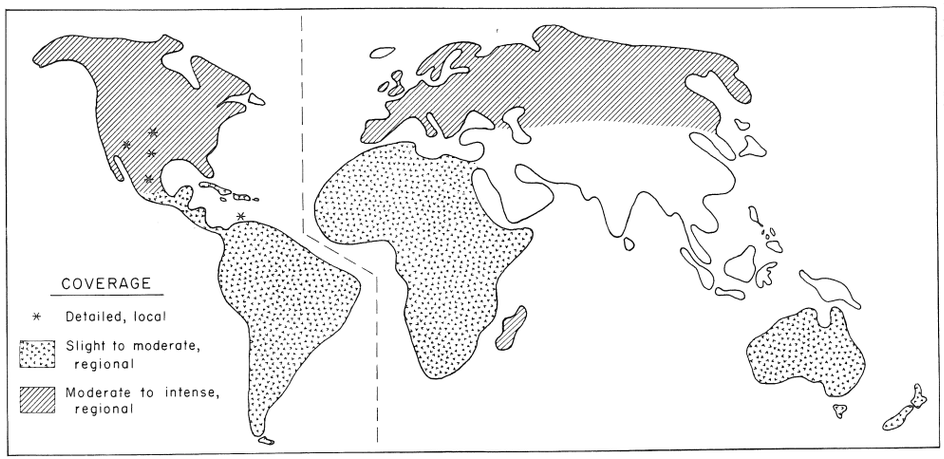

World coverage of Pleistocene extinction as discussed by contributors to this volume. Unshaded areas are not treated.

PLEISTOCENE EXTINCTIONS
The Search for a Cause

Volume 6 of the Proceedings of the VII Congress of the International Association for Quaternary Research

Sponsored by the National Academy of Sciences–National Research Council

Editors

P. S. MARTIN AND H. E. WRIGHT, JR.

NEW HAVEN AND LONDON, YALE UNIVERSITY PRESS, 1967

KAZIMIERZ KOWALSKI
Institute of Systematic Zoology
Polish Academy of Sciences
Kraków, Poland

THE PLEISTOCENE EXTINCTION OF MAMMALS IN EUROPE

Abstract

In Europe—which, because of its geographic situation had only limited possibilities of faunal migrations between north and south—the Ice Age caused the impoverishment of fauna. This depletion affected all groups of mammals (except, perhaps, bats), but it especially influenced the larger mammals, which were not able to survive in the small refuges of southern Europe. Their limited populations approached more easily the point at which the lack of genetic plasticity, accidental change of sex ratio, epidemics, and other factors could bring about their extinction.

The hunting activity of primitive man, even over a very long period, does not necessarily bring the extinction of his prey. Extensive literature concerning the hunting habits of European Paleolithic man indicates that all large phytophagous mammals were hunted, but it is very difficult to judge the size of the human population and the degree to which hunting influenced the population of particular species. Reindeer, red deer, aurochs, wild horse—all extensively hunted—were able to survive, whereas some mammals, which were probably more difficult for primitive man to kill (mammoth, woolly rhinoceros, cave bear) or were of no interest to him (lion, hyena), became extinct. When the density of the prey dropped, man with his primitive weapons could not get enough game and began to hunt other animals, migrated, or finally died of hunger. Not only in the forests of Europe but also in the steppes of Asia, numerous herds of large herbivorous mammals were able to persist in spite of centuries of hunting, until in modern times they were decimated with firearms. The extinction (local, at least) of many mammals was caused only by the development of agriculture and/or the raising of domestic animals, which make the human population independent of game animals.

In the forest zone of Europe, only extensive deforestation in the late Middle Ages brought the danger of extinction to such species as the aurochs and the bison. No doubt, the preservation of the European bison, as well as of other

mammals (such as beaver, elk, red deer, and brown bear) is now possible only through active protection.

The extinction of large mammals at the end of the last glaciation is less dramatic in Europe than in North America. Its main cause, in Europe, was the disappearance of the specific habitat represented by the "steppe–tundra" of the Pleistocene. The species connected with this biotope became extinct, while others were able to survive in the zone of warm steppes (horse and saiga) or of tundra (reindeer).

The extinction of large mammals in Europe needs further research, especially in radiocarbon dating and the stratigraphy of Paleolithic sites, chiefly in caves.

A comparison of Europe and North America can be of interest in the study of the Pleistocene extinction of animals. Although the climatic and geologic conditions were similar, man coexisted much longer with the fauna in Europe than in North America, where the primitive human population appeared dramatically at the decline of the Ice Age. Knowledge of the composition of the European Quaternary mammalian fauna is extensive but still far from complete.

Using Guilday's conclusions (this volume) I shall try to distinguish between extinction through evolution—the disappearance of a species through its transformation into another—and true extinction—the disappearance of an evolutionary line without descendants. The first type of extinction proves the success of a phylogenetic branch, and the second, its failure; the types are therefore antithetical. Sometimes, however, this distinction is not simple. In the fauna of European small mammals, the rodent genus *Mimomys* disappeared in the early-Pleistocene and was replaced in northwestern Europe by a similar genus, *Arvicola*, representing a higher stage in the development of molar teeth. It was recently discovered, however, that in southeastern Europe *Arvicola* appeared earlier and coexisted during a long period with the latest species of *Mimomys*. *Arvicola* apparently developed from one of the kinds of *Mimomys*, probably outside Europe. In some regions, then, *Mimomys* experienced "extinction through evolution." In regions characterized by the "true extinction" of the genus, *Arvicola* appeared when some species of *Mimomys* still existed and perhaps caused their extinction through active competition. The same systematic unit can therefore disappear partly through evolutionary and partly through true extinction.

