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Late Pleistocene Mammal Fauna of Siberia

N. K. Vereshchagin and I. Ye. Kuz'mina

The Late Pleistocene mammal fauna of Arctic and southern Siberia became known at the turn of the century from the fragmentary data of Academicians P. S. Pallas, I. F. Brandt, A. F. Middendorf (1869), I. D. Cherskiy (1891), M. V. Pavlova (1910), and others. By the 1950s, new light had been shed on the fauna of central and southern Siberia by the remarkable excavations of Paleolithic campsites by Soviet archaeological work and through the paleozoological studies of Gromov (1948).

A series of new studies on paleontologic materials now makes it possible to characterize the Late Pleistocene mammal fauna of individual regions of northern Asia on the basis of the remains of 65 species recovered from geologic sites (Alekseyeva, 1980; Vangengeym, 1977; Vereshchagin, 1959a, 1959b; Vereshchagin and Barishnikov, 1980; Galkina, 1975; Yermolova, 1978; Kuz'mina, 1971, 1977; Sher, 1971). The indicator and widely distributed species in this region (Table 21-1) include wolf, red fox, arctic fox, brown bear, sable, wolverine, cave lion, northern pika, Eurasian beaver, bank vole, woolly mammoth, woolly rhinoceros, Siberian roe deer, red deer, moose, reindeer, and steppe wisent. Some of these species, inhabitants of forested and rocky biotopes, lived in intrazonal elements of the landscape zone of cold Pleistocene steppe.

Western Siberia

Sites with skeletal remains of the following Late Pleistocene animals are confined in western Siberia to the eastern slopes of the southern Urals, the Ishim-Irtysh interfluvium, the Kuznetsk Basin, and the Western Altay: corsac fox, small cave bear, steppe ferret, gray marmot, Siberian mole-rat, and wide-hoofed horse.

In Zyryanka and Sartan time, as the northern half of western Siberia became free of the sea, it was settled from the west, south, and east. On the Yamal Peninsula, in the lower reaches of the Ob', and on the Gydan Peninsula

were found wolf, brown bear, polar bear, woolly mammoth, Lena horse, reindeer, and musk ox. Remains of saiga antelope were found in the lower reaches of the Ob'. Remains of woolly rhinoceros and bison were not found on the Gydanskiy Peninsula (Kuz'mina, 1977). No remains of arctic fox have been found thus far in northwestern Siberia in the Late Pleistocene.

Farther south, cave lion, mammoth, Lena horse, woolly rhinoceros, red deer, and moose inhabited the basin of the lower course of the Irtysh during Zyryanka time (Vangengeym, 1977). Giant deer occurred 100 km north of Tomsk near Krasnyy Yar on the Ob' (Alekseyeva, 1980). The Kuznetsk Basin, according to the data of Galkina (1975), was inhabited by bank vole, collared lemming, Siberian brown lemming, steppe lemming, water vole, narrow-headed vole, tundra vole, and Siberian mole-rat. Among large mammals the following also inhabited the Kuznetsk Basin and the western slopes of the Altay: cave hyena, cave lion, Asiatic wild ass, argali sheep, Siberian ibex, yak, and aurochs.

Thus, three regions with a greatly similar mammal fauna can be distinguished in western Siberia in the Late Pleistocene as follows: a northern part, with a predominance of cold-tolerant species (musk ox, Lena horse, polar bear); a southern region, with a predominance of warmth-loving species (red deer, giant deer, corsac fox, wide-hoofed horse, Asiatic wild ass) and with species associated with forest biotopes (sable, wolverine, roe deer, beaver, water and bank voles, etc.); and a southeastern part, with a fauna very similar to that of eastern Siberia.

