C. C. Flerow

18. THE EVOLUTION OF CERTAIN MAMMALS DURING THE LATE CENOZOIC

Extensive information has been accumulated on the faunas of the northern hemisphere, and on the patterns of their evolution and dispersal during intervals of the Pliocene and Quaternary periods. This knowledge is based on a study of abundant factual data discussed in numerous papers on the systematics, paleoecology, phylogeny, and stratigraphy of mammals for the period under question (see the figures at the end of this paper). There are many articles and summaries on the continents of Europe, Asia, and North America which give a more or less clear idea of the composition and distribution of mammals in the northern part of both hemispheres. On the basis of these researches we are now able to reconstruct the fundamental stages in the development of Quaternary and Recent forms of mammals.

First it is necessary to show the role played by the changes in the fauna itself and in the living conditions of the mammals during the Pliocene and Pleistocene on the developmental processes of Recent complexes. The composition and general nature of mammalian faunas in tropical and subtropical zones had taken their present form by the end of the Pliocene. The population of African savannas, as indicated by the history of its development, represents in composition and origin the descendants of the so-called Hipparion faunas, which were widely developed during the Neogene in the present tropical and temperate zones of Europe, Asia, and Africa. It is known that areas which are now characterized by temperate zone conditions had a much warmer climate and, correspondingly, a different vegetational cover during the period of the Hipparion fauna. Mammals included in this fauna belong to thermophilic species mostly inhabiting forest-steppes and savannas and partly humid plains and vast river valleys with forest thickets along the banks. Their composition is well known and need not be discussed here. During the Pliocene this complex was subjected to certain changes and by the early Quaternary had become virtually the present savanna type.

Similarly, mammals inhabiting the Indo-Malayan area have their roots in the Pliocene, but they are characterized by a predominance of forest and swamp species. Typical for the fauna of this area are Indian elephants and rhinoceroses,

tapirs, wild boars, tragulides, deer, and oxen; among the carnivores are the various bears and big cats, tree-climbing rodents, and primitive primates—squirrel shrews, true apes, etc.

In genera, and to a great extent even in species, this entire association is apparently a direct successor of the Pliocene complex. Especially striking confirmations of this fact are the tapirs, tragulides, deer, and bears. Axis deer and samburs, some of the oldest representatives of the family Cervidae, have been known in Asia and Europe since the middle Pliocene. Although in the Palaearctic region of the Eurasian continent these groups, like the muntjacs (Cervulinae), were not preserved in their original state and disappeared at the end of the Pliocene and early Pleistocene, having left numerous descendants represented by more specialized genera and subgenera (*Elaphurus, Przewaliskum*), in the Indo-Malayan area they continue to exist even now. Especially striking is the pattern of changes in the former dispersal of various chevrotains—tragulides of the families Gelocidae and Tragulidae. Tragulides are living now in forest and swamp areas of tropical Asia and Africa (genera *Tragulus, Moschiola, Hyaemoschus*); in the Palaearctic region they disappeared completely during the second half of the Pliocene, whereas the Oligocene and Miocene are characterized by a wide development in Europe and in the northern half of Asia of their numerous representatives—*Lophiomeryx, Miomeryx, Prodremotherium, Dorcatherium,* and many others. During the post-Tertiary the place of chevrotains in the north is occupied by their descendants the musk deer (Moschidae), artiodactyls that stand close to them in many morphological features, but are much more highly adapted to cold climatic conditions and have specific traits for a life in low-temperature areas having a snow cover and providing a boreal or alpine vegetation for their food. An analogous picture can be observed for many other groups of mammals.

In contrast to African savanna faunas, India is characterized by many typically forest animals that are virtually absent in Africa. The reason for this difference lies in the physical and geographical conditions of the time, when Hipparion faunas formed on the Asian continent migrated to Africa. There they undoubtedly encountered obstacles that served as insurmountable barriers to the dispersal of forest animals—like vast expanses of steppes that can be easily crossed by horses, steppe rhinoceroses, elephants, antelopes, wild boars, giraffes, and big cats. Later many of these produced an abundant community species of steppe dwellers, like antelopes for instance. In India, on the contrary, real steppe mammals, like horses and the majority of antelopes, are almost completely absent.