When discussing the Quaternary fauna of European mammals and its changes, we must keep in mind the peculiar geographic situation of that continent. Europe, which could be considered a peninsula of Asia, is wide open to migrations from the east. At the same time, the Mediterranean Sea and the European mountain ranges that run mostly

from east to west limit to a great degree the possibility of migration from north to south. In the cold periods typical of the Pleistocene, elements of the thermophilous fauna could find shelter in the forest regions of Southern Europe, but the Pyrenean and Apennine regions and the Balkan peninsulas were limited in space and were isolated.

In spite of many studies, we still do not know enough about the change in the European Quaternary faunas to be able to correlate them with the pattern of four glaciations described by geologists. Many paleozoologists, primarily in unglaciated regions of Europe, prefer therefore to use special names for the periods of the faunal development, independent of the names of glaciations (Kretzoi, 1965). Farther north the connection of the faunal changes with the course of glaciations, especially later ones, is evident.

The Ice Age, as a whole, caused the extinction of the rich Pliocene fauna of Europe, with its numerous subtropical elements. In the oldest Pleistocene (Villafranchian) a successive extinction of many evolutionary lines occurred (e.g. of mastodonts, tapirs, gazelles, *Parailurus*, and many groups of deer). The same is true for small mammals and also for many plants (*Azolla*, *Tsuga*, *Pterocarya*, *Magnolia*). Even in the Mediterranean regions, where the modern climate is similar to that of Central Europe in the late Pliocene, the fauna is much poorer as a result of Pleistocene extinction. The family Soricidae, for example, is represented in the Pliocene of central Europe by the genera *Sorex*, *Neomys*, *Crocidura*, *Petenyia*, *Beremendia*, *Blarinoides*, *Petenyiella*, *Soriculus*, and *Allosorex*, with numerous species. In similar climatic conditions in southern Europe, the same family recently contained only four genera: *Sorex*, *Neomys*, *Crocidura*, and *Suncus*, with few species. This depletion of the fauna of Europe has not yet been compensated, because migrations in the Holocene were somewhat restricted by geographical barriers. In eastern Asia, where the migrations from north to the south were not impeded, the fauna of Insectivora is much more diversified—comparable to that of preglacial Europe. Many ecological niches are therefore unoccupied in the recent fauna of Europe, particularly in glaciated islands (e.g. Ireland, where moles, voles, and many other mammalian species are lacking, and their niches apparently empty).

The spatial limitations of the refuges of European thermophilous fauna during the Ice Age had different effects on different species. In many cases large mammals became extinct, whereas small mammals were able to survive in limited territories but were sometimes no longer able to expand when conditions improved. For example, water-moles (Desmaninae), widely distributed over Europe in the Pliocene and early Pleistocene (Fig. 1), now live only in two refuges, the Pyrenees (*Desmana*

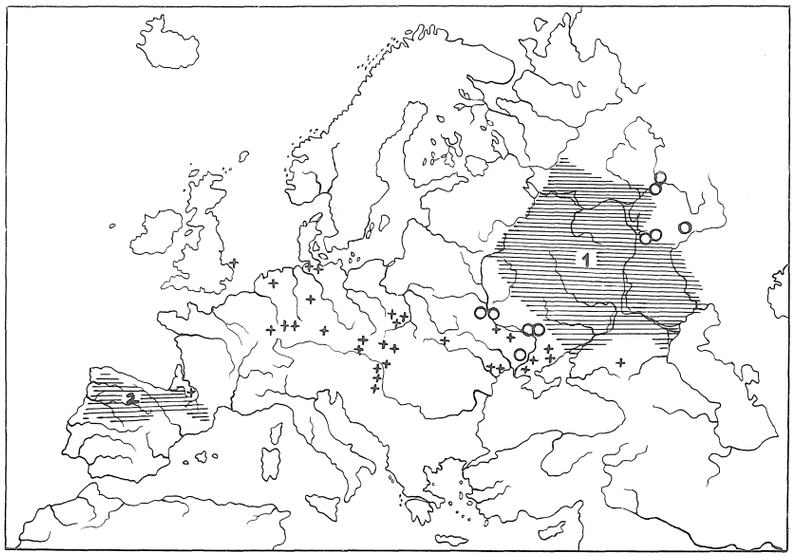

FIG. 1. Distribution of *Desmana* in Europe. 1, *D. moschata;* 2, *D. pyrenaica;* +, fossil localities; O, localities of recent artificial introduction. Once continuous areas are now limited to refuges because of the Ice Age.

pyrenaica) and the Ukraine (*D. moschata*). Other species, when the ice retreated, managed to spread again into central and northern Europe. The moles (*Talpa europaea*) of Europe are clearly differentiated into three forms—western, central, and eastern—each of which expanded in postglacial time from other refuges (Fig. 2) (Stein, 1963).

Thus the Pleistocene brought the gradual extinction of many mammalian elements of the "warm" Tertiary fauna. Particular species died out during different glaciations. The extinction affected large as well as small mammals, although the latter had a better chance of surviving in refuges; sometimes their isolation during cold periods brought the evolution of new subspecies or even species.

