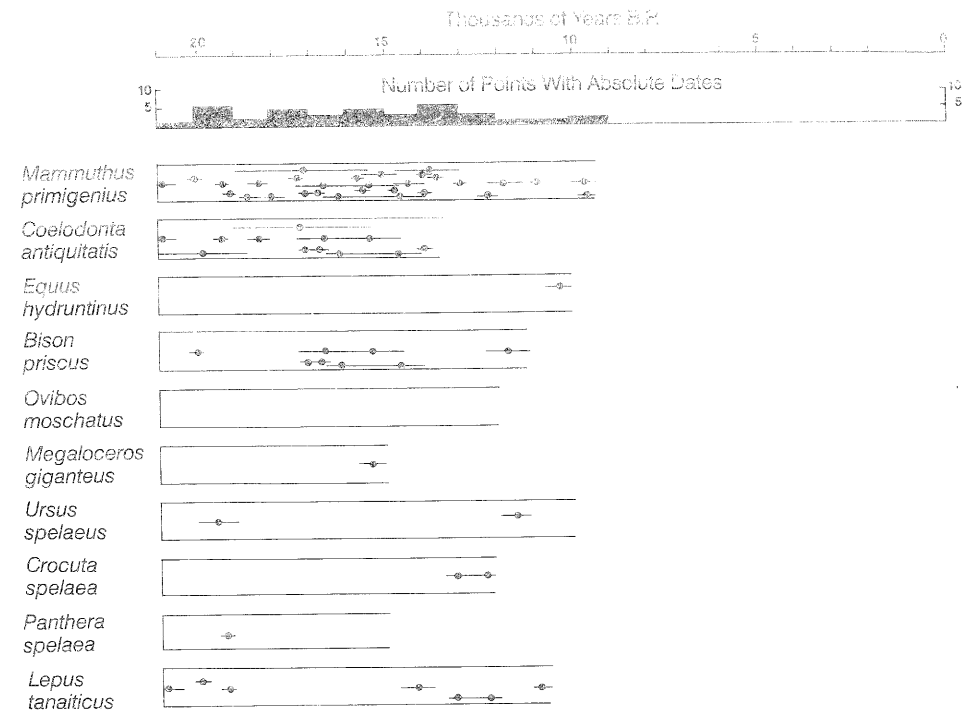


Figure 22.4. The latest radiocarbon dates for remains of Pleistocene mammals in eastern Europe and the Caucasus.

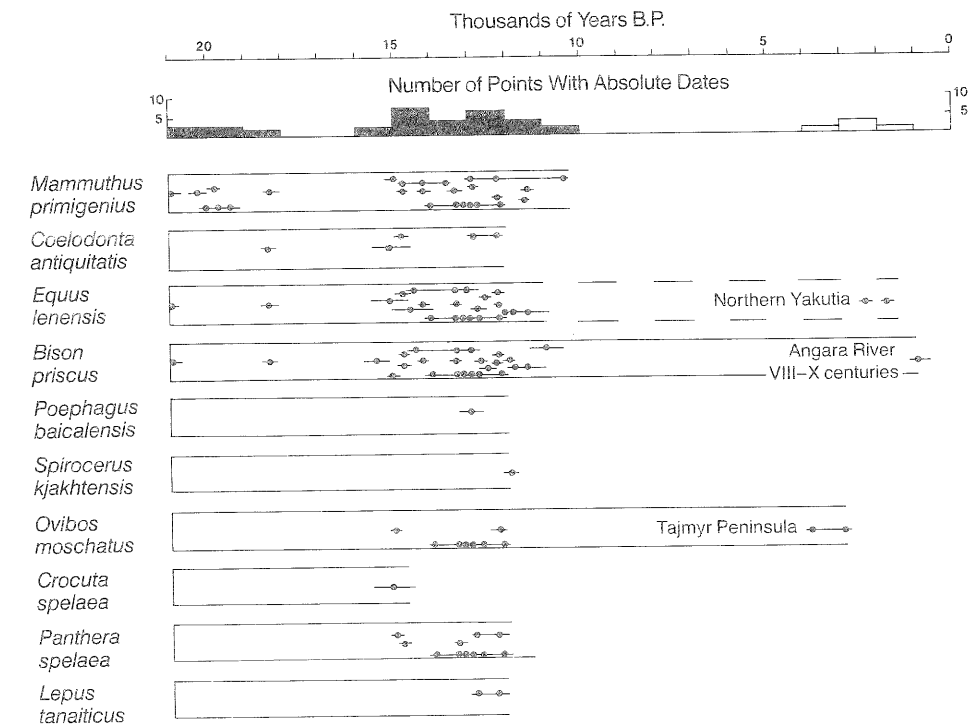


Figure 22.5. The latest radiocarbon dates for remains of Pleistocene mammals in Siberia.