In contrast to the south, the composition of mammals inhabiting the Holarctic sharply differs from both the Pliocene and early Pleistocene complexes. In preglacial Pleistocene the animals here included many thermophilic species; the glacial and postglacial population of the Holarctic consists of species to a greater or lesser degree adapted for a life under cold conditions with a snow cover. With the beginning of a colder spell many Pliocene species of mammals became extinct, others retreated to the south, and the rest were sufficiently adaptable to adjust themselves quickly to new conditions, in some cases undergoing fundamental morphological and physiological changes. Certain adaptive traits have appeared: cold-resistance, seasonally changing hair, an alteration of coloring, and the winter hair of the mature animal always being different from that of the young animals as well as from species of the same genera living in warmer regions. Various adaptations appeared in the limbs for movement on snow and ice.

The developmental period of the Quaternary fauna of the Holarctic is characterized by a rapid extinction of some genera widely developed in the Pliocene. At the end of the Pliocene, *Hipparion* had become extinct because of shrinkage of extensive humid plains, and tapirs completely disappeared in Europe and Palaearctic Asia; on the other hand, a substantial number of the genera remained and in a changed state became parts of newly formed complexes. Rhinoceroses and elephants, for instance, acquired a peculiar appearance. At the same time new species and genera were appearing—*Elasmotherium,* southern elephants (*Archidiscodon meridionalis*), big-horned deer (*Megaloceros*), *Alces latifrons,* and many others.

Presently available data on the Quaternary fauna indicate that the climate not only became colder but fluctuated considerably, which caused complicated changes in the entire physico-geographical medium and in the animal kingdom throughout this period. New species emerged, some species adapted to new conditions and others migrated, and new biocoenoses were formed.

At the present time we cannot trace details of this complicated sequence of events over the territory that has been inhabited by boreal faunas. It is most distinct in the Asian and especially in the European regions during the upper Paleolithic. One can assume that during the Quaternary period the vast areas for the various components of the early Quaternary faunistic complexes were gradually shrinking. There was more pronounced discontinuity in the distributions of many faunal species. This was a typical condition for a Recent fauna.

Let us summarize the main events and moments of especially distinct changes in the history of mammalian fauna that took place from the end of the Pliocene up to the Recent.

1. At the end of the Pliocene a number of species became extinct. The areal distribution of many mammals shrank considerably. Thermophilic forms—tragulides, southern species of deer (muntjacs, axis deer, samburs), tapirs, the majority of rhinoceroses and elephants, mastodonts, apes, etc.—disappeared completely in the northern parts of Asia and Europe. At the same time, during the late Pliocene and early Pleistocene, a number of new groups appeared, typical of the Pleistocene and Holocene (*Elasmotherium,* gigantic deer, true deer—*Cervus elaphus L.* and *C. nippon* Temminek—and others). In the U.S.S.R. the Taman and Tiraspol faunistic complexes correspond to this period of time.

2. At the beginning of the middle Pleistocene there was extensive development in the northern parts of Asia, Europe, and North America of truly

arctic and subarctic genera and species like the reindeer, snow sheep, musk-ox, long-horned bison, woolly rhinoceros, mammoth, polar fox, polar bear, wolverine, various lemmings, etc. These events are characteristic of the upper Paleolithic faunistic complex.

3. At the end of the Pleistocene there was an extinction of species adapted to life under glacial conditions: woolly rhinoceros, mammoth, and to a lesser degree the musk-ox and long-horned bison. The last two having survived to our time, they were gradually restricted in distribution, retreating to regions in which prevailing conditions are associated with ice; they became extinct in Europe and Asia but are preserved in North America and in Greenland.