The influence of the last glaciation (Würm) on the fauna of Europe is better known than that of earlier glaciations. The small-mammal fauna of the last interglacial (Eemian) in Europe is very similar to the recent one. Not a single species of micromammalia of the European Eemian forest fauna is completely extinct today, but the fauna of the large mammals contains extinct as well as extant species, the former including the forest elephant *Palaeoloxodon antiquus*, the rhinoceros *Dicerorhinus kirchbergensis*, the hippopotamus *Hippopotamus amphibius*, and fallow deer *Dama dama*. The hippopotamus and fallow deer

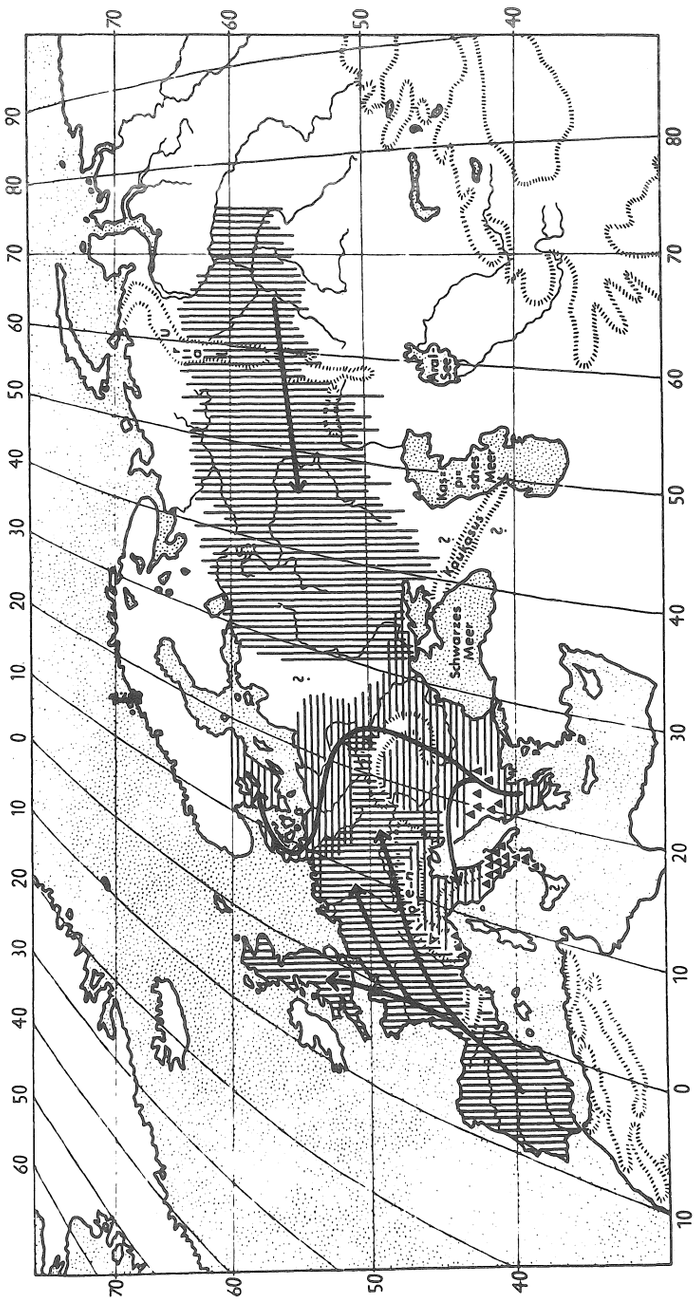

FIG. 2. Distribution of *Talpa europea* in Europe. Vertical lines, populations with narrow skulls; horizontal lines, populations with broad skulls; solid triangles, *T. e. romana.* Repopulation of central Europe after glaciations starting from different refuges (after Stein, 1963).

disappeared in Europe but still exist outside its limits (fallow deer was later reintroduced in Europe for hunting). The extinction of these species can be explained by changes in climate. The last glaciation limited the suitable biotope of enumerated species to a few areas in southern Europe. The population of elephant and rhinoceros in each of the refuges was so small that even a local factor could bring extinction. Man was present at that time in Europe, but there is almost no evidence for his role in extermination of animals; at such a primitive stage of culture he probably was not a real danger for animals as large as elephant or rhinoceros. The disappearance of these large mammals at the end of the last interglacial is the last episode in the great extinction of European fauna caused by Quaternary climatic changes in conjunction with the geographical configuration of the continent. According to the quantity of their populations and the extent of individual areas, large and small mammals were affected differently by the climate.

The Würm glaciation brought a great extension of the Scandinavian ice sheet and the total destruction of the fauna of northern Europe. The European climate became increasingly continental as a permanent center of high atmospheric pressure developed above the ice sheet and the extent of the sea diminished (because of the glaciation of the Baltic and North seas and by the isostatic lowering of the world oceanic level). The great area of the "steppe–tundra" was formed, connecting central and western Europe with the steppe regions of western and central Asia, with the rich fauna of open country. The composition of the rodent fauna, as well as pollen analysis, shows that the character of Pleistocene vegetation at the time was different from that of the recent Arctic tundra in northern Europe and from that of the recent dry steppes in southeastern Europe and southwestern Asia. In the Pleistocene of central Europe the lemmings *Lemmus* and *Dicrostonyx*, which are now limited to the tundra, lived side by side with the small hamsters (*Cricetulus*), now confined to the steppes far south of the lemming area. *Microtus gregalis*, a characteristic rodent of the Würm glaciation in Europe, lives today in the tundra and steppe regions of central and eastern Asia. In general, Pleistocene vegetation from the time of the Würm glaciation is most analogous to the vegetation of eastern Asia, which developed under the influence of a cold continental climate in middle latitudes.