Eastern Siberia

During the Late Pleistocene, the mammals of eastern Siberia constituted a single complex that in the present state of knowledge is difficult to divide according to landscape-geographic zones. Deposits dated as Zyryanka and Sartan

Table 21-1. Late Pleistocene Mammals of Siberia (Including the Arctic Zone)

Taxon	Common Name	Western Siberia	Eastern Siberia	Far East, South
LAGOMORPHA				
<i>Caprolagus brachyurus</i> Temm.	Manchurian hare			x
<i>Lepus tanaiticus</i> Gureev.	Don hare		x	
<i>Lepus timidus</i> L.	Arctic hare	x		x
<i>Ochotona alpina</i> Pall.	Alpine pika	x	x	x
RODENTIA				
<i>Arvicola terrestris</i> L.	Water vole	x	x	
<i>Castor fiber</i> L.	Eurasian beaver	x	x	x
<i>Citellus glacialis</i> Vinog.	Indigirka long-tailed ground squirrel		x	
<i>Citellus undulatus</i> Pall.	Long-tailed ground squirrel		x	
<i>Clethrionomys</i> sp.	Bank vole	x	x	x
<i>Dicrostonyx torquatus</i> Pall.	Collared lemming	x	x	
<i>Lagurus lagurus</i> Pall.	Steppe lemming	x	x	
<i>Lemmus sibiricus</i> Kerr	Siberian brown lemming	x	x	
<i>Marmota baibacina</i> Kastsch.	Gray marmot	x		
<i>Marmota camtschatica</i> Pall.	Black-capped marmot		x	
<i>Marmota sibirica</i> Radde	Tarbagan marmot		x	
<i>Microtus gregalis</i> Pall.	Narrow-headed vole	x	x	
<i>Microtus oeconomus</i> Pall.	Tundra vole	x		
<i>Myospalax myospalax</i> Laxm.	Siberian mole-rat	x		
CARNIVORA				
<i>Alopex lagopus</i> L.	Arctic fox	x	x	
<i>Canis lupus</i> L.	Gray wolf	x	x	x
<i>Crocota spelaea</i> Gold.	Cave hyena	x		
<i>Cuon alpinus</i> Pall.	Dhole		x	x
<i>Felis bengalensis</i> Kerr.	Leopard cat			x
<i>Felis lynx</i> L.	Eurasian lynx		x	x
<i>Gulo gulo</i> L.	Wolverine	x	x	x
<i>Lutra lutra</i> L.	Eurasian otter			x
<i>Martes flavigula</i> Bodd.	Yellow-throated marten			x
<i>Martes zibellina</i> L.	Sable	x	x	x
<i>Meles meles</i> L.	Eurasian badger			x
<i>Mustela eversmanni</i> Less.	Steppe ferret	x		
<i>Mustela sibiricus</i> Pall.	Siberian weasel			x
<i>Nyctereutes procyonoides</i> Gray	Raccoon dog			x
<i>Panthera pardus</i> L.	Snow leopard			x
<i>Panthera spelaea</i> Gold.	Cave lion	x	x	x
<i>Panthera tigris</i> L.	Tiger			x
<i>Spelaeartcos rossicus</i> Boris.	Small cave bear	x		
<i>Ursus arctos</i> L.	Brown bear	x	x	x
<i>Ursus maritimus</i> Phipps	Polar bear	x	x	
<i>Vulpes corsac</i> L.	Corsac fox	x		
<i>Vulpes vulpes</i> L.	Red fox	x	x	x
ARTIODACTYLA				
<i>Alces alces</i> L.	Moose (Eurasian elk)	x	x	x
<i>Bison priscus</i> Boj.	Steppe wisent	x	x	x
<i>Bos baikalensis</i> N. Ver.	Baikal yak	x	x	
<i>Bos primigenius</i> Boj.	Aurochs	x	x	
<i>Capra sibirica</i> Pall.	Siberian ibex	x		
<i>Capreolus pygargus</i> Pall.	Siberian roe deer	x	x	x
<i>Cervus elaphus</i> L.	Red deer (wapiti)	x	x	x
<i>Gasella gutturosa</i> Gmel.	Mongolian gazelle		x	
<i>Megaloceros giganteus</i> Blum.	Giant deer	x	x	
<i>Moschus moschiferus</i> L.	Musk deer		x	x
<i>Nemorhaedus caudatus</i> Milne-Edw.	Common goral			x
<i>Ovibos moschatus</i> Zimm.	Tundra musk ox	x	x	
<i>Ovis ammon</i> L.	Argali sheep	x	x	
<i>Ovis nivicola</i> Eschsch.	Snow sheep		x	
<i>Parabubalis capricornis</i> V. Gromova	Goat-horned antelope		x	
<i>Rangifer tarandus</i> L.	Reindeer	x	x	
<i>Saiga tatarica</i> L.	Saiga antelope	x	x	
<i>Spirocerus kiakhtensis</i> M. Pavl.	Twisted-horned antelope		x	
<i>Sus scrofa</i> L.	Wild boar			x
PERISSODACTYLA				
<i>Coelodonta antiquitatis</i> Blum.	Woolly rhinoceros	x	x	x
<i>Equus</i> sp.	Wild horse			x
<i>Equus hemionus</i> Pall.	Asiatic wild ass	x	x	
<i>Equus latipes</i> Gromova	Wide-hoofed horse	x		
<i>Equus lenensis</i> Russ.	Lena horse	x	x	
PROBOSCIDEA				
<i>Mammuthus primigenius</i> Blum.	Woolly mammoth	x	x	x