This time is characterized by the shrinkage or, to be more exact, a northward displacement of the habitat of the majority of arctic species that had previously been displaced from the areas covered by masses of continental ice and had migrated during the second half of the Pleistocene (during the period of maximum glaciation) far to the south. Examples are the reindeer, polar fox, lemmings, wolverines, and others. It should be remarked that some species apparently migrated during postglacial time farther north than their present distribution, which indicates that in many areas the climate of the early Holocene was warmer than at present.

It should be stated that the formation of recent zoogeographic groups in the Holarctic must have taken place during the last stages of the geological and paleogeographical history of Asia, Europe, and North America. We should regard the Holocene as the time when typically arctic forms were retreating to the northeast, inasmuch as their life was associated with conditions created by the presence of continental ice. The last representatives of a truly glacial fauna—the musk-ox and the wood bison—are living testimonials of this phenomenon.

All the above evidence proves beyond dispute that a knowledge of Pliocene and early Pleistocene faunas and floras is of decisive importance for the understanding of the recent development of mammals (as well as of many other animals and certainly of plants) in the tropical and subtropical zones; to appreciate their distribution in the temperate and arctic zones one has to know the faunas and floras of the Pleistocene and early Holocene.

Some influence pertaining to the effect of man upon the changes in mammalian fauna was undoubtedly felt most in places of lengthy habitation—the Tigris-Euphrates interfluve, the Nile Valley, India, China, and Europe. The influence of man proceeded in two ways—first in a passive way determined by the development of territories in the expansion of agriculture, felling of forests, and plowing. This resulted in a displacement of, mainly, large species, a destruction of harmful animals, a transformation of the fauna by domestication, and the development of animal breeding. Second, man effects changes in the fauna by the active extermination of animals. The latter became especially effective with the invention of firearms and the development of hunting techniques.

We know that in Asia and in northern regions of America bisons became

extinct in the early Holocene. In this case, apparently, we have a pattern analogous to the development of the musk-ox which became extinct all over the Palaearctic but was preserved in North America and Greenland. In other words it survived in places where climatic and general landscape conditions are associated with the presence of continental ice. Even in North America the musk-ox retreated gradually from the western bank of the Mackenzie River toward the east, closer to glacial territories. With the recession of the ice and the beginning of a warmer spell in Europe and northern Asia, followed by a change in vegetation, the retreat of the musk-ox began. Like the musk-ox, the forest bison also retreated gradually eastward, its grazing area shrinking until it found its last refuge in the forests of the Great Slave Lake area.

What can explain this extinction over a vast territory of Siberia and the northern parts of North America? Many scientists believe that the exterminating activity of man was one of the main reasons for the extinction of large Pleistocene mammals. There is no doubt that it was extensive (during the last two to three millennia especially). However, hunting was not sufficient during Paleolithic and Neolithic times to reduce substantially the number of such animals as mammoths, woolly rhinoceroses, cave bears, and lions. It has been said that elephants and rhinoceroses are still present in Africa because the population there has not been dense, but southern Asia, India, and Indochina have been very densely populated and yet elephants, rhinoceroses, and many other large mammals are still living there.

The ideas of population density of Europe and areas of Siberia held by those who believe man to have been the main cause for the extinction of large mammals will not stand up to scrutiny. According to their reasoning, Europe must have been very sparsely populated—or at least much less densely than eastern and western Siberia—because big-horned deer, aurochs, and (until recently) wisents are still preserved there, whereas they had been exterminated all over Siberia by man. This approach to the anthropic factor is demonstrably false.

It is generally known that in North America bisons flourished until the Union Pacific Railroad was built, despite the fact that the Indians had always hunted them. When the railway was completed, the Americans shot nearly all the millions of bisons. The same can be said about elephants, rhinoceroses, and quaggas in Africa, where these species have been killed by Europeans. But men of the Paleolithic, Neolithic, and even of the Bronze Age were certainly, absolutely, unable to destroy completely the populations of large animals.

What, then, are the actual causes for the extinction of Pleistocene mammals? First it should be said that extinction is determined by a *set* of causes. For different species, however, different factors are of decisive importance.