At the decline of the Würm glaciation in Europe, small mammals of the steppe and tundra retired toward the north or southeast, unable to live in rapidly developing forests. During the same period six species of the larger mammals became extinct: mammoth (*Mammuthus primigenius*), woolly rhinoceros (*Coelodonta antiquitatis*), Irish deer (*Megaceros giganteus*), cave bear (*Ursus spelaeus*), cave lion (*Panthera spelaea*), and

cave hyena (*Crocuta spelaea*). The extant European bison (*Bison bonasus*) may be the direct offspring of the extinct primitive bison (*Bison priscus*). The musk-ox (*Ovibos maschatus*) became extinct in the Old World but still lives in America. The wild horse (*Equus przewalskii*) lives in Central Asia; the saiga antelope (*Saiga tatarica*) persisted in Asia as well as on the outskirts of Europe; and the reindeer (*Rangifer tarandus*) was preserved partly as a wild, partly as a domestic animal, in extreme northern Eurasia.

Mammoth (*Mammuthus primigenius*) developed from the steppe elephant (*Elephas trogontherii*) in the penultimate (Riss) glaciation. Its makeup is well known, because, besides numerous skeletal remains, many specimens with soft parts are preserved in the permafrost of Siberia, and one in a layer of silt, impregnated with petroleum and salt in Starunia on the northern slope of the Carpathians (Garutt, 1964). The mammoth's adaptation to the cold climate is provided, for example, by its long hair, small ears, and tusks shaped to drive away snow in the search for food in winter. The geological situation of mammoth fossil remains, and the accompanying fauna and flora indicate that it lived in an open, woodless landscape.

The mammoth, whose Old World fossil remains are distributed from the Atlantic to the Pacific and from the Arctic to the Mediterranean and to Central Asia, probably had a more limited range at any one time. Carbon-14 dates of mammoth corpses discovered in Siberia range between 32,500 and 39,000 years B.P. (Heinz and Garutt, 1964) and thus suggest correlation with the relatively warm oscillation (Göttweig) within the last glaciation. The mammoth from Taimyr was dated by the above authors as 11,450 ± 250 years B.P. (an indication of the Allerød warmer oscillation at the end of the last glaciation). The stratigraphy of the European sites with mammoth also suggests its disappearance at the end of the Würm.

There is no doubt that Upper Paleolithic man hunted the mammoth. Probably it was done mostly by stampede, but pitfalls were also in use. The important role of mammoth in the engravings and sculptures of primitive man in Europe also suggests that it was hunted (Fig. 3).

The problem of the extinction of mammoth has been widely discussed. Earlier hypothetical explanations—e.g. that its extinction was a consequence of its poor adaptation to the conditions of life (Neuville, 1921)—now have only historical significance. The suppositions about a larger number of specimens with pathological characteristics immediately before extinction find no confirmation in an analysis of broader materials (Kubiak, 1965). The role of Paleolithic hunters in the extinction of mammoth is difficult to estimate, but mammoth was probably never

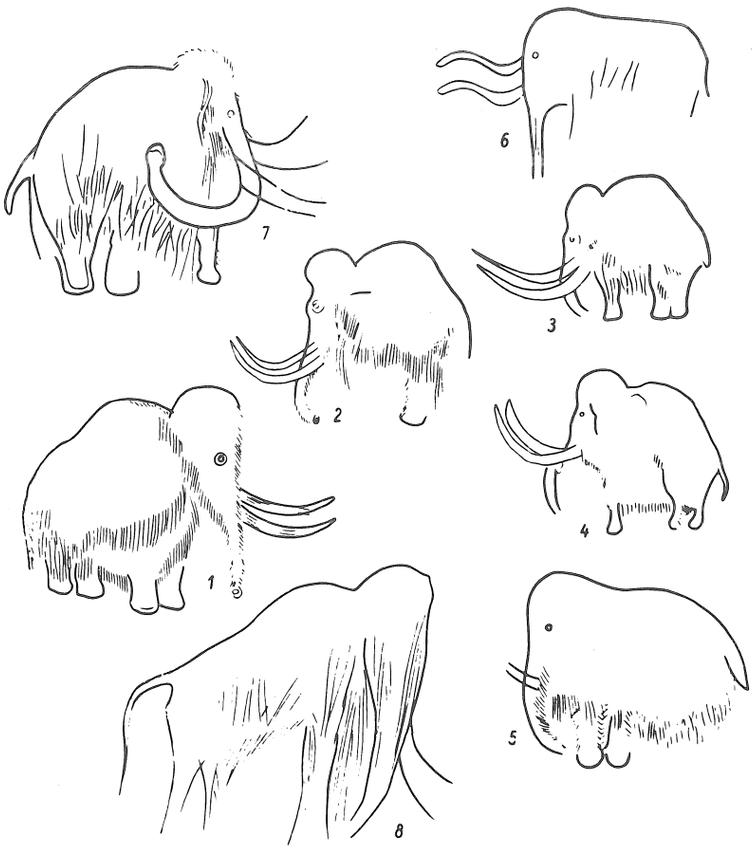

FIG. 3. Paleolithic drawings of mammoth (*Mammuthus primigenius*) (from different sources, after Garutt, 1964).

the principal game of human groups, and the traces of human colonization of Siberia at that time are very scarce.

The most logical explanation of the extinction of mammoth seems to be that it was caused by the disappearance of its habitat at the end of the Würm glaciation. The Pleistocene vegetation during this glaciation was different from that of the northern tundra as well as from that of the present steppes in Europe and western Asia. The adaptation of mammoth to the cold climate precluded life in the southern steppes, with their warm and dry summers. The present tundra, north of the Polar Circle, is very different from the steppe–tundra of the late Pleistocene; long polar nights and abundant snowfall in winter create

quite peculiar conditions of life. Central and western Europe, independent of temperature changes in the Pleistocene, had the same geographical latitude as today and, of course, no polar night; the snowfall was probably slight. The development of forests in the postglacial of Europe and Siberia (Vangengeim, 1961) restricted the habitat of mammoth and finally caused its extinction.