(Vangengeym, 1977; Sher, 1971) in the basins of the Nizhnyaya Tunguska, Angara, Aldan, Lena, Vilyuy, and Markha Rivers were found to contain skeletal remains of wolf, red fox, arctic fox, brown bear, wolverine, cave lion, Don hare, alpine pika, long-tailed ground squirrel, Indigirka ground squirrel, black-capped marmot, beaver, collared lemming, Siberian brown lemming, steppe lemming, water vole, and narrow-headed vole.

In addition, complete or partial carcasses of mammoth, horse, woolly rhinoceros, and steppe wisent have been preserved in the frozen state in deposits of eastern Siberia (Rusanov, 1968; Vereshchagin, 1981; Lazarev, 1980; Vereshchagin and Lazarev, 1977).

Mountain animals were abundantly represented. The region was inhabited by the dhole, musk deer, twisted-horned antelope, Siberian ibex, argali sheep, snow sheep, and Baikal yak.

Somewhat apart faunistically stood the Transbaikalian region, in southeastern Siberia, inhabited by animals of xerophytic landscapes and a sharply continental climate: tarbagan marmot, Mongolian gazelle, Asiatic wild ass, and saiga antelope. These species have survived in the steppes and semideserts of Kazakhstan and Mongolia to this day, and during the Late Pleistocene the saiga antelope occurred widely in western and eastern Siberia up to the shores of the Polar Basin. Its fossil remains are also known on the Novosibirsk Islands. Such a wide distribution of saiga antelope remains can be explained not only by the considerable spread of open steppe landscapes in the Late Pleistocene but also by the distant migrations very typical of this animal.

Thus, 43 species of mammals known from fossil remains (Table 21-1) inhabited the territory of eastern Siberia during the Late Pleistocene. Skeletal remains of 8 species were found only in eastern Siberia: black-capped and tarbagan marmots, long-tailed and Indigirka ground squirrels, Mongolian gazelle, twisted-horned antelope, goat-horned antelope, and snow sheep.

An extensive exchange of species between Eurasia and North America occurred during the Pliocene and Pleistocene (Hibbard et al., 1965; Vereshchagin, 1971). Eastern Siberia was last connected to North America during the Late Pleistocene via the Bering region. Apparently, cave lion, northern pika, moose, musk ox, snow sheep, saiga antelope, and yak entered North America at that time. Mammoth and short-horned bison moved back into America. In addition, collared lemming, reindeer, and, apparently, horse and marmot reentered America, their place of origin (Kuz'mina, 1977).