We know that in western Siberia the elk (moose) does not live in all areas having a deep snow cover, and the northern limit of its distribution beyond the Urals sharply descends southward along the Ob River to the extreme southern margins of the forest zone, rising again far to the north in eastern Siberia where the snow cover is much thinner.

The American wood bison lives in the very severe conditions of Athabasca and the Great Slave Lake area. The latter remains frozen for seven months of the year. The temperatures range to –54°C. The average temperature in January is about –24°C. Winter begins in the middle of October and lasts until the end of April.

All this, however, does not interfere with the normal existence of the wood bisons. What is the reason? It happens that the snow cover in Athabasca does not exceed an average depth of half a meter. Permanently frozen ground is at a depth of 10 cm. There is also no permanently frozen ground on the European plain, but the snow cover is thicker and the European bisons retreated for this reason to the west and south into regions with less snow. During the winter the American bison can be satisfied with snow alone and does not need water. The European bison, on the contrary, needs drinking water. In the steppes of the Transbaikal area, in Manchuria, and in Mongolia there is often no snow in winter. This fact alone created unfavorable conditions for the existence of the bisons in western Siberia and Alaska which are characterized, as is well known, by the deepest snow covers.

The European bison and the wood bison need leaves and thin branches for their food, from such trees as willow, aspen, oak, lime, mountain ash, etc. In addition, both these animals cannot live without definite types of grass fodder which are completely absent in northern Siberia and Alaska. Moreover, both species try to avoid the vast sphagnum peat muskeg and its associated plant assemblages; these muskegs and plants are widely distributed in Siberia.

The Evolution of Bisons

The earliest bisons are known from the late Pliocene of the Siwaliks and China. They represent a separate, morphologically well-defined group of the oldest bisons of the *Eobison* subgenus.

Bisons probably originated in southern Asia during the late Pliocene. Their ancestors stand close to *Leptobos*. Real *Bison* appeared in the early Pleistocene and was widely disseminated in the temperate zones of Asia and Europe. Southern Europe up to the Caucasian plains in the east was inhabited by short-horned forms—*B. tamanensis*, later *B. voigtstedtensis*, *B. lagenocornis*, and *B. schoetensacki*. By the beginning of middle Pleistocene *Bison* disappeared in southern Asia, but was widely distributed in the Holarctic (*B. schoetensacki*). During the middle Pleistocene, Europe, Asia, and the northern half of North America were inhabited by long-horned bisons: *B. priscus priscus*, *B. priscus crassicornis*, *B. priscus gigas*.

Landscape conditions throughout these territories were similar, and bisons occupied the entire area. From Asia the bisons dispersed into America (*B. chaneyi*) before the maximum glaciation (Illinoian). During the Illinoian glaciation of Canada they were forced southward and inhabited only the territory of the present United States, developing there into the gigantic *B. latifrons*. During