The history of the woolly rhinoceros (*Coelodonta antiquitatis*) is similar. It is also known from the corpses with soft parts preserved in the permafrost of Siberia and particularly in the salt- and petroleum impregnated silt in Starunia on the northern slope of the Carpathians (Fig. 4). Hypsodont molars, reduced front teeth, and the anatomy of the upper lips prove that it was a grass-eating animal; the long hair and the paleontologic and geologic data suggest its adaptation to cold climate. The woolly rhinoceros did not develop until the late Pleistocene. The remains found on the Indigirka River in Siberia are radiocarbon-dated at 38,000 years B.P. (Heinz and Garutt, 1964); the species became extinct in Europe at the end of the Würm glaciation. Although *Coelodonta antiquitatis* was sometimes represented in Paleolithic art, few data suggest that it was hunted in the older Stone Age. In all probability its extinction may be explained by the disappearance of its proper habitat, as in the case of mammoth.

The Irish deer (*Megaceros giganteus*) also developed in the late-Pleistocene. Its older forms (*M. g. antecedens*), provided with smaller antlers, could have been forest animals, but later populations (*M. g. giganteus*) lived in an open landscape, as is suggested at least by the enormous antlers, which probably would have made movements in forests impossible. The Irish deer, probably confined to milder climate than was the contemporaneous reindeer, was still living in the Allerød, when the warming climate caused the expansion of forests, and died out in the beginning of the Dryas period about 10,000 years B.P. (Guenther, 1960).

The European primitive bison (*Bison priscus*) undoubtedly inhabited open, treeless country of the late Pleistocene. Its relation to the extant forest bison (*B. bonasus*) needs further study (Degerbøl and Iversen, 1945). *B. priscus* might be the ancestor, or both forms might have lived side by side in different habitats, and *B. priscus* might have disappeared with the decline of grassland in Europe at the end of the last glaciation, while the other persisted. The steppe bison was important game for primitive man and was often represented in Paleolithic art.

Musk-ox (*Ovibos moschatus*) developed from a species adapted to mild climate and was not confined to an arctic environment until the late-Pleistocene. Its extinction in the Old World is difficult to explain,

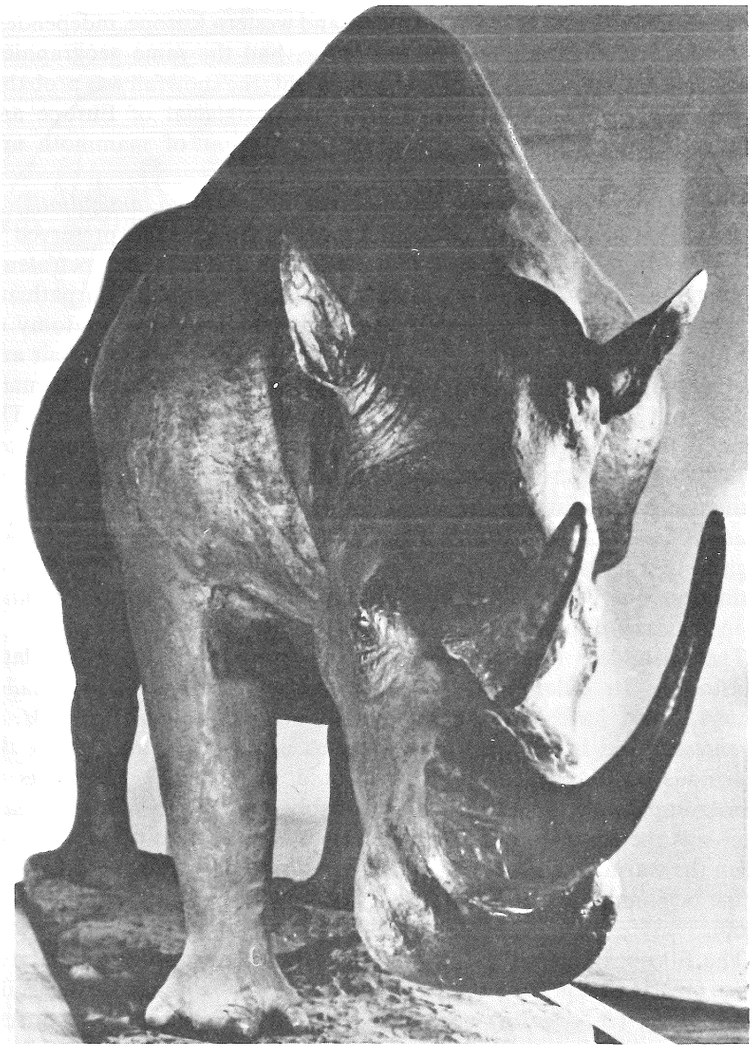

FIG. 4. Woolly rhinoceros (*Coelodonta antiquitatis*), specimen preserved with soft parts in Starunia, now in the museum of the Institute of Systematic Zoology, Kraków (photo by L. Sych).

because it seems to have been well adapted to life in the Eurasian tundra. Few data indicate that it was hunted by Paleolithic man; its distribution was probably always limited to the sparsely inhabited periglacial regions.