Bering Region and Asian-American Faunistic Links

Skeletal remains of Late Pleistocene mammals are particularly abundant in deposits of Zyryanka-Sartan (Wisconsin) age over all of northeastern Siberia, including the Novosibirsk Islands, Wrangel Island, Maritime Lowland, Chukotka Peninsula, and Kamchatka. There, the remains of soft tissues, horn sheaths, and fur from many species of

Pleistocene wild animals are found in frozen ground more often than anywhere else. The shelf of the Laptev and East Siberian Seas in some places (Oyagosskiy and Khaptashinskiy Yar, Ayon Island, etc.) is covered with bones of horse, reindeer, bison, musk ox, and mammoth washed up by tidal waters. Occasionally, bones of wolf, brown bear, cave lion, and (rarely) woolly rhinoceros, moose, and saiga antelope are also found.

Sites in Alaska and in the valley of the Yukon River and its tributaries, similar in age and taxonomy, contain essentially similar fauna (Guthrie, 1968; Irving et al., 1977) but not woolly rhinoceros, which apparently did not live east of the Kolyma Basin. This similarity of Pleistocene mammal complexes from the plains of the two adjacent continents, now separated once again by the sea, confirms the existence, during the epoch of maximum cooling, of wide continental links at the location of the shelf zone and Bering Straits, that is, the Bering Land Bridge.

Similar features are also preserved in the modern mammal fauna of extreme northeastern Siberia and Alaska. This fauna includes Bering brown bear, arctic fox, red fox, wolverine, stag moose (*Cervalces*), reindeer, and long-tailed and Indigirka ground squirrels among other species.

At the same time, secondary and marked differences in the mammal fauna of these regions are apparent as a result of ecologic barriers and older migration routes. Such are the subspecies differences among the modern snow sheep and Dall sheep of Chukotka and Alaska, the absence of the mountain goat of Alaska on the Chukotka Peninsula and the Koryak Highland, species differences among others, and so on (Chernyavskiy, 1976).

South of the Far East

The south of the Far East was faunistically the most unusual region of the Late Pleistocene. Deposits in caves of the Maritime Territory have been found to contain skeletal remains of species not found farther northeast: raccoon dog, Siberian weasel, yellow-throated marten, badger, otter, leopard cat, tiger, leopard, Manchurian hare, horse, wild boar, and mountain antelope. In addition, species common in southeastern Siberia also inhabited the Far East, namely, dhole, lynx, and musk deer in addition to 15 species widely distributed in the Palearctic: wolf, red fox, brown bear, sable, wolverine, cave lion, northern pika, beaver, red-backed vole, mammoth, woolly rhinoceros, roe deer, red deer, moose, and bison (Table 21-1). Remains of cave hyena are known from cave deposits of western Siberia and the Far East.

The mammal fauna of the Far East indicates that the climate there during the Late Pleistocene was milder than that in Siberia. The species diversity was due to the penetration from the south of certain species more characteristic of the Indo-Malayan zoogeographic region.

Conclusions

Comparison of species compositions of the mammal fauna of western and eastern Siberia and the south of the Far East

showed that differences can be traced even for the Late Pleistocene. Remains of corsac fox, small cave bear, steppe ferret, gray marmot, Siberian mole-rat, and wide-hoofed horse were found only in western Siberia. Remains of turgan marmot, black-capped marmot, long-tailed ground squirrel, Indigirka arctic ground squirrel, Mongolian gazelle, and snow sheep were found only in eastern Siberia. There were many more species in the south of the Far East, namely, raccoon dog, Siberian weasel, yellow-throated marten, badger, otter, leopard cat, tiger, leopard, Manchurian hare, horse, wild boar, and mountain antelope.

Paleontological data indicate a later Late Pleistocene settlement by mammals of northern regions of western Siberia, where cold-tolerant species predominated widely. The southern part was inhabited by warmth-loving species, associated either with forest biotopes or with steppe and semidesert biotopes. The Late Pleistocene mammal fauna of eastern Siberia was more uniform. In this complex one can distinguish only the faunas of the Transbaikalian region and southeastern Siberia, including species of mountain and plains landscapes adapted to a dry, sharply continental climate. The composition of Far Eastern mammals in the Maritime Territory indicates a milder and more humid climate than in Siberia, and the penetration from the south of representatives of the Indo-Malayan zoogeographic region. All the latest studies confirm the hypothesis offered by Sushkin (1925) that there were different conditions of formation and development of western Paleartic, eastern Paleartic, and Far Eastern faunas.