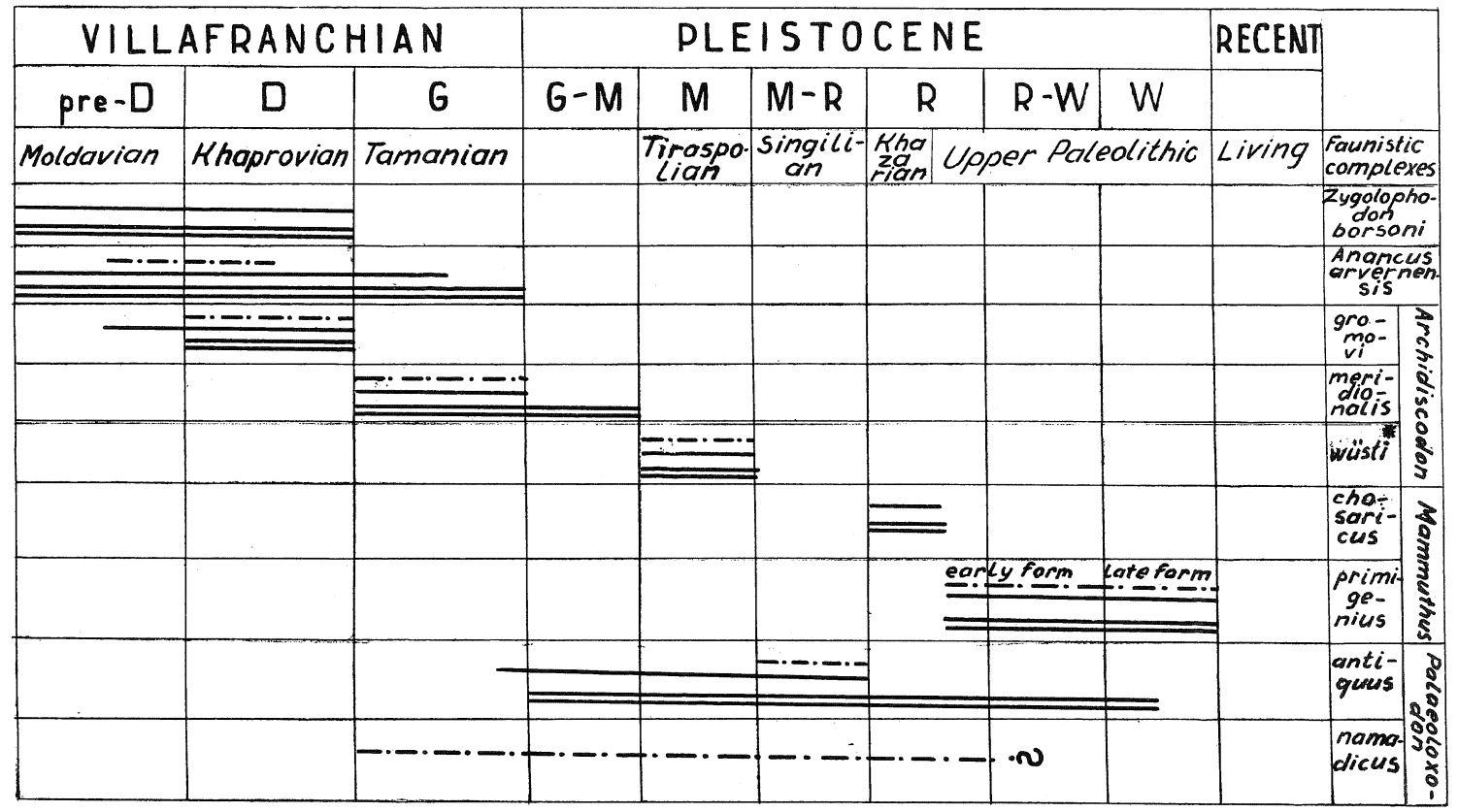
Wisconsin time the southern population was completely isolated from the northern population that continued to live in Asia, Beringia, and Alaska. During this time in the United States the ancestors of steppe bisons (*B. alleni*) and the later steppe bisons (*B. bison*) were developed. After the disappearance of the Canadian glacial sheet bisons again penetrated into Canada from the northwest and Alaska.