In spite of voluminous literature devoted to the wild horse, a clear picture of its extinction in Europe is difficult to obtain. In the open areas of the late Pleistocene, the wild horse was very common and was a principal prey of Paleolithic hunters. In the postglacial, the range of the wild horse contracted, beginning with western Europe, and *Equus przewalskii* now lives only in the semideserts of Central Asia (Mohr, 1959), on the verge of extinction. Historical data prove the existence of wild horses in the Ukrainian steppes as late as the middle of the nineteenth century. These horses were described as a separate species, *Equus gmelini*, but they were more probably feral. Vetulani (1933) supposed that the peculiar forest form of *E. gmelini* was extant in western Europe in the Middle Ages and in Poland as late as the eighteenth century. Primitive domestic horses in Poland were, according to him, the direct descendants of these wild horses, and he started to reconstruct this form by breeding the Polish primitive strain in wild conditions (Vetulani, 1948). In these continuing experiments, the animals have developed some apparently primitive characters (not necessarily related to ancestral genotypes). The existence of a sylvan form of the horse seems ecologically improbable, and the supposed "forest tarpan" was probably a feral domestic horse. The postglacial development of forests made the existence of the wild horse in western and central Europe impossible, and the final limitation of its area to the semideserts of central Asia was the result of predation by man.

The extinction of the cave bear (*Ursus spelaeus*), the remains of which are very abundant in European caves, has been widely discussed (Kurtén, 1958). The cave bear appeared during the Mindel Glaciation, survived two later glaciations and two interglacials, and became extinct at the end of the Würm glaciation; its latest remains are from Würm III. It coexisted in Europe with the brown bear (*U. arctos*), but these two species were seldom found together. The cave bear can be distinguished from the brown bear by its larger dimensions, by many details of the skeleton and dentition, and by its probably strictly phytophagous habits.

Abel's suggestion (1929) that the extinction of the cave bear was anticipated by the appearance of degenerated, pathological specimens and by the excess of male births was rejected by Kurtén (1958) as being based on fragmentary or erroneously interpreted material. Another hypothesis holds Paleolithic man responsible for the extermination of the cave bear; according to some archaeologists, tribes of Mousterian man living mostly in mountains specialized in hunting bears. These suppositions also lack an adequate factual basis, and they concern the time of the Eemian Interglacial, long before the process of extinction of cave bear began. Kurtén (1958) stated that the extinction of cave bear was gradual,

and that in many regions the species disappeared long before its final extinction elsewhere. Before extinction, isolated populations with a limited number of specimens revealed the effects of inbreeding in the diminished variation of morphological characters.

There is no defense for Kurtén's explanation that cave bears disappeared because of the occupation by Paleolithic man of caves used as bear dens. Most of the remains of cave bear were found in caves only because of the much better conditions for the preservation of bones in cave sediments than outside, and not because of a narrow specialization of cave bear to wintering in caves. In the Tatra Mountains of Poland, where brown bears still exist, their subfossil remains are found exclusively in caves. The animals hibernate sometimes in caves, but even in the calcareous Tatras, where caves are abundant, the hibernation places are generally located below uprooted trees in the forests. The preservation of bones outside caves, especially in mountains where erosion prevails over accumulation, is very unlikely. Because of the highly irregular distribution of caves in Europe, it is hard to imagine a species of large mammals that depended on the caves for its existence. In the same period, Paleolithic settlement of caves, except for some regions in France and Spain, was irregular and sporadic. In Poland the caves with bear remains have only scarce traces of human habitation, and the high mountains (e.g. Tatra), where cave bear remains are numerous, had no Paleolithic habitation at all. The competition for shelter between Paleolithic man and cave bear, therefore, cannot be the principal cause of the reduction of the once numerous population of this animal to scattered small groups as a prelude to extinction. Here again, the disappearance of the proper biotope seems to be the most probable cause of extinction.

Cave lion (*Panthera spelaea*) and cave hyena (*Crocuta spelaea*) became extinct in the final stages of the Würm glaciation. They were probably never regularly hunted by Paleolithic man.

Most large Pleistocene forest mammals able to survive the last glaciation still live in Europe: the elk (*Alces alces*), red deer (*Cervus elaphus*), roe deer (*Capreolus capreolus*), wild boar (*Sus scrofa*), and others. Two of them have faced extinction in historical times: the aurochs (*Bos primigenius*), which disappeared in the wild and survived only as domestic cattle, and the European bison (*Bison bonasus*), which was saved through active protection when it was on the verge of extinction.

Aurochs appeared in Europe during the Holsteinian or Great Interglacial (Mindel–Riss) and survived two glaciations. It was principally a member of the forest community but was also able to live in open areas. Aurochs was distributed through Europe except for the northernmost regions, northern and temperate Asia and northern Africa. Important

game of Paleolithic man, it was hunted also in later prehistoric times, in antiquity, and in the Middle Ages. The rapid process of its extinction began in the late Middle Ages, probably as a result of extensive deforestation. In the thirteenth century aurochs were still present in France, Germany, Sweden, Poland, and Russia. In the fourteenth and fifteenth centuries they virtually disappeared as wild animals (Fig. 5). In Poland the hunting of aurochs was early reserved for monarchs and sovereigns, who prohibited general hunting of the animal and commanded their protection (e.g. Prince Boleslaus of Masovia in 1298, Prince Ziemovit of