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Late Pleistocene Insects

S. V. Kiselev and V. I. Nazarov

Systematic studies of fossil insects in the USSR did not begin until the 1960s. Since that time, data have been published on the composition of Pleistocene insect faunas of the European USSR (Panfilov, 1965; Medvedev, 1968a, 1968b, 1976; Nazarov, 1979; Voznyachuk, Makhnach, et al., 1979; Voznyachuk, San'ko, et al., 1979), Siberia (Kiselev, 1973), Yakutiya (Grushevskiy and Medvedev, 1962, 1970; Grunin, 1973; Medvedev and Voronova, 1977; Sher et al., 1979; Kiselev, 1981; Kaplina et al., 1980), Chukotka (Kiselev, 1980a, 1980b; Boyarskaya and Kiselev, 1981), and some other regions of the Soviet Union (Kiselev et al., 1981). The locations of the main sites of fossil insect remains in this country are shown in Figure 22-1).

To date, only two regions of the USSR—Belorussia and northeastern Siberia, primarily the Kolyma Lowland—have been studied extensively in the paleoentomological sense. This makes it possible to compare the development of the insect fauna in the West and East of the country, that is, in regions of markedly different environmental history.

Northeastern Siberia

In the Kolyma Lowland, the Late Pleistocene entomofaunas can be grouped into tundra, tundra-taiga, and steppe species. Among the most typical members of the steppe group are the weevil genera *Coniocleonus* and *Stephanocleonus*. Today, species of the subfamily Cleoninae, which includes these weevils, are confined to the steppe and mountain-steppe regions of southern Siberia and Mongolia, although some penetrate into central Yakutiya through steppe-type extrazonal areas (*Stephanocleonus eruditus* Faust, *S. fossulatus* Disch.) and as relicts known even from areas of Taimyr, western Chukotka, and Wrangel Island (*Coniocleonus ferrugineus* Fahr., *C. astragali* Ter-Min. et Korot., *C. cimerascens* Hochh.) (Korotyayev, 1977; Korotyayev and Ter-Minasyan, 1977). Almost all

fossil sites of these weevils in the Northeast are quite distant from their modern ranges, indicating a previous greater extent of steppe and meadow-steppe than at present. Analysis of weevil fossils indicates cyclic climatic changes in the occurrence of steppe and tundra-taiga species.

Steppe assemblages dominate the fossil fauna; tundra assemblages consist almost exclusively of inhabitants of comparatively dry biotopes, such as grass and herb meadows or shrub-herb gentle slopes (e.g., the carabids *Pterostichus sublaevis* Sahlb., *Curtonotus alpinus* Payk., and *Amara glacialis* Munch. and the leaf beetles *Chrysolina septentrionalis* Dej., *C. subsulcata* Munh., and *C. cavigera* Sahlb.). Taiga and tundra (*sensu stricto*) beetle species play a secondary role in this type of fauna. Thus, a steppe-tundra must have predominated in a severe continental and arid or semiarid climate similar to, or more severe than, the present ultracontinental climate of the intermontane basins of Yakutiya (Verkhoyansk, Oymyakon).

The opposite type of Late Pleistocene entomofauna includes taiga insects (e.g., *Trachypachus zetterstedti* Gyll., *Pissodes gyllenchali* Gyl., and *Camponotus herculeanus* L.) and tundra mesophiles (e.g., *Pterostichus costatus* Men., *P. agonus* Horn., and *Cryobius* spp.) typical of forest-tundra or sparse larch forests. The presence of a few steppe insects in such faunas indicates a somewhat more severe climate than the present one in the Kolyma Lowland even during the "warm" interstadial of the Late Pleistocene.

Belorussia

The situation in Belorussia was entirely different. During the Mikulino Interglaciation, the entomofauna differed little from the present one, although it did include insects that now live farther south and west, such as the carabids *Epaphius rivularis* Gyll., *Oodes gracillis* Villa, and *Chisenius tristis* Schall.; the click beetles *Ampedus nigrinus* Hbst.