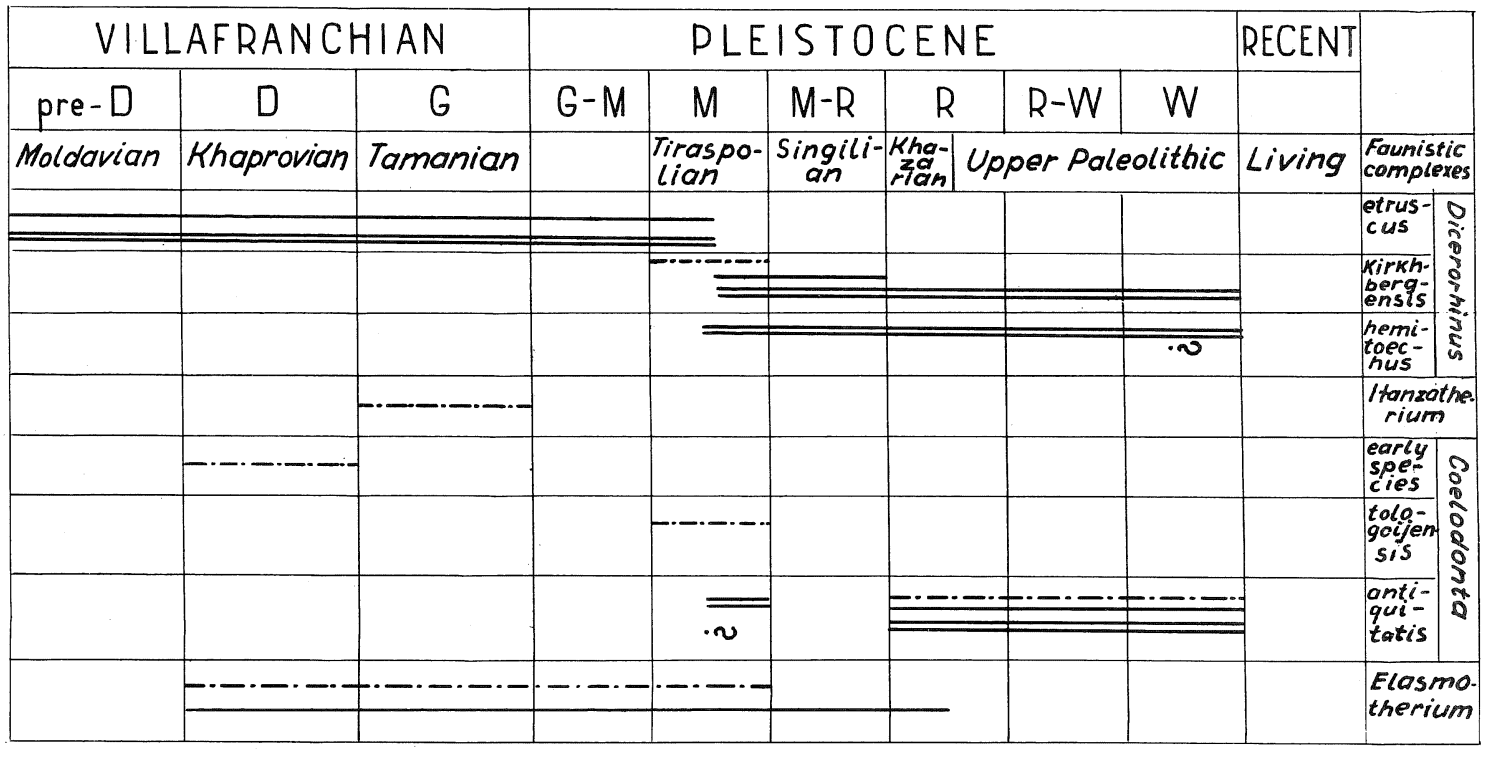
As the ice sheet disappeared the bisons began to get smaller. The long-horned *B. priscus priscus* and *B. priscus crassicornis* were replaced by short-horned *B. priscus mediator* and *B. priscus athabascae*. They also inhabited a very extensive area. At the end of the Würm that area was broken up into parts and by the beginning of the Holocene it was completely separated. Bison were preserved only in Europe (excepting its northern part), eastern Siberia, Alaska, Canada, and the United States. Independent populations were being formed and the bisons began to differentiate. An endemic form originated in Europe—*B. bonasus*.

A large *B. priscus athabascae* lived in eastern Siberia, Alaska, and Canada, which soon became extinct in Asia and is now preserved only in Canada.

By the beginning of the Holocene three geographically isolated populations had originated, with independent lines of historical development, very different ecologically and morphologically and well adapted to different conditions: *B. bonasus* inhabiting broad-leaved and mixed forests of Europe with a temperate climate and thin snow cover; the plains bison (*B. bison*) lived in the open expanses of the southern half of North America; and the woods bison (*B. priscus athabascae*) lived in the severe climate of the northern taiga forests of Canada.