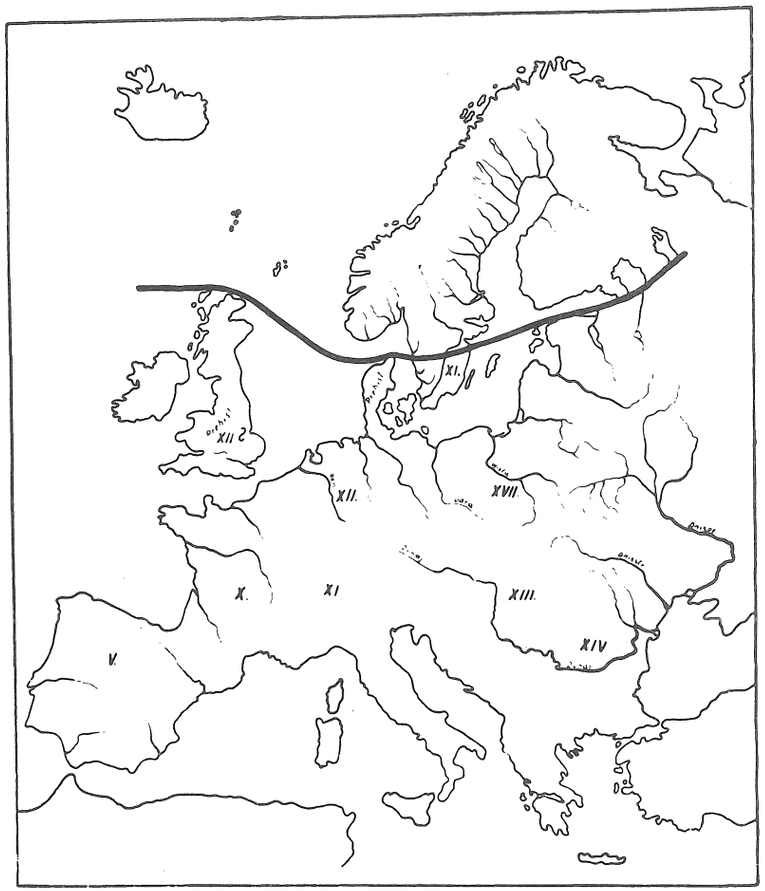

FIG. 5. The dates (by century) of extinction of aurochs (*Bos primigenius*) in different countries in Europe. Solid line, northern limit of distribution (after Lukaszewicz, 1952).

Masovia in 1359, and others). In the sixteenth century, aurochs existed only in the Jaktorov primeval forest near Warsaw, where, under official protection, they were guarded by the inhabitants of surrounding villages, who gave them hay in winter. Reports about the aurochs reservation in the Jaktorov Forest—prepared by royal officers between 1510 and 1630 and published recently by Lukaszewicz (1952)—offer interesting data not only on the final extinction of *Bos primigenius* in spite of its protection but also on their biology and on the ecological conditions in which the last of them lived. In 1557 there were still about fifty in Jaktorov Forest, and in 1562 there were thirty-eight (eleven of them bulls). At that time all hunting was forbidden, but the deforestation and the grazing of domestic cattle in the forest were disastrous for the population. In 1599, in spite of numerous decrees commanding their protection, there were only twenty-four aurochs living in Jaktorov. In 1601, a plague killed all but four, only one of them a female. In 1630 the royal officer noted that he found no aurochs in Jaktorov, but was told that the last animal, a female, died in 1627 (Fig. 6).

It is interesting to note that in Germany experiments were started to "reconstruct" aurochs through the hybridization and selection of some primitive forms of cattle resembling their extinct ancestors (Lengerken, 1953).

The European bison (*Bison bonasus*) was also on the verge of extinction. Whether it is the descendant of *B. priscus* or the latest stage of the independent line of forest bison, it appears in the postglacial and is

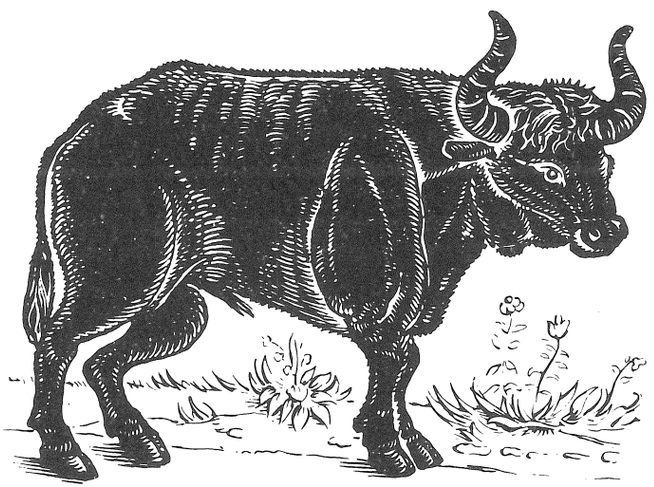

FIG. 6. A drawing of aurochs (*Bos primigenius*) from A.D. 1557 (after Lengerken, 1953).

limited in its distribution to Europe. In antiquity it was common on the whole continent. The process of its extinction began in the Middle Ages, and in the eighteenth century it disappeared everywhere but in the Bialowieza primeval forest and in the Caucasus. The lowland population from Bialowieza and the mountain population in the Caucasus were in contact via the forested valley of the Don as late as the Middle Ages. The Caucasian bison is smaller and of darker color.

In 1803 Bialowieza, then in the Russian empire, was declared the private hunting ground of the czars. The herd of bison numbered 300 to 500. In 1860 there were as many as 1,500 bison there, but at the beginning of World War I the population once more declined to 750. The main reason for the weak birth rate and the later decline of the bison population was the destruction of forest vegetation in Bialowieza by an excessive number of red deer, maintained there for hunting purposes. During the nineteenth century some of the bison from Bialowieza were sent to different places as gifts from the czars. Four specimens presented to Pszczyna in Silesia propagated in 1920 to a herd of seventy head.

During World War I, when the Russian army retreated, German soldiers killed about 500 bison; the remainder were exterminated by poachers when Bialowieza passed successively into the hands of the Lithuanian, Russian, and Polish armies. At the same time, the Pszczyna herd, the largest outside Bialowieza, was decimated, and only three specimens survived; other bison lived in zoological gardens. There were at that time no more than fifty purebred European bison in the world. Their breeding in Poland, Germany, Sweden, and the Netherlands increased the number in 1939 to ninety-four. During World War II some centers of bison breeding were destroyed, but the herd in Bialowieza survived. Now there are several hundred bison in Europe, 213 of them in 1966 in Poland, where some live in reservations, and three herds live freely in large forest regions such as Bialowieza.

