THE REPEATED REPLACEMENT OF *Mammuthus-* AND *Elephas* FAUNAS IN CENTRAL EUROPE

Wighart v. KOENIGSWALD

University of Bonn, Dept. of Paleontology, Nussallee 8, D-53115 Bonn, Germany; Koenigswald@uni-bonn.de

During the Middle and Upper Pleistocene, two ecologically very different faunas occurred repeatedly in Central Europe. They are characterized by the proboscideans *Mammuthus primigenius* and *Elephas antiquus*, respectively. The multiple faunal exchange was caused by climatic oscillations which affected Central Europe more severely than most other parts of the world. This is due to the specific geographic position of Central Europe which led to a shift from a strongly continental climate during glacial periods to a more maritime climate during warm periods. Thus, very antithetic species like *Ovibos* and *Hippopotamus* were able to inhabit the same area, e.g., the Rhine valley, but at different times. A new model of repeated immigration and local extinction is presented. It focuses on the distinction between temporarily inhabited areas and core areas for the various species. The model sheds a new light on which geographic areas were crucial for the survival or the extinction of the Pleistocene mammals.

INSECTS AND GRAZING MAMMALS IN THE PLEISTOCENE OF NORTHEASTERN SIBERIA

Svetlana KUZMINA

Paleontological Institute, Russian Academy of Sciences, 123 Profsoyuznaya St., 117997 Moscow, Russia; skuz@orc.ru

The environment that supported large herbivorous mammals, such as mammoth, horse, bison, and others in arctic Siberia in the Pleistocene is commonly called “tundra-steppe”. The existence of the tundra-steppe landscape, which has no complete modern analogues, is proven by various fossils, including insects. Chances to be preserved as fossils are good for the insects with the most solid exoskeleton elements. Most common are fossils of coleopterans (beetles), but some remains of ants, hemipterans (true bugs), caddis-flies and flies can be preserved.

The composition of various fossil beetle assemblages shows certain regularities and is believed to reflect the relative abundance of species in the past and, eventually, to give some idea on the former occurrence of their preferred habitats and the proportion of those habitats in the landscape. The most typical feature of fossil insect assemblages of the tundra-steppe type is that they include species which do not occur together at present. Besides that, these assemblages often demonstrate uncommon proportions of the ecological groups of insects, which are not observed in the modern fauna. Each fossil assemblage usually includes more or less abundant remains of species currently widespread in northeastern Siberia. Many of them have very broad ranges covering several natural zones. Some species are now restricted to the tundra zone, but are very common there (*Chrysolina subsulcata*, *Tachinus arcticus)*, while the others are currently

known from a few tundra areas, but were much more widespread in the Pleistocene (*Sitona borealis, Cholevinus sibiricus, Isochnus arcticus).* Among the species that are known in the modern fauna of northeastern Siberia, some are very common or even dominate the fossil assemblages, although their present distribution is limited to a few isolated areas, representing the remnants of the past much broader ranges (*Morychus viridis, Poecilus nearcticus, Phyllobius kolymensis*). On the other hand, tundra-steppe insect assemblages include some species which are currently distributed much further south (e.g., in the steppe zone) and are either not known in northeastern Siberia at present at all (e.g., *Stephanocleonus tricarinatus*), or occur there in narrow refugia, isolated from their main southern range, thus demonstrating discontinuous relict distribution. The latter group is quite large, and includes several species of weevils (*Stephanocleonus eruditus* and others), ground beetles and leaf beetles of steppe origin, having their main present ranges in southern Siberia and Mongolia, and surviving in scattered refugia in Central Yakutiya and the Yana-Indigirka-Kolyma upstreams. Finally, the tundra-steppe assemblages include some extinct species (a few weevils, a leaf beetle, and a dung beetle). The recent discoveries of these extinct species provide additional evidence of the peculiar character of the tundra-steppe insect fauna.

In accordance with the pollen spectra, picturing wide distribution of grass-herb vegetation, and with the general grazing character of fossil mammal fauna, insect assemblages of the tundra-steppe type include many species, related to grasses and herbaceous plants. Some beetles feed on grasses, like *Curtonotus alpinus,* a ground beetle, very common and often abundant in the Pleistocene. Several species are related to legumes (weevils *Sitona borealis, Hypera ornata* and others), many to *Artemisia*, crucifers, some to chenopods and caryophylls. Tundra-steppe assemblages also include species, related to shrubs, mostly willows (weevils *Lepyrus, Isochnus, Dorytomus*), or to trees, like weevils *Pissodes* living on larch, or some ants, often dwelling in tree trunks. Although shrub and tree insects (except willow weevils) are usually much less abundant than grass and herb species, they occur quite often. That shows a complex pattern of tundra-steppe vegetation.

Many insect species in tundra-steppe assemblages, like their host plants, prefer scattered vegetation communities of pioneering character. That is in agreement with the presence of many ruderal plants in plant macrofossil spectra (Kienast *et al*, 2001; Schirrmeister *et al.*, 2002) One of the best examples of this kind is a pill beetle *Morychus viridis*. It occurs in almost all Pleistocene assemblages, and sometimes is very abundant or even the absolute dominant. Currently it lives in floristically very impoverished biotopes, where the main plants are short-stem xerophilic sedges and some mosses. Well-drained in summer and almost snow-free in winter, these habitats are basically very dry, but subjected to a huge range of soil temperature variations. These plant communities are classified as hemicryophitic steppe (Yurtsev, 1981, Berman *et al.*, 2001) or “sedge heath”; they are a kind of pioneering community, and were a common element of the Pleistocene landscape.

In most cases, the high abundance of *Morychus viridis* is accompanied by the presence of true steppe species and is well correlated with a relatively high proportion of various xerophilic insects, indicating more diverse herbaceous vegetation, which is often confirmed by pollen spectra with an increasing proportion of various herb families. That allows us to assume that in tundra-steppe mosaic the sedge heath patches were associated with (or surrounded by) richer grass-herb communities, more productive for the mammalian grazers. The grazing by itself could, besides physical reasons, contribute to the wide distribution of very low productive sedge heath, a consequence of trampling and selective consuming of more nutritious plants by mammals.

Insect species directly associated with large mammals, which are quite numerous in true (zonal) steppe, are surprisingly rare in tundra-steppe fossil assemblages. Dung beetles are represented by a few species of the genus *Aphodius*, and only one of them is common (most likely, an extinct species). Meanwhile, the dung beetles are one of the main groups of coleopterans in the true steppe. The tundra-steppe faunas include almost no carrion beetles. It seems likely that the main role in utilization of mammal metabolic products and their dead bodies belonged to dipterans (flies). There are many occurrences of fossil bones, such as mammoth mandibles, filled with fly puparia. It can be assumed that, along with the preservation effect of permafrost, the lack of carrion beetles and other necrophilous insects was one of the factors responsible for excellent preservation of mammalian fossils in northeastern Siberia.

The earliest known insect assemblages of the tundra-steppe type in northeastern Asia come from the Early Olyorian - the regional Land Mammal Age that started about 1.5 million years ago (Kiselev, 1981; Sher, 1986). Though peculiar for many extinct mammals, the Olyorian fauna was a typical grazing assemblage that existed in an open grass and herb dominated environment. Since at least that time, and through the whole Pleistocene, large mammals and tundra-steppe insect faunas coexisted in northeastern Siberia and actually were components of the same very peculiar biome. It is reasonable to assume that complex interactions and feedbacks between mammals, insects and vegetation existed in that biome, probably similar to those of the extant biomes of pasture type with diverse grazing mammals; these interactions and feedbacks are still to be understood in further detail. Although insects are more resistant to unfavorable environments, surviving in small refugia, the tundra-steppe insect fauna disappeared in the Early Holocene, very soon after the mass extinction of mammals and the collapse of the Pleistocene "mammoth" biome.

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INFLUENCE OF LATE QUATERNARY PALEOENVIRONMENTAL CONDITIONS ON THE DISTRIBUTION OF MAMMALS IN THE LAPTEV SEA REGION

Tatiana V. KUZNETSOVA[1], Leopold D. SULERZHITSKY[2], Andrei ANDREEV[3a], Christina SIEGERT[3b], Lutz SCHIRRMEISTER[3c], and H.-W. HUBBERTEN[3d]

[1] Department of Paleontology, Faculty of Geology, Moscow State University, Vorob’evy Gory, Moscow, 119992, Russia; tatkuz@orc.ru
[2] Geological Institute RAS, Moscow, 109017, Russia;
[3] Alfred Wegener Institute for Polar and Marine Research, Research Unit Potsdam, Telegrafenberg A43, D-14473 Potsdam, Germany; [3a] aandreev@awi-potsdam.de; [3b] csiegert@awi-potsdam.de; [3c] lschirrmeister@awi-potsdam.de; [3d] hubbert@awi-potsdam.de

Understanding of the paleoenvironment is only possible through multidisciplinary studies of terrestrial deposits from the shelf land. Perennially frozen sediments along the Laptev Sea coast and New Siberian Islands contain various bioindicators of the past environment including mammal bones, fragments of insects, mollusk shells, remains of plant macrofossils, diatoms, pollen, ostracods etc. The study of these indicators, supplemented by ^{14}C dating, provides excellent archives of past life and Pleistocene environmental conditions.

In the frame of the joint Russian-German “Lena Delta Expeditions” (1998-2002), carried out under the umbrella of the Russian-German cooperation “System Laptev Sea 2000”, we investigated Late Pleistocene and Holocene deposits on the Laptev Sea coast, southwest coast of the East Siberian Sea and New Siberian Islands. Our collection of large mammal bones contains more than 3000 samples. It is unique because all bone findings were collected and registered, in contrast to former collections. Such an approach combined with radiocarbon dating of bone collagen (more than 300 dates) makes it possible to bring out some important aspects of date distribution of large animals in the studied area during the Late Quaternary. It is the first time that we have had such complete and well-dated material from the Arctic region.

A large part of the collection consists of *Mammuthus primigenius* bones (nearly 38%) and mammoth dates in our database are predominant (about 200 dates). The distribution of the bone ages is heterogeneous, especially for the mammoths. All dates may be divided into three groups. The first group consists of dates from ca 50 ka BP to 35-34 ka BP with a maximal number of dates around 40-38 ka BP. The second group (33 ka BP - 23-22 ka BP) has two periods with maximum numbers of dates: 33-32 ka BP and 25-24 ka BP. The last large number of dates belongs to the period from 15 ka BP to 9 ka BP with a maximum number of dates around 11-10 ka BP.