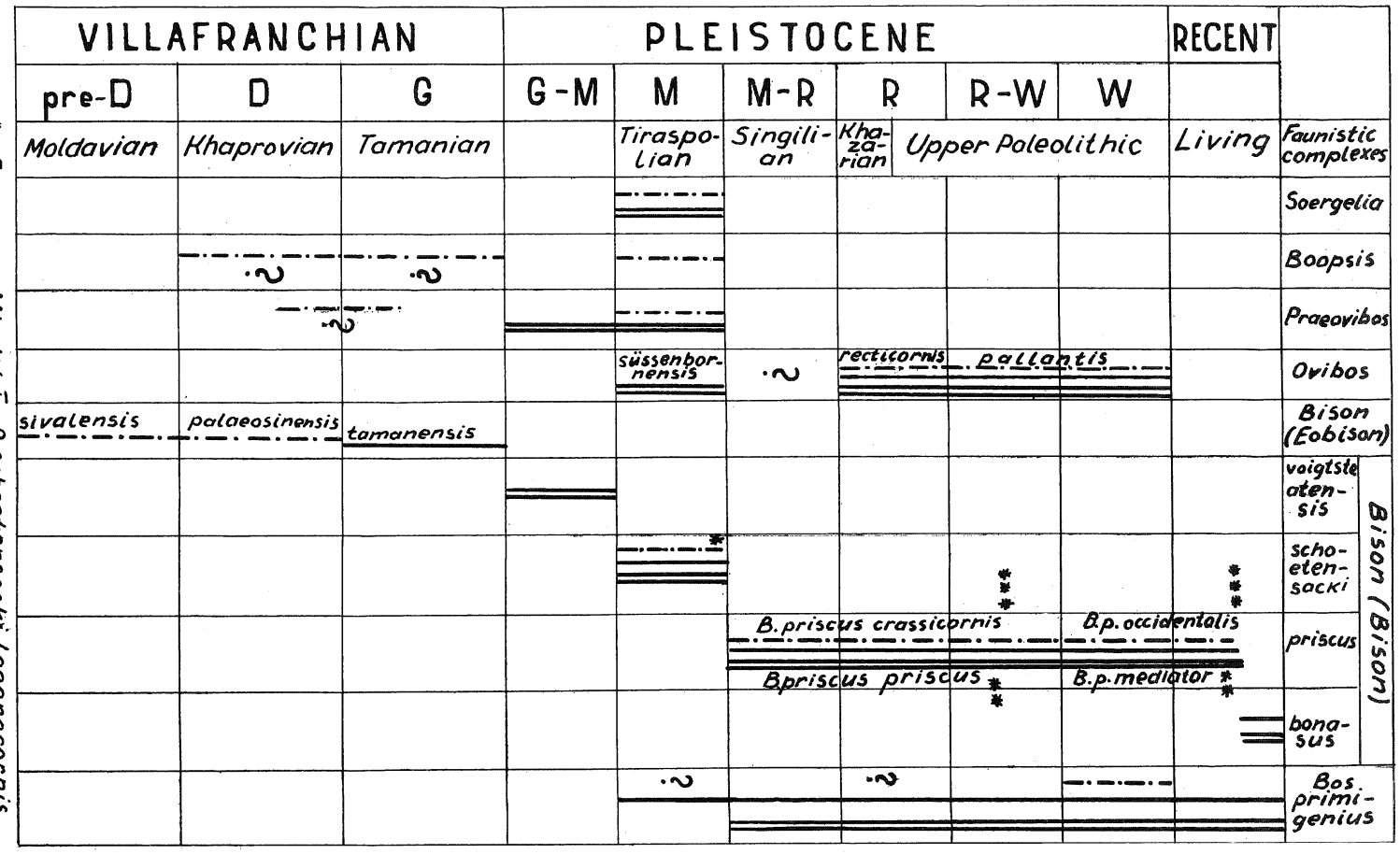
Stratigraphical Ranges of the Main Mammalian Groups
of Europe and Northern Asia





VILLAFRANCHIAN			PLEISTOCENE						RECENT	
pre-D	D	G	G-M	M	M-R	R	R-W	W		
Moldavian	Khaprovian	Tamanian		Tiraspolian	Singilian	Khazarian	Upper Paleolithic		Living	Faunistic complexes
										Hipparion
										Proboscidipparion
										stenonis-group — plesippus
										süssenbornensis-gr. — plesippus
sivalensis	sanmeniensis early form			late form						E. sivalensis-sanmeniensis-group
										Simionescui — Equus
										mosbachensis-group — Equus
										caballus — Equus
					large		small			

VILLAFRANCHIAN			PLEISTOCENE						RECENT	
pre-D	D	G	G-M	M	M-R	R	R-W	W		
Moldavian	Khaprovian	Tamanian		Tiraspolian	Singilian	Khazarian	Upper Paleolithic		Living	Faunistic complexes
										Paracamelus
				·?·						Camelus
										Euctenoceros Eucladoceros
	·?·									Praemegaceros
										Praedama
										Megaloceros
			·?·							Libralces
		·?·			A.l. postremus					latifrons — Alces
		·?·								alces — Alces
					·?·					Rangifer

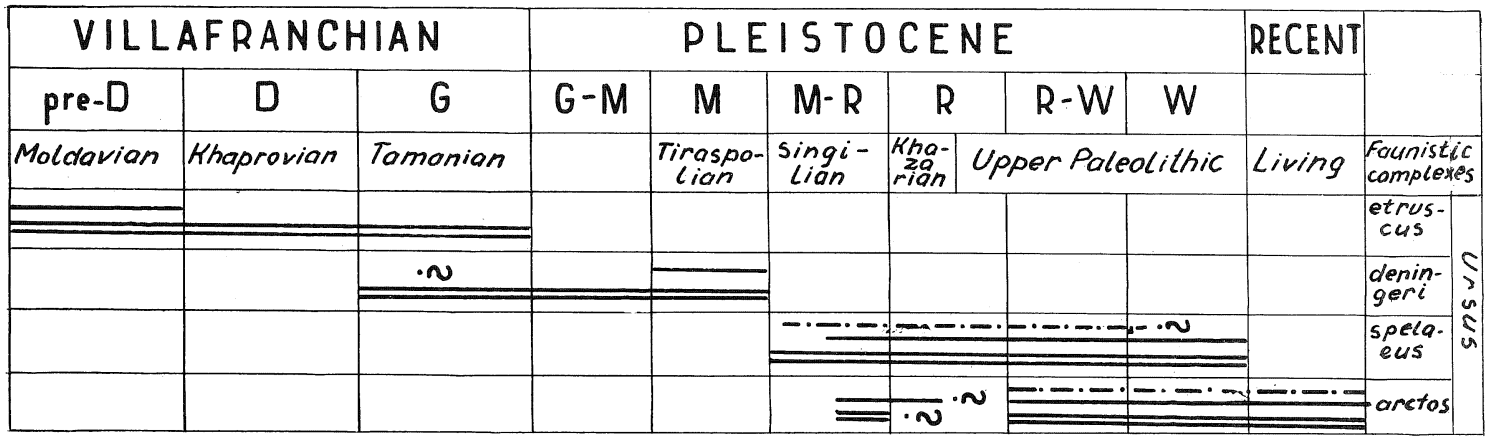


* In European Mindel I - B. schoetensacki lagenocornis, in the end of Mindel I and Mindel II B.S. schoetensacki.

** In Europe and West Siberia.

*** In East Siberia.

Note: In Russian of Southern Siberia and Mongolia - Bison priscus gigas.



Legend

— · — · — · — . Northern Asia

_____ Eastern Europe (within U.S.S.R.)

═══ Western Europe

Compiled by C. C. Flerow and A. V. Sher after their original work and after papers by: W. Gromova, *Brief Review of Quaternary Mammals of Europe* (in Russian), 143 pp., Moscow, 1965; and E. Vangengeim and V. Zazhigin, in *The Main Problems of Anthropogene Geology in Eurasia*, pp. 47–59, Moscow, 1969. W = Würm, R = Riss, M = Mindel, G = Günz, D = Donau.