The Caucasian herd of bison numbered about a thousand specimens in the second half of the nineteenth century. It diminished gradually, and the last known specimen was killed in 1926. Only one Caucasian bison, a bull, was transported from Russia before World War I; it mated with the lowland bison from Bialowieza and left numerous hybrid offspring. The issue of this line is kept separately and now forms quite a large population in Russian and Polish reservations.

We can hope that the European bison has been saved as a species, although it is almost completely dependent on continuous protection from man.

References

Abel, O., 1929, *Paläobiologie und Stammesgeschichte:* Jena, Fischer, 423 p.

Degerbøl, M., and Iversen, J., 1945, The bison in Denmark: København, *Danmarks geol. unders.* R. *II*, no. *73*, p. 1–62

Garutt, W. E., 1964, Das Mammut: Wittenberg, *Neue Brehm-Bücherei*, no. *331*, p. 1–140

Guenther, E. W., 1960, Funde des Riesenhirsches in Schleswig-Holstein und ihre zeitliche Einordnung, p. 201–06, in *Steinzeitfragen d. Alten u. Neuen Welt;* Zotz-Festschrift: Bonn, L. Röhrscheid Verlag

Guilday, J. E., Differential extinction during late-Pleistocene and Recent times (this volume)

Heinz, A. E., and Garutt, W. E., 1964, Determination with radioactive carbon of the absolute age of fossil remains of mammoth and woolly rhinoceros found in permanently frozen ground of Siberia (in Russian): Moscow, *Doklady Akad. Nauk SSSR*, v. *154*, p. 1367–70

Kretzoi, M., 1965, Die Nager und Lagomorphen von Voigtstedt in Thüringen und ihre chronologische Aussage: Berlin, *Paläont. Abh., A*, v. *II*, no. *2/3*, p. 585–660

Kubiak, H., 1965, Examples of abnormalities in the dentition of fossil elephants (in Polish): Krakow, *Folia. Quatern.*, v. *19*, p. 45–61

Kurtén, B., 1958, Life and death of the Pleistocene cave bear: *Acta. zool. fennica*, v. *95*, p. 1–59

Lengerken, H., 1953, Der Ur und seine Beziehungen zum Menschen: Wittenberg, *Neue Brehm-Bücherei*, no. *105*, p. 1–80

Lukaszewicz, K., 1952, The Ure-ox (in Polish): Krakow, *Ochrona Przyrody*, v. *20*, p. 1–33

Mohr, E., 1959, Das Urwildpferd: Wittenberg, *Neue Brehm-Bücherei*, no. *249*, p. 1–144

Neuville, H., 1921, On the extinction of the Mammoth: *Smithson. Inst. Ann. Report for 1919*, p. 327–38

Stein, G., 1963, Unterartengliederung und Nacheiszeitliche Ausbreitung des Maulwurfs, Talpa europaea L.: Berlin, *Mitteil. zool. Mus.*, v. *39*, p. 379–402

Vangengeim, E. A., 1961, Paleontologic materials for the stratigraphy of the Quaternary sediments of northeastern Siberia (in Russian): Moscow, *Trudy geol. inst. Akad. Nauk SSSR*, v. *48*, p. 1–182

Vetulani, T., 1933, Zwei weitere Quellen zur Frage des europäischen Waldtarpans: Berlin, *Zeit. Säugetierkunde*, v. *8*, p. 281–82

Vetulani, T., 1948, Premières observations sur la régénération du Tarpan sylvestre européen dans la forêt vierge de Bialowieza: *Bull. int. Acad. Pol. Sci. Lettres, Cl. Sci. Math. Nat.*, B, 1947, p. 1–22

N. K. VERESHCHAGIN
Zoological Institute
Academy of Sciences of the U.S.S.R.
Leningrad, U.S.S.R.

PRIMITIVE HUNTERS AND PLEISTOCENE EXTINCTION IN THE SOVIET UNION

Abstract

Archaeological investigations undertaken in the ranges of the U.S.S.R. have yielded very important documentary material for studying the mammalian fauna. In different Pleistocene epochs nearly all the U.S.S.R. was inhabited by the mammoth fauna, characterized by mammoth, cave hyena, cave lion, horse, reindeer, giant and red deer, bison, saiga, etc. In the Russian plain, along the rivers in Siberia, in karst regions of the Crimea, Caucasus, the Urals, Middle Asia, East Siberia, and the Far East, game animals were used by Paleolithic and later tribes. Numerous remains found in the Crimea and in the Ukraine testify to the hunting for large animals.

The largest sites of the Upper Paleolithic are estimated by radiocarbon to be 9,000–14,000 years old.

At the boundary between the Paleolithic and Neolithic, complex changes in the fauna and ecological assemblages of different areas took place. About ten species of large Pleistocene mammals became extinct in the U.S.S.R. Other species underwent a reduced distributional range in the Holocene. Some species, having expanded their range into the taiga, increased their populations (moose, brown bear, beaver). In the Neolithic, man began to exploit fish and marine mammals.

The main reason for the absolute extinction of animals of the mammoth complex and for the reduction of range in some species is the change in climate and terrain, especially the change in the regime of winter weather. The destructive effect of man supplemented and intensified the influence of climatic factors.

As many as two thousand years ago ancient Greek and Roman philosophers wondered how our distant ancestors had mastered the animal world. Titus Lucretius thought primitive man had been a brutal plunderer: