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RUDOLF MUSIL
Department of Geology and Palaeontology J. E. Purkyně University, Brno

PALEOBIOGRAPHY OF TERRESTRIAL COMMUNITIES IN EUROPE DURING THE LAST GLACIAL

CONTENTS

METHOD OF PROCESSING

When processing the monograph on cave bears from the whole of Europe (MUSIL 1980, 1982) I collected all literature from all European countries that was available for me. The individual articles dealt not only with cave bears but gave outlines of entire faunistic communities, sometimes in great detail and with respect to the particular layers very exactly defined temporally. This overall outline that is available with me inspired me to try to present the development of faunistic communities of Europe in this paper.

I considered it the most suitable to limit myself only to the Last Glacial into certain sectors which I process in the same way so as to by finds, that it is best known from all aspects and that is exhibits a great variety of climatic oscillations. It also immediately precedes the Holocene, i.e. an epoch of the final formation of present-day fauna, and from this very point of view it is immensely important.

The modern stratigraphic scale of Würm could not be used as a whole. This is because I have used a great variety of articles from different times, not only the recent ones. This fact affected the division of the Last

Glacial into certain sectors which I process in the same way so as to obtain comparable results. Even so, due to articles of different age, it is possible to expect some minor time discrepancies in some cases, chiefly concerning time relation from more distant areas which are hard to remove. In spite of these possible — and I believe only isolated — shortcomings the outline of the development of communities given below corresponds to reality.

I divide the Last Glacial into the following substages from the point of view of the faunas processed:

H the late part of Stadial W_3 (Magdalenian)
G the latter half of W_3 (Solutrean)
F substages $W_{2/3}$ and W_3 (Gravettian)
E Stadial W_2
D Mousterian (without exact time classification)
C Interstadial $W_{1/2}$ (Mousterian)
B W_1 (Mousterian)
A Early Würm

Originally I wanted to divide the area of the whole of Europe regularly into the individual provinces and process these independently. But at the very beginning it became evident that it would not be quite possible. This is because the finding places of fossil fauna are not distributed evenly, but they concentrate into only some regions. Thus there appear places with a great concentration of finds and, on the other hand, areas with only isolated finds or those where all finds are lacking. The degree of investigation of the individual regions is another obvious feature.

For the above reasons I have specified regions with a major number of localities and with roughly the same climatic conditions at the same time. The conclusions can be then be generally interpreted into the other surrounding areas. The individual independently processed regions from the west to the east are as follows:

Region 1 the northern part of the Iberian Peninsula (with the exception of the Pyrenees, prevailingly its NW part)
2 the Pyrenees and their slopes
3 southern and central France
4 northern and central parts of Italy, Yugoslavia near the Adriatic coast
5 the Alps and their extensive promontory
6 southern part of the Federal Republic of Germany
7 central Germany (FRG, German Democratic Republic)
8 northern part of the FRG, Jutland and its southern surroundings
9 the region of Belgium
10 Czechoslovakia, particularly Moravia, to a lesser degree Bohemia and Slovakia
11 Poland, mostly its central and southern half
12 the Pannonian lowland, mainly its northern part
13 the inland of Rumania
14 the environs of the Danube delta
15 the region around the Dniester River (U.S.S.R.)
16 the region south of the City of Kiev (U.S.S.R.)
17 the Krimea
18 the region between the rivers Don and Volga (U.S.S.R.)
19 the Caucasus and its slopes
20 the southern part of the South Ural Mountains
21 the northern part of the Pechora River (the North Urals)

These regions delimited mainly from the point of view of the concentration of localities thus constitute a skeleton for solving the problems of the development of European communities in the course of Würm.

Analyzing the fauna I concentrated my attention to most of the species described. Their ecological requirements are, of course, different. This concerns also vegetation to which most of them are bound. That is why I have specified the main plant zones and species typical of them. If a species is found in several zones, I do not neglect this fact. The other species depending on other conditions than temperature or the plant cover are listed separately.

Species dominating the community of the given time and the given region are marked separately (printed in capital italics).

The areas of the main distribution of the individual species:

■ The tundra:

Rangifer tarandus, Ovibos moschatus, Gulo gulo, Lepus timidus, Coelodonta antiquitatis, Alopex lagopus, Mammonteus primigenius, Dicrostonyx torquatus, Dicrostonyx henseli, Lemmus lemmus.

○ The subarctic forest including the taiga:
Ursus arctos, Lynx lynx, Cervus elaphus, Rangifer tarandus, Bos primigenius, Marmota marmota, Alces alces, Sciurus vulgaris, Megaloceros giganteus, Canis lupus, Castor fiber.

▲ The arctic steppe, the loess steppe, the steppe:
Citellus citellus, Citellus rufescens, Cricetus cricetus, Equus sp., Bison priscus, Ochotona pusilla, Spermophilus rufescens, Mammonteus primigenius, Saiga tatarica, Alopex lagopus, Lepus timidus, Coelodonta antiquitatis, Rangifer tarandus, Ovibos moschatus, Marmota marmota, Alces alces, Equus (A.) hydruntinus, Equus (A.) hemionus, Megaloceros giganteus, Vormela sp., Alactaga jaculus, Dicerorhinus hemitoechus.

● The mild zone forest, meadows, water:
Ursus arctos, Ursus priscus, Lynx lynx, Martes martes, Martes foina, Lutra lutra, Canis lupus, Vulpes vulpes, Castor fiber, Sus scrofa, Cervus elaphus, Capreolus capreolus, Bos primigenius, Dama dama, Glis glis, Felis silvestris, Panthera leo, Oryctolagus cuniculus, Sciurus vulgaris.

All the other species described in the present paper have a climatically broad range of toleration. Characteristic of significantly warm climate are above all: *Dicerorhinus kirchbergensis, Hippopotamus amphibius, Palaeoloxodon antiquus, Testudo hermanni, Canis aureus, Canis lupaster, Sus scrofa, Hystrix cristata.*

THE TIME ANALYSIS OF THE FAUNAS OF THE INDIVIDUAL REGIONS

Early Würm

The finds described evidently include the beginning of the Last Glacial with its first interstadials and stadials. Finds marked in this way were limited only to the region of the Iberian Peninsula and Central Europe. The species composition in the individual regions looks as follows:

Region 1: Species living in the forest prevail, steppe elements are, however, quite frequently represented. Main species of the community (printed in capital italics).

● *D. kirchbergensis, H. amphibius, Sus scrofa, Capreolus capreolus, Vulpes vulpes.*
● ○ *Castor fiber, CERVUS ELAPHUS, Canis lupus, BOS PRIMIGENIUS, Lynx lynx.*
▲ ○ *Marmota marmota, Megaloceros giganteus.*
▲ *Equus* sp., *Bison priscus.*

■ ▲ ○ *Rangifer tarandus.*
■ ▲ *Lepus timidus.*
Other species described: *Panthera pardus, Panthera spelaea, RUPICAPRA RUPICAPRA, URSUS SPELAEUS, Meles meles, Capra ibex, Sorex sp.*

Region 4: A small number of species indicates that the community is not complete. The main species of the community.
● *D. kirchbergensis, Vulpes vulpes.*
● ○ *Cervus elaphus, Canis lupus.*
▲ ○ *Marmota marmota, Alces alces.*
■ ▲ *Lepus timidus.*
The following are listed from among the other species: *Ursus spelaeus, Crocuta spelaea.*

Region 6: Despite a low number of species represented rather steppe and tundra elements seem to prevail. The chief species of the community.
● *Capreolus capreolus.*
● ○ *CERVUS ELAPHUS, Bos primigenius.*
▲ *Equus sp., Bison priscus.*
■ ▲ ○ *RANGIFER TARANDUS.*
■ ▲ *M. PRIMIGENIUS, C. antiquitatis.*

Region 10: Animals of the taiga, the tundra and the steppe prevail. Chief community species.
● *Capreolus capreolus.*
● ○ *Castor fiber, Cervus elaphus, Canis lupus, Ursus arctos, Bos primigenius.*
▲ *Saiga tatarica, EQUUS* sp., *Bison priscus, Equus (A.) hydruntinus.*
▲ ○ *Alces alces.*
■ ▲ ○ *Rangifer tarandus.*
■ ○ *Gulo gulo.*
■ ▲ *Lepus timidus, Alopex lagopus, M. PRIMIGENIUS, C. ANTIQUITATIS.*
From among the other species the following are given: *Panthera spelaea, Rupicapra rupicapra, Ursus spelaeus, Ovis sp., Crocuta spelaea, Capra ibex.*

Region 11: Elements of the taiga, the tundra and the steppe prevail. Main community species.
● *Martes martes, Vulpes vulpes.*
● ○ *Castor fiber, Cervus elaphus, Canis lupus, Ursus arctos, Bos primigenius, Lynx lynx.*
▲ *Ochotona pusilla, Equus* sp., *Bison priscus.*
▲ ○ *Alces alces.*
■ ▲ ○ *Rangifer tarandus.*
■ ▲ *Lepus timidus, Alopex lagopus, M. primigenius, C. antiquitatis.*
■ *Dicrostonyx sp., Lemmus lemmus.*
From among the other species the following are given: *Panthera spelaea, Panthera pardus, URSUS SPELAEUS, Talpa europaea, Crocuta spelaea, Sorex* sp.

Region 12: Relatively frequent are forest species, those of the central European forest and of the tatra. Steppe elements are also frequent. Main species of th ecommunity.
● *Martes martes, Sus scrofa, Felis silvestris, Vulpes vulpes, Sciurus vulgaris, Capreolus capreolus.*
● ○ *Castor fiber, Cervus elaphus, Canis lupus, Ursus arctos, Lynx lynx.*
▲ *Ochotona pusilla, Cricetus cricetus, Equus* sp., *Bison priscus.*
▲ ○ *Alces alces, Megaloceros giganteus.*
■ ▲ ○ *Rangifer tarandus.*
■ ▲ *Lepus timidus, Alopex lagopus, M. primigenius, C. antiquitatis.*
From the other species the following are represented: *Hystrix cristata, Panthera pardus, Panthera spelaea, Rupicapra rupicapra, Ursus spelaeus, Ovis sp., Erinaceus sp., Talpa europaea, MELES MELES, Lepus europaeus, Mustela* sp., *Putorius* sp., *Sorex* sp.

Region 14: Steppe elements strongly prevail. Main community species.
● *Martes martes.*
● ○ *Cervus elaphus, Canis lupus, Ursus arctos.*

▲ *Saiga tatarica, EQUUS* sp., *Bison priscus, Equus (A.) hydruntinus.*
▲ ○ *Megaloceros giganteus.*
■ ▲ ○ *Rangifer tarandus.*
■ ▲ *Alopex lagopus, M. primigenius, C. antiquitatis.*
From among the other species the following are listed: *URSUS SPELAEUS, Crocuta spelaea, Capra ibex.*

The period of Early Würm is a stretch of time with a relatively warm climate all over Europe. Forests, however, are not continuous, but interchange with areas of steppes, irrespective of the average annual temperature. This means that the whole area of Europe was relatively arid.

The warmest region at that time appear to be the northern part of the Iberian Peninsula, northern Italy and Yugoslavia. Both central and southern France will no doubt belong here as well. In the Pannonian lowland there also prevailed a relatively warm climate at that time. As the coldest there appear to be the southern part of the FRG, the area of Czechoslovakia and that of the Danube delta. In those regions not only the amount of tundra elements increases, but there is also a sharp increase in the steppe elements. This is evidently due to an extensive spread of steppes, of course in any case with the presence of continuous forests of the taiga or of central European forest types. Of interest is the region of Poland which might have had somewhat more advantageous climatic conditions than regions situated immediately south of it.

Climatically, in the relation of this time space the regions studied can be evaluated as follows:

very warm climate: 1, 4
warm climate: 12
mildly cold climate: 10,11
very cold climate: 6, 14
extremely cold climate: —

Species explicitly requiring warm climate are found in Region 1 (*D. kirchbergensis*, P. *antiquus*), in Region 4 (*D. kirchbergensis*) and in Region 12 (*Hystrix cristata*). Steppe species, like *Ochotona pusilla* and *Saiga tatarica* are currently found in the area of central Europe. *Ovibos moschatus* is documented from the Alps, the westernmost finds of *Dicrostonyx* sp. and *Lemmus lemmus* come from Poland.

Stadial W_1

The finds thus marked can evidently come from a fairly long time period, from the end of the Last Interglacial up to Interstadial $W_{1/2}$. They are limited chiefly to the area of western, central and southern Europe. The species composition in the individual regions is as follows:

Region 1: All species point to a very warm climate, with forests and steppes present. Main species of the community.
● *D. kirchbergensis, P. antiquus, Sus scrofa, Oryctolagus cuniculus, Capreolus capreolus.*
● ○ *Cervus elaphus, Canis lupus, Ursus arctos, BOS PRIMIGENIUS.*
▲ ○ *Marmota marmota.*
▲ *Equus* sp., *Bison priscus.*
■ ▲ ○ *Rangifer tarandus.*
From the other species the following are given: *Rupicapra rupicapra, Ursus spelaeus, Crocuta spelaea, Capra pyrenaica.*

Region 3: The dominant element are animals living in the forest, the steppe element is not negligible. Chief species of the community.
● *D. kirchbergensis, Dama dama, H. amphitius, Sus scrofa, Felis silvestris, ORYCTOLAGUS CUNICULUS, Sciurus vulgaris, Capreolus capreolus, Vulpes vulpes.*
▲ ○ *Marmota marmota, Megaloceros giganteus.*
● ○ *Cervus elaphus, Canis lupus, Ursus arctos, Bos primigenius, Lynx lynx.*
▲ *Ochotona pusilla, Equus* sp., *Bison priscus.*

■ ▲ ○ *Rangifer tarandus.*
■ ▲ *M. primigenius, C. antiquitatis.*
The other species include: *Panthera spelaea, Panthera pardus, Rupicapra rupicapra, Ursus spelaeus, Erinaceus* sp., *Talpa europaea, Meles meles, Crocuta spelaea, Capra ibex.*

Region 4: Forest elements dominate, relatively frequently also steppe animals are represented. Chief species of the community.
● *P. antiquus, D. kirchbergensis, H. amphibius, Sus scrofa, Martes martes, Felis silvestris, Glis glis, Sciurus vulgaris, Capreolus capreolus, Vulpes vulpes.*
● ○ *CERVUS ELAPHUS, Canis lupus, Ursus arctos, Bos primigenius, Lynx lynx.*
▲ ○ *Marmota marmota.*
▲ *Cricetus cricetus, Equus* sp., *Bison priscus.*
▲ ○ *Alces alces, Megaloceros giganteus.*
■ ▲ *Lepus timidus.*
From among the other species the following are included: *Panthera pardus, Panthera spelaea, Cuon alpinus, Rupicapra rupicapra, URSUS SPELAEUS, Erinaceus* sp., *Meles meles, Crocuta spelaea, Putorius putorius, Sorex* sp., *Mustela nivalis, Capra ibex.*

Region 5: Animals of all environments are represented. Chief community species.
● *Martes martes, Felis silvestris, Glis glis, Vulpes vulpes.*
● ○ *Cervus elaphus, Canis lupus, Ursus arctos, Bos primigenius, Lynx lynx.*
▲ ○ *Marmota marmota.*
▲ *Cricetus cricetus, Equus* sp., *Bison priscus.*
■ ▲ ○ *Rangifer tarandus.*
■ ○ *Gulo gulo.*
■ ▲ *Alopex lagopus, Lepus timidus.*
■ *Dicrostonyx* sp.
From among the other species the following are listed: *Panthera spelaea, Panthera pardus, Cuon alpinus, Rupicapra rupicapra, URSUS SPELAEUS, Sorex* sp., *Putorius putorius, Mustela nivalis, Capra ibex.*

Region 6: Steppe and tundra elements are very frequent. Of course, also animals of the central European forest are represented. Main species of the community.
● *Sus scrofa, Felis silvestris, Glis glis, Capreolus capreolus, Vulpes vulpes,*
● ○ *Cervus elaphus, Canis lupus, Ursus arctos, Bos primigenius, Lynx lynx.*
▲ *Ochotona pusillla, Cricetus cricetus, Spermophilus* sp., *EQUUS* sp., *Bison priscus, Alactaga jaculus.*
▲ ○ *Megaloceros giganteus.*
■ ▲ ○ *Rangifer tarandus.*
■ ▲ *Ovibos moschatus, Lepus timidus, Alopex lagopus, M. PRIMIGENIUS, C. antiquitatis.*
■ *Dicrostonyx* sp., *Lemmus lemmus.*
From the other species the following are listed: *Panthera spelaea, Cuon alpinus, Rupicapra rupicapra, Ursus spelaeus, Erinaceus* sp., *Crocuta spelaea, Sorex* sp., *Mustela nivalis.*

Region 10: The number of species listed is lower, the steppe and tundra elements seem to prevail. Main species of the community.
● *Vulpes vulpes.*
● ○ *Canis lupus, Bos primigenius.*
▲ *Saiga tatarica, Equus* sp.
■ ▲ ○ *Rangifer tarandus.*
■ ▲ *Lepus timidus, M. primigenius, C. antiquitatis.*
From the other species the following are listed: *Ursus spelaeus, Crocuta spelaea.*

Region 11: Tundra and steppe elements prevail. Main species of the community:
● *Martes martes.*
● ○ *Cervus elaphus, Canis lupus, Bos primigenius.*
▲ *Ochotona pusilla, Cricetus cricetus, Citellus citellus, EQUUS* sp., *Bison priscus.*
■ ▲ ○ *Rangifer tarandus.*

■ ▲ *Ovibos moschatus, Lepus timidus, M. primigenius, C. antiquitatis.*
■ *Dicrostonyx* sp., *Lemmus lemmus.*
From the other species the following are given: *URSUS SPELAEUS, Talpa europaea, Crocuta spelaea, Sorex* sp., *Mustela nivalis.*

Region 17: Steppe forms prevail. The presence of the finds of *D. kirchbergensis* is not in accord with the other species. The main species of the community.
● *D. kirchbergensis.*
● ○ *Cervus elaphus.*
▲ *Saiga tatarica, Equus* sp., *Bison priscus, Equus (A.) hydruntinus.*
▲ ○ *Megaloceros giganteus.*
■ ▲ *M. PRIMIGENIUS.*
The following are listed from among the other species: *Ursus spelaeus, Crocuta spelaea.*

Region 18: A small amount of finds, nevertheless indicating an open steppe. Chief species of the community:
● *Vulpes vulpes.*
▲ *Saiga tatarica, Equus* sp., *BISON PRISCUS.*
■ ▲ *M. primigenius.*

Region 19: Forest elements dominate, steppe elements being also relatively frequent. Main species of the community.
● *D. kirchbergensis, Dama dama, Martes martes, Sus scrofa, Capreolus capreolus, Vulpes vulpes.*
● ○ *CERVUS ELAPHUS, Canis lupus, Ursus arctos, Lynx lynx.*
▲ *CANIS AUREUS, Bison priscus, Equus (A). hydruntinus.*
▲ ○ *Megaloceros giganteus.*
■ ▲ *Gulo gulo, Lepus timidus.*
Other species described: *Panthera pardus, Panthera spelaea, Rupicapra rupicapra, URSUS SPELAEUS, Ovis* sp., *Meles meles, Capra ibex.*

Substage W_1 is characterized — on the basis of the faunistic community — by an increased average annual temperature when compared with the latter half of Würm, which holds for the entire area studied. An essential increase in temperature is, however, perceptible in the northern part of the Iberian Peninsula, in southern and central France, in the north of Italy and Yugoslavia, in the Crimea and in the Caucasus. Nowhere in the regions studied extremely cold climate is observed; the coldest seem to be the regions of Czechoslovakia and Poland.

Despite the increased average temperature great aridity of the climate evidently persists. Steppe elements are represented not only in the colder regions, but relatively amply also in the warmest ones. This is due to the fact that in this substage areas of the forest and of the steppe alternate irrespective of the average annual temperature. There are, of course, also regions where the distribution of the steppe is strongly influenced by the underlying rocks, such as the Crimea.

Climatically the studied areas in relation of this very substage can be evaluated as follows:

very warm climate: 1, 2, 3, 17, 19
warm climate: 13
mildly cold climate: 6
very cold climate: 10, 11
extremely cold climate: —

Of interest is the position of the Alps and their northern adjacent part (the southern part of the FRG) from the point of view of average temperature. Their climate was more favourable than that in Czechoslovakia or in Poland.

As for the individual species, animals requiring explicitly warm climate occur all over the south of Europe.

Region 1 (NW part of the Iberian Peninsula): *D. kirchbergensis, P. antiquus.*

Region 3 (southern and central France): *D. kirchbergensis, P. antiquus, Dama dama, H. amphibius.*

Region 4 (the north of Italy and Yugoslavia): *D. kirchbergensis, P. antiquus, H. amphibius.*

Region 19 (the Caucasus): *D. kirchbergensis, Dama dama.*

The area of distribution of *Sus scrofa, Felis silvestris* and other species of the central European forest ends in the north by the Alps or by southern part of the FRG, i. e. it is relatively small. In Spain and in France *Oryctolagus cuniculus* is present. Only the species *Cervus elaphus* inhabits the whole European area, the same as *Bos primigenius* and *Bison priscus.*

Interesting is also a great distribution of *Ochotona pusilla* (up to the south of France). *Saiga tatarica,* on the other hand, reaches only up to central Europe. Relatively rare are the finds of *Alces alces* and *Megaloceros giganteus* in that substage.

Ovibos moschatus has been recorded in the southern part of the FRG, finds of mammonths are relatively infrequent, but they are registered even from the region of southern France, i. e. from a region with very warm climate. The same holds for *C. antiquitatis.* Frequent are finding places of typical tundra animals such as *Dicrostonyx* and *Lemmus* which are often found in the western part of Europe as far as in the Alps and in the southern part of the FRG.

Substage $W_{1/2}$

The substage of the so-called First Würm Interstadial ($W_{1/2}$, Hengelo, Podhradem, Middle-Würm Interstadial, etc.) is a substage of relatively mild to warm climate all over Europe. The whole of eastern Europe is missing in our outline, but it can be judged that climatic conditions there might have been analogical to those of central or western Europe. The species pattern in the individual regions looks as follows:

Region 3: Most animals are characteristic of the central European forest zone. The presence of *P. antiquus* and *D. kirchbergensis* points to very warm climate. Chief species of the community.

- ● *P. antiquus, D. kirchbergensis, Dama dama, Sus scrofa, Martes martes, Panthera leo, Oryctolagus cuniculus, CAPREOLUS CAPREOLUS, Vulpes vulpes.*
- ● ○ *CERVUS ELAPHUS, Canis lupus, Ursus arctos, Bos primigenius, Lynx lynx.*
- ▲ *Citellus citellus, EQUUS* sp., *BISON PRISCUS, Equus (A). hydruntinus.*
- ■ ▲ ○ *Rangifer tarandus.*
- ■ ▲ *Alopex lagopus.*
- ▲ ○ *Marmota marmota, Megaloceros giganteus.*

Other species described: *Panthera pardus, Panthera spelaea, Rupicapra rupicapra, Ursus spelaeus, Ovis* sp., *Lepus europaeus, MELES MELES, Talpa europaea, Erinaceus* sp., *CROCUTA SPELAEA, CAPRA IBEX,* Putorius putorius, Cuon alpinus.

Region 4: Despite a great prevalence of forest animals also elements typical of the northern regions appear. Despite this, the climate must have been significantly warm. Main species of the community.

- ● *D. kirchbergensis, Sus scrofa, Martes martes, Felis silvestris, Sciurus vulgaris, Glis glis, Capreolus capreolus, Vulpes vulpes.*
- ● ○ *Castor fiber, CERVUS ELAPHUS, Canis lupus, Ursus arctos, Bos primigenius, Lynx lynx.*
- ▲ *Citellus citellus, Cricetus cricetus, Equus* sp., *Bison priscus.*
- ■ ▲ *Lepus timidus, Alopex lagopus, M. primigenius.*
- ▲ ○ *Marmota marmota, Megaloceros giganteus, Alces alces.*
- ■ ○ *Gulo gulo.*

Other species mentioned: *Panthera pardus, Panthera spelaea, Cuon alpinus, Rupicapra rupicapra, URSUS SPELAEUS, Ovis* sp., *Lepus europaeus, Meles meles, Talpa europaea, CROCUTA SPELAEA, Putorius putorius, Mustela nivalis, Sorex* sp., *Capra ibex.*

Region 5: Forest and taiga elements prevail, tundra animals in relation to them are in a subordinate amount. Chief species of the community.

- ● *Sus scrofa Martes martes, Capreolus capreolus, Vulpes vulpes.*
- ● ○ *Cervus elaphus, Canis lupus, Ursus arctos, Lynx lynx.*
- ■ ○ *Gulo gulo.*
- ▲ ○ *Marmota marmota, Alces alces.*
- ▲ *Cricetus cricetus, Citellus citellus, Bison priscus.*
- ■ ▲ *Ovibos moschatus, Lepus timidus, C. antiquitatis.*
- ■ ▲ ○ *Rangifer tarandus.*

Other species described: *Panthera spelaea, Rupicarpra rupicapra, URSUS SPELAEUS, MELES MELES, CROCUTA SPELAEA, Capra ibex.*

Region 7: Besides animals of the central European forest and of the taiga a number of typically tundra and steppe elements occur. Main species of the community.

● *Sus scrofa, Capreolus capreolus, Vulpes vulpes.*
● ○ *CERVUS ELAPHUS, Canis lupus, Ursus arctos, Bos primigenius.*
▲ ○ *Megaloceros giganteus.*
■ ▲ ○ *Rangifer tarandus.*
■ ▲ *Lepus timidus, Alopex lagopus, M. PRIMIGENIUS, C. antiquitatis.*
▲ *Citellus citellus, EQUUS* sp., *Bison priscus, Equus (A). hydruntinus.*
■ ○ *Gulo gulo.*

Other species described: *Panthera spelaea, Rupicapra rupicapra, URSUS SPELAEUS, Meles meles, Crocuta spelaea, Capra ibex.*

Region 10: The prevailing element are animals of the tundra, the steppe and the taiga. Chief species of the community.

● *Martes martes, Lutra lutra, Sus scrofa, Felis silvestris, Vulpes vulpes.*
● ○ *Castor fiber, Cervus elaphus, Canis lupus, Ursus arctos, Bos primigenius.*
▲ ○ *Marmota marmota, Megaloceros giganteus, Alces alces.*
▲ *Saiga tatarica, Citellus citellus, Equus* sp., *Bison priscus, Equus (A.) hydruntinus.*
■ ▲ ○ *Rangifer tarandus.*
■ ○ *Gulo gulo.*
■ ▲ *Lepus timidus, Alopex lagopus, M. primigenius, C. antiquitatis.*

Other species described: *Panthera panthera, Panthera spelaea, Rupicapra rupicapra, URSUS SPELAEUS, Meles meles, Crocuta spelaea, Putorius putorius, Capra ibex.*

Region 11: Quite eminently animals of the tundra and of the steppe dominate, elements of the central European forest are missing altogether. Chief community species.

● ○ *Canis lupus, Ursus arctos, Bos primigenius.*
▲ *Ochotona pusilla, Cricetus cricetus, Equus* sp., *Bison priscus.*
■ ▲ ○ *Rangifer tarandus.*
■ ○ *Gulo gulo.*
■ ▲ *Lepus timidus, Alopex lagopus, C. antiquitatis.*
■ *Dicrostonyx* sp., *Lemmus lemmus.*

From among other species the following are mentioned: *Panthera spelaea, Rupicapra rupicapra, URSUS SPELAEUS, Talpa europaea, Mustela nivalis, Sorex* sp.

Region 12: The amounts of tundra, steppe and taiga animals are more or less quantitavely the same, animals of the central European forest being also present. Main species of the community.

● *Martes martes, Sus scrofa, Felis silvestris, Vulpes vulpes.*
● ○ *Cervus elaphus, Canis lupus, Ursus arctos, Lynx lynx.*
▲ *Ochotona pusilla, Cricetus cricetus, Citellus citellus, Equus* sp., *Bison priscus.*
▲ ○ *Megaloceros giganteus, Alces alces.*
■ ▲ ○ *Rangifer tarandus.*
■ ▲ *Lepus timidus, Alopex lagopus, M. primigenius, C. antiquitatis.*
■ *Dicrostonyx* sp.

Some other species described: *Panthera spelaea, URSUS SPELAEUS, Erinaceus* sp., *Talpa europaea, Meles meles, Crocuta spelaea, Mustela nivalis, Sorex* sp., *Capra ibex, Putorius putorius.*

Region 13: Elements of the steppe and of the taiga prevail. Animals of the central European forest are also present. Main species of the community.

● *Lutra lutra, Martes martes, Sus scrofa, Vulpes vulpes.*
● ○ *Cervus elaphus, Canis lupus, Bos primigenius.*
▲ *Saiga tatarica, Equus* sp., *Bison priscus, Equus (A). hydruntinus.*
▲ ○ *Megaloceros giganteus, Alces alces.*
■ ▲ ○ *Rangifer tarandus.*
■ ▲ *M. primigenius, C. antiquitatis.*

Other described species: *Rupicapra rupicapra, URSUS SPELAEUS, Ovis* sp., *Meles meles, Talpa europaea, Crocuta spelaea, Putorius putorius, Capra ibex.*

Region 14: Only a small number of finds described, which does not yield the possibility of further evaluation. Main species of the community.

■ ▲ *M. primigenius, C. antiquitatis.*

Mentioned from among other species: *Ursus spelaeus.*

Region 15: Steppe elements clearly predominate. Chief species of the community.

● *Vulpes vulpes.*
● ○ *Cervus elaphus, Canis lupus.*
▲ ○ *Megaloceros giganteus.*
▲ *Equus* sp., *Bison priscus.*
■ ▲ ○ Rangifer tarandus.
■ ▲ M. primigenius, C. antiquitatis.

Other species described: *Panthera spelaea, URSUS SPELAEUS, Crocuta spelaea.*

Region 17: Steppe elements prevail, animals of all zones, however, occurring as well. Main community species.

● *Sus scrofa, Capreolus capreolus.*
● ○ *Cervus elaphus, Canis lupus, Bos primigenius.*
▲ *Saiga tatarica, Equus* sp., *Bison priscus, EQUUS (A.) HYDRUNTINUS.*
▲ ○ *Megaloceros giganteus.*
■ ▲ ○ *Rangifer tarandus.*
■ ▲ *Alopex lagopus, M. primigenius, C. antiquitatis.*

Other species described: *Ursus spelaeus, Lepus europaeus, Crocuta spelaea, Putorius putorius.*

Region 19: From the substage studied a small number of species is described, which does not allow further conclusions. Main species of the community.

● *Sus scrofa.*
● ○ *Cervus elaphus.*
▲ *Bison priscus.*

From among other species the following are mentioned: *URSUS SPELAEUS, Capra ibex.*

This substage is climatically very strongly differentiated in Europe. Even though steppe elements are strongly represented everywhere, a typical arctic steppe comes into consideration in a small number of cases. Tundra animals recede strongly, forest animals, on the other hand, being relatively frequent. A number of regions has explicitly warm climate, in many cases the climate is mild.

Very warm climate is found in the region of south and central France and further along the northern coast of the Adriatic. This is supported not only by the dominating species of the central European forest and a weak representation of tundra elements, but also by the presence of species requiring explicitly warm environment, such as *D. kirchbergensis* and *P. antiquus.* Despite the explicitly warm climate a great variety of steppe species indicates in both cases a large spread of steppes. It is therefore necessary to assume that the climatic conditions were rather arid.

Relatively strongly is climatically differentiated the region of central Europe. At that time the coldest part is the region of Poland; central Germany, Czechoslovakia and the Pannonian lowland have more or less a mild and dry climate. The situation is somewhat different in the region of the Alps and their promontories and in relation with them also the region of the Carpathians in Rumania. A relatively high amount of forest zone species indicates a warm climate, but still with the presence of steppe elements. This looks like the two mountain ranges forming a definite temperature and climatic inversion due to greater relative height.

The region around the Dniester River and the Crimea indicate widely spread steppes, but a number of species typical of the central European forest and the taiga are present.

In the relation of this substage the regions studied can be climatically evaluated as follows:

very warm climate: 3, 4
warm climate: 5, 13
cold climate: 7, 15

mildly cold climate: 10, 12
very cold climate: 11
extremely cold climate: —

On the whole, an average warmer climate can be observed all over Europe, as well as a relatively high aridity. Irrespective of temperature steppes are widely extended, the landscape everywhere has a character of alternating areas of forests and open steppes. Open steppes are intensely represented mainly in the eastern parts of Europe.

As for the individual species, forest animals with higher temperature requirements do not exceed the region of south and central France and the northern coast of the Adriatic. The limit of animals typical of the central European forest coincides roughly with the 50th parallel in western and central Europe. A variety of species living both in the central European forest and in the taiga occur all over the area of Europe.

Typical steppe elements penetrate from the east only to the region of central Europe. Thus the species *Ochotona pusilla* has the western boundary of its distribution in Poland and in central Germany, in the south in the Pannonian lowland. The same also concerns the species *Saiga tatarica.*

A warmer climate is also indicated by the finds of *Equus (A.) hydruntinus* situated relatively high in the north of Europe.

Species adapted to a cold climate leave out the region of France and mostly also that of the Adriatic coast. *Ovibos* is documented only from the Alps, the mammoth occurs westernmost in central Germany and in northern Italy, the same goes roughly also for the woolly rhinoceros. Explicitly tundra species, such as *Dicrostonyx* and *Lemmus* have a distribution similar to that of *Ochotona* and *Saiga.*

Mousterian

A number of localities were not geologically dated, paleontological finds being found in cultural layers with the tools of Mousterian. Even though this stage persisted for a relatively long time, including a variety of climatic oscillations of different intensity, I think that to a certain extent it characterizes — as a whole — a definite average and in many cases it completes former data. The outline is, therefore, to be understood like this.

Region 1:

● *Sus scrofa, ORYCTOLAGUS CUNICULUS, Vulpes vulpes.*
● ○ *Ursus arctos, Bos primigenius.*
▲ ○ *Marmota marmota.*
▲ *Bison priscus.*

Other species mentioned: *Panthera spelaea, Cuon alpinus, Rupicapra rupicapra, Ursus spelaeus, Crocuta spelaea, Capra ibex.*

Region 2:

● *Sus scrofa, Felis silvestris Vulpes vulpes.*
● ○ *Castor fiber, CERVUS ELAPHUS, Canis lupus, BOS PRIMIGENIUS, Lynx lynx.*
▲ *Equus sp., BISON PRISCUS, D. hemitoechus.*
■ ▲ ○ *Rangifer tarandus.*
■ ○ *Gulo gulo.*
■ ▲ *C. antiquitatis, Ovibos moschatus.*

Other species described: *Panthera pardus, URSUS SPELAEUS, Meles meles.*

Region 3:

■ *SUS SCROFA, ORYCTOLAGUS CUNICULUS, Capreolus capreolus, Vulpes vulpes.*
■ ○ *Castor fiber, CERVUS ELAPHUS, Canis lupus, Ursus arctos, BOS PRIMIGENIUS, Lynx lynx.*
▲ ○ *Marmota marmota, Alces alces.*
▲ *Saiga tatarica, EQUUS* sp., *Bison priscus, Equus (A). hydruntinus.*
■ ▲ ○ *Rangifer tarandus.*
■ ▲ *C. antiquitatis.*

From among other species the following are described: *Panthera spelaea, Rupicapra rupicapra, URSUS SPELAEUS, CROCUTA SPELAEA, CAPRA IBEX.*

Region 5:

● *D. kirchbergensis, Sus scrofa, Martes martes, Vulpes vulpes, Felis silvestris, Sciurus vulgaris.*
● ○ *Cervus elaphus, Canis lupus, Ursus arctos, Bos primigenius, Lynx lynx.*
▲ ○ *Marmota marmota.*
▲ *Cricetus cricetus, Equus* sp., *Bison priscus.*
■ ▲ ○ *Rangifer tarandus.*
■ ○ *Gulo gulo.*
■ ▲ *Lepus timidus, Alopex lagopus.*
■ *Dicrostonyx* sp.

Other species mentioned: *Panthera spelaea, Panthera pardus, Cuon alpinus, Rupicapra rupicapra, Ursus spelaeus, Crocuta spelaea, Putorius* sp., *Mustela* sp., *Capra ibex.*

Region 6:

● *Capreolus capreolus, Vulpes vulpes.*
● ○ *Cervus elaphus, Canis lupus.*
▲ ○ *Marmota marmota, Megaloceros giganteus.*
▲ *Equus* sp., *Bison priscus.*
■ ▲ ○ *Rangifer tarandus.*
■ ○ *Gulo gulo.*
■ ▲ *Lepus timidus, Alopex lagopus, M. primigenius, C. antiquitatis.*

Other described species: *PANTHERA SPELAEA, Rupicapra rupicapra, Ursus spelaeus, Crocuta spelaea, Capra ibex.*

Region 9:

● ○ *Canis lupus, URSUS ARCTOS.*
▲ *Equus* sp.
■ ▲ *M. primigenius.*

Other species mentioned: Ursus spelaeus, *CROCUTA SPELAEA.*

Region 12:

● *Martes martes, Capreolus capreolus, Vulpes vulpes.*
● ○ *Cervus elaphus, Canis lupus, Lynx lynx.*
▲ ○ *Megaloceros giganteus.*
▲ *Equus* sp., *Bison priscus.*
■ ▲ ○ *Rangifer tarandus.*
■ ▲ *Lepus timidus, C. antiquitatis.*

Other species described: *Panthera spelaea, Rupicapra rupicapra, URSUS SPELAEUS, Meles meles, Crocuta spelaea.*

Region 13.

● *Vulpes vulpes.*
▲ ○ *Marmota marmota.*
● ○ *Canis lupus, Ursus arctos.*
▲ *Equus* sp.
■ ▲ *C. antiquitatis.*

From among other species the following is described: *Ursus spelaeus.*

Region 14:

● *Vulpes vulpes.*
● ○ *Cervus elaphus, Canis lupus, Bos primigenius.*
▲ *Canis aureus, Saiga tatarica, Citellus citellus, Equus* sp., *Bison priscus, Equus (A.) hydruntinus.*
● *Vulpes vulpes.*
■ ▲ *C. antiquitatis.*

Other species described: *URSUS SPELAEUS, Crocuta spelaea, Mustela* sp.

Region 17:

● *Sus scrofa, Vulpes vulpes.*
● ○ *Cervus elaphus, Canis lupus, Ursus arctos, Bos primigenius, Lynx lynx.*
▲ ○ *Marmota marmota, Megaloceros giganteus.*
▲ *Ochotona pusilla, Saiga tatarica, Cricetus cricetus, Equus* sp., *Bison priscus, Equus (A) hydruntinus, Alactaga jaculus.*

■ ▲ ○ *Rangifer tarandus.*
■ ▲ *Alopex lagopus, M. primigenius, C. antiquitatis.*
Other species mentioned: *RUPICAPRA RUPICAPRA, Ursus spelaeus, MELES MELES, Ovis* sp., *Crocuta spelaea.*

Region 18:
● *Vulpes vulpes.*
▲ *Saiga tatarica, Equus* sp., *BISON PRISCUS.*
■ ▲ *M. primigenius.*

Region 19:
● *Sus scrofa, Martes martes, Lutra lutra, Capreolus capreolus, Vulpes vulpes*
● ○ *Cervus elaphus, Canis lupus, Bos primigenius.*
▲ *Canis aureus, Saiga tatarica, Equus* sp., *BISON PRISCUS, Equus (A). hydruntinus.*
▲ ○ *MEGALOCEROS GIGANTEUS, Alces alces.*
■ ▲ ○ *Rangifer tarandus.*
■ ▲ *Lepus timidus, M. primigenius.*
Other species mentioned: *URSUS SPELAEUS, Crocuta spelaea, Capra ibex.*

Substage W_2

The substage of the Second Würm Stadial means for central Europe the onset of pronouncedly cold climate, substantially different from the climate of the preceding part of Würm. This change is comparatively quick and very conspicuous, as could be stated at a number of localities.

Unfortunately localities in the east of Europe that could be stratigraphically exactly fitted into this Stadial are almost missing. The species pattern in the individual regions looks as follows:

Region 1: Most animals are characteristic of the central European forest zone, tundra elements are relatively scanty. Main species of the community.
● *Panthera leo, Felis silvestris, CAPREOLUS CAPREOLUS, Vulpes vulpes, Oryctolagus cuniculus, Sus scrofa, D. kirchbergensis.*
● ○ *CERVUS ELAPHUS, Bos primigenius, Lynx lynx, Castor fiber, Canis lupus, Ursus arctos.*
▲ *EQUUS* sp., *Bison priscus, D. hemitoechus.*
■ ▲ ○ *Rangifer tarandus.*
■ ▲ *Lepus timidus, C. antiquitatis.*
▲ ○ *Marmota marmota.*
Other species mentioned: *RUPICAPRA RUPICAPRA, Talpa europaea, Sorex* sp., *Mustela* sp., *Capra pyrenaica, PANTHERA PARDUS, URSUS SPELAEUS, Meles meles, Crocuta spelaea, Crocuta crocuta, Putorius putorius.*

The pattern of the community indicates very warm climate, as can be seen from the presence of *D. kirchbergensis.*

Region 2: Relatively strongly are represented elements of the central European forest and steppe, numerous are, however, also elements of the tundra and of the taiga. This is evidently due to the height variation in this region. Most frequent are, however, steppe animals. Chief species of the community.
● *Fellis silvestris, Martes martes, Sus scrofa, Capreolus capreolus, VULPES VULPES.*
● ○ *CERVUS ELAPHUS, CANIS LUPUS, Ursus arctos, BOS PRIMIGENIUS.*
▲ *Saiga tatarica, EQUUS* sp., *Bison priscus.*
▲ *Megaloceros giganteus.*
■ ▲ ○ *RANGIFER TARANDUS.*
■ ▲ *Lepus timidus, Alopex lagopus, M. primigenius, C. antiquitatis.*
Other species described: *Panthera spelaea, Panthera pardus, Cuon alpinus, RUPICAPRA RUPICAPRA, Ursus spelaeus, Crocuta spelaea, Sorex* sp.

The community pattern indicates prevailingly warm climate, cold adapted coming evidently from higher situated areas.

Region 3: Relatively few tundra elements, animals of the central European forest prevail, steppe animals being amply represented. Chief species of the community.

● *Sus scrofa, Oryctolagus cuniculus, Capreolus capreolus, Vulpes vulpes, Dama dama, Lutra lutra, Martes martes.*
● ○ *Cervus elaphus, CANIS LUPUS, BOS PRIMIGENIUS, Lynx lynx, Ursus arctos.*
▲ *EQUUS* sp., *Equus (A.) hydruntinus.*
▲ ○ *Marmota marmota, Megaloceros giganteus, BISON PRISCUS, Citellus citellus.*
● ▲ ○ *RANGIFER TARANDUS.*
■ ▲ *M. primigenius, C. ANTIQUITATIS, Lepus timidus, ALOPEX LAGOPUS.*

Other described species: *Panthera pardus, Rupicapra rupicapra, Ursus spelaeus, CROCUTA SPELAEA, CAPRA IBEX, Panthera spelaea, Meles meles, Talpa europaea, Mustela* sp.
The community pattern indicates warm climate.

Region 4: The quantitative representation of animals of the individual climatic zones is roughly the same. Main species of the community.

● *Capreolus capreolus.*
● ○ *Castor fiber, Cervus elaphus, Canis lupus, Bos primigenius, Lynx lynx.*
▲ *Ochotona pusilla, Saiga tatarica, Bison priscus.*
▲ ○ *Marmota marmota, Alces alces.*
■ ▲ ○ *Rangifer tarandus.*
■ *Gulo gulo.*
■ ▲ *Lepus timidus, Alopex lagopus, C. antiquitatis.*

Other species mentioned: *Panthera spelaea, RUPICAPRA RUPICAPRA, URSUS SPELAEUS, Capra ibex, Mustela* sp.
The pattern of the community indicates essentially mild, but rather cold climate.

Region 6: Steppe elements are represented relatively frequently, the others are roughly balanced. Chief species of the community.

● *Vulpes vulpes.*
● ○ *Cervus elaphus, Canis lupus.*
▲ *Ochotona pusilla, EQUUS* sp., *Bison priscus.*
▲ ○ *Megaloceros giganteus.*
■ ▲ ○ *Rangifer tarandus.*
■ ▲ *Lepus timidus, M. PRIMIGENIUS, C. antiquitatis.*

Other species described: *Panthera spelaea, Rupicapra rupicapra, Ursus spelaeus, Meles meles, Mustela* sp.
The pattern of the community indicates mildly cold climate.

Region 9: The quantitative number of species of the individual zones is roughly balanced, despite its position which is shifted relatively high to the north a freat number of species of the central European forest occur. A strong effect of the sea on the climate is evident. Main species of the community.

● *Sus scrofa, VULPES VULPES.*
● ○ *Cervus elaphus, Canis lupus, Bos primigenius.*
▲ *Equus* sp.
■ ▲ ○ *Rangifer tarandus.*
■ ▲ *Lepus timidus, ALOPEX LAGOPUS, M. primigenius, C. antiquitatis.*

Other species mentioned: *URSUS SPELAEUS, Crocuta crocuta, Capra ibex.*
The community pattern indicates mildly cold climate.

Region 10: Animals of the steppe and of the tundra are greatly prevalent, others are strongly shifted to the background. Chief species of the community.

● *Vulpes vulpes.*
● ○ *Canis lupus.*
▲ *Ochotona pusilla, Saiga tatarica, Cricetus cricetus, Equus* sp., *Alactaga* jaculus.
■ ▲ ○ *Rangifer tarandus.*
■ ○ *Gulo gulo.*
■ ▲ *Lepus timidus, Alopex lagopus, M. primigenius, C. antiquitatis.*
■ *Dicrostonyx* sp., *Lemmus lemmus.*

Other species described: *Rupicapra rupicapra, URSUS SPELAEUS, Crocuta spelaea, Mustela* sp., *Putorius putorius.*

The community pattern indicates extremely cold climate.

Region 12: Animals of the central European forest and of the taiga prevail. Steppe elements are very frequent. Main species of the community.

● ○ *Cervus elaphus, Canis lupus, Ursus arctos.*
▲ *Ochotona pusilla, Saiga tatarica, Cricetus cricetus.*
■ ▲ ○ *Rangifer tarandus.*
■ ▲ *Lepus timidus.*

Other species mentioned: *Rupicapra rupicapra, Ursus spelaeus, Talpa europaea, Crocuta spelaea, Putorius putorius, Mustela* sp., *Capra ibex.*

The pattern of the community indicates warm climate.

Region 14: Steppe elements prevail, animal typical of the taiga and the tundra are abundant. Chief species of the community.

● ○ *Cervus elaphus.*
■ ○ *Megaloceros giganteus.*
▲ *Equus* sp., *Bison priscus, Equus (A.) hydruntinus.*
● ▲ ○ *RANGIFER TARANDUS.*
■ ▲ *OVIBOS MOSCHATUS, ALOPEX LAGOPUS.*

Other species described: *Ursus spelaeus, CROCUTA SPELAEA, Putorius putorius.*

The species pattern indicates very cold climate.

The prevailing element of Stadial W_2 in Europe is the steppe. Steppe elements are represented in different amounts, almost always being dominant, particularly as for the southern part of the FRG, Czechoslovakia and the region about the Danube delta. Very abundant are also tundra animals, particularly in those regions where steppe elements dominate. Central European forest animals or those of the taiga are found chiefly in NW Spain where they are dominant and also in the Pyreneees, in the northern part of Yugoslavia at the Adriatic, in the central and chiefly in the southern part of France, in Belgium and surprisingly also in the northern part of the Pannonian lowland.

Th coldest regions at that time were the territory north of the Alps and the western coast of the Black Sea, mainly, however, the territory of Czechoslovakia (as far as regions with a major number of finds of that substage are concerned).

The studied regions can be climatically evaluated within that substage as follows:

very warm climate: 1, 3
warm climate: 2,12
cold climate: 6
mildly cold climate: 4, 9
very cold climate: 14
extremely cold climate: 10

The northern part of the Mediterranean Sea proves to have great moderating effects as far as temperature is concerned, on the whole coast (the same holds for the coast of Belgium). The coldest, evidently continental climate was that of the regions of central Europe proper and, as can be judged, also the whole of the Ukraine. The Pannonian lowland, protected from the north, was an exception in central Europe.

Animals of the central European forest are concentrated mostly to the southern parts, such as the Iberian Peninsula, central and southern France, northern Yugoslavia and certainly also the north of Italy, penetrating to the north mainly along the Atlantic coast. All those phenomena indicate a decrease in average annual temperature and cold continental climate with cold arctic steppes being formed in extensive areas of central and evidently also eastern Europe. Forest stands in those regions must have been very limited and only of the taiga type.

Steppe elements are therefore the most widespread. *Ochotona pusilla* penetrates from the east up to the Alps, the species *Alactaga jaculus* does not penetrate so far westwardes. Saigas, on the other hand, are found as far as in the Pyrenees. The dominant presence of horses in the south of France safely indicates the fact that also in that region which was climatically warmer extensive open steppe areas must have existed.

An interesting community is that of the region of Istria and northern Yugoslavia. On the one hand animals of the central European forest are abundant, but together with a veriety of steppe elements. They indicate a continued connection of that region with the east from where the steppe fauna comes and despite the warmer climate

finds favourable living conditions there. Similar is the situation at the coast of Belgium.

An extensive geographical distribution can be seen in the reindeer. It is a dominating animal not only in the region of the Danube delta, but also in southern and central France, but it is also found in NW Spain. The conditions of its existence were evidently ideal at that time all over Europe.

The meridian Adriatic — Czechoslovakia is essentially the western limit of the distribution of the wolverines, as well as the species *Lemmus lemmus* and *Dicrostonyx torquatus*. On the other hand, the mammoth and the woolly rhinoceros are spread up to the westernmost parts of Europe.

Greatly distributed is the species *Capra ibex* (dominant in southern France and northern Yugoslavia) and also the chamois. The latter can at that time be found all over western and central Europe (dominant in northern Yugoslavia).

This substage is thus characterized by a marked differentiation of the individual regions and by a great spread of cold steppes chiefly in the broad zone of central Europe. Expressively tundra elements mostly end at the meridian going between Istria and Czechoslovakia.

Substage $W_{2/3}$—W_3

This relatively long substage includes the climatical oscillation $W_{2/3}$ and particularly the first half of the Last Würm Stadial. The species pattern of the community of the individual regions is as follows:

Region 3: Most frequent are animals characteristic of the steppes, relatively abundant are, however, also elements of the central European forest and of the taiga. Main species of the community.

● *Sus scrofa, Vulpes vulpes.*
● ○ *Cervus elaphus, Canis lupus, Ursus arctos, BOS PRIMIGENIUS, Lynx lynx.*
▲ *Equus (A.) hydruntinus, Saiga tatarica, EQUUS* sp., *BISON PRISCUS.*
■ ▲ ○ *Rangifer tarandus.*
■ ▲ *Ovibos moschatus, M. primigenius, Alopex lagopus.*
▲ ○ *Megaloceros giganteus, Alces alces, Gulo gulo.*
■ *Dicrostonyx* sp., *Lemmus lemmus.*

Other species mentioned: *Rupicapra rupicapra, Ursus spelaeus, Crocuta spelaea, Capra ibex, Mustela* sp.

The pattern of the community indicates a relatively warm region.

Region 4: Animals of the central European forest and of the taiga are dominant elements. Relatively infrequent are animals of the tundra. The find of the species *Hystrix cristata,* if it comes from this time horizon at all, is an exception. Chief species of the community.

● *Hystrix cristata, Vulpes vulpes, Felis silvestris, Sus scrofa, Martes martes, Capreolus capreolus.*
● ○ *Castor fiber, Cervus elaphus, Canis lupus, Ursus arctos, Bos primigenius, Lynx, lynx.*
▲ *Ochotona pusilla, Saiga tatarica, Cricetus cricetus, Equus* sp., *Bison priscus, Alactaga jaculus, Equus (A) hydruntinus.*
■ ▲ ○ *Rangifer tarandus, Lepus timidus, Alopex lagopus, M. primigenius.*
▲ *MARMOTA MARMOTA, ALCES ALCES, Megaloceros giganteus.*
■ ○ *GULO GULO.*
■ *Dicrostonyx* sp.

Other species described: *Panthera spelaea, Cuon alpinus, Rupicapra rupicapra, URSUS SPELAEUS, Talpa europaea, Meles meles, Crocuta crocuta, Capra ibex, Mustela* sp., *Putorius putorius, Sorex* sp.

The community pattern indicates a relatively warm region.

Region 5: The prevailing element are steppe animals, but almost to the same extent also all other environments are represented. This is due to great differences of the plant cover of this region. Chief species of the community.

● *Felis silvestris, Capreolus capreolus.*
● ○ *Cervus elaphus, Canis lupus.*
▲ *Ochotona pusilla, Citellus citellus.*

■ ▲ ○ *Rangifer tarandus.*
▲ ○ *Marmota marmota, Megaloceros giganteus.*
■ ▲ *Lepus timidus, Alopex lagopus.*
Other species described: *Rupicapra rupicapra, URSUS SPELAEUS, Talpa europaea, Erinaceus* sp.
The community pattern indicates a mildly cold region.

Region 9: Steppe elements prevail, but relatively frequent are also animals typical of the tundra and of the central European forest. Main species of the community.
● *Sus scrofa, Vulpes vulpes.*
● ○ *Cervus elaphus, Canis lupus.*
▲ *Saiga tatarica, EQUUS* sp.
■ ▲ ○ *RANGIFER TARANDUS.*
■ ▲ *Lepus timidus, M. primigenius, C. antiquitatis.*
Other species mentioned: *Ursus spelaeus, Meles meles, Crocuta spelaea, Capra ibex, Mustela* sp.
The community pattern indicates a mildly cold region.

Region 10: Elements of the steppe, the tundra and the taiga prevail. Isolated elements of the central European forest are rather exceptional. Chief species of the community.
● *Panthera leo, Capreolus capreolus, Vulpes vulpes.*
● ○ *Castor fiber, CANIS LUPUS, Ursus arctos, Bos primigenius.*
▲ *Equus* sp., *Equus (A.) hydruntinus, Bison priscus.*
■ ▲ ○ *Rangifer tarandus.*
■ ▲ *Ovibos moschatus, LEPUS TIMIDUS, Alopex lagopus, M. primigenius, C. antiquitatis.*
■ *Dicrostonyx* sp., *Lemmus lemmus.*
▲ ○ *Marmota marmota, Alces alces, Megaloceros giganteus.*
■ ○ *Gulo gulo.*
Other species mentioned: *Panthera pardus, Panthera spelaea, Rupicapra rupicapra, URSUS SPELAEUS, Lepus europaeus, Meles meles, Erinaceus* sp., *Crocuta spelaea, Capra ibex.*
The community pattern indicates a very cold region.

Region 11: Animals of the individual zones are found in roughly the same amounts, none of them being dominant. Main species of the community.
● *Glis glis, Capreolus capreolus.*
● ○ *Cervus elaphus, Canis lupus, Bos primigenius.*
▲ *Cricetus cricetus, Equus* sp., *Bison priscus.*
■ ▲ ○ Rangifer tarandus.
■ ▲ *Lepus timidus, Alopex lagopus.*
■ *Lemmus lemmus, Dicrostonyx* sp.
Other species mentioned: *Rupicapra rupicapra, Ursus spelaeus, Erinaceus* sp., *Crocuta spelaea, Putorius putorius, Mustela* sp.
The community pattern indicates a mildly cold region.

Region 12: Animals of the central European forest and those of the steppe are roughly balanced as for their numbers. The other elements fall into the background. Chief species of the community.
● *Felis silvestris, Martes martes, Sus scrofa, Vulpes vulpes.*
● ○ *Cervus elaphus, Lynx lynx.*
▲ *Ochotona pusilla, Cricetus cricetus, Equus* sp., *Bison priscus.*
■ ▲ ○ *Rangifer tarandus.*
■ ▲ *LEPUS TIMIDUS, Alopex lagopus.*
■ *Dicrostonyx* sp.
Other species mentioned: *Rupicapra rupicapra, URSUS SPELAEUS, Erinaceus* sp., *Crocuta spelaea, Capra ibex, Mustela* sp., *Sorex* sp.
The community pattern indicates a relatively warm region.

Region 13: The number of finds mentioned is very small and indicates rather steppe conditions in this region. Principal species found.
▲ *Ochotona pusilla, Citellus citellus, Cricetus cricetus.*
■ ▲ *Lepus timidus.*

Other species described: *Ursus spelaeus, Talpa europaea, Sorex* sp.

Region 14: Steppe elements are quite dominant in this region, all the others are only weakly represented. Chief species found.

○ ● *Cervus elaphus.*
▲ *Saiga tatarica, Equus* sp., *Bison priscus.*
▲ ○ *Megaloceros giganteus.*
■ ▲ ○ *Rangifer tarandus.*
■ ▲ *Alopex lagopus.*

Other species mentioned: *Crocuta spelaea.*
The community pattern indicates a very cold region.

Region 15: The dominant element are clearly animals of the steppe, somewhat less numerous are those typical of the tundra and the taiga. Main species found.

● *Capreolus capreolus.*
● ○ *Cervus elaphus, CANIS LUPUS, Ursus arctos.*
▲ ○ *Marmota marmota, Alces alces, Megaloceros giganteus.*
▲ *Citellus citellus, EQUUS* sp., *Equus (A.) hydruntinus, Bison priscus.*
■ ▲ ○ *RANGIFER TARANDUS.*
■ ▲ *OVIBOS MOSCHATUS, Lepus timidus, ALOPEX LAGOPUS, M. PRIMIGENIUS, C. ANTIQUITATIS.*
■ ○ *Gulo gulo.*
■ *DICROSTONYX* SP.

The community pattern indicates an extremely cold region.

Region 16: Animals of the steppe prevail, relatively frequently also elements of the tundra and of the taiga are found. Main species discovered.

● *Capreolus capreolus.*
● ○ *Bos primigenius.*
▲ *Citellus citellus, EQUUS* sp., *Bison priscus.*
▲ ○ *Alces alces, Megaloceros giganteus.*
■ ▲ ○ *RANGIFER TARANDUS.*
■ ▲ *Ovibos moschatus, M. primigenius, C. antiquitatis.*

The community pattern indicates an extremely cold region.

Region 17: The dominant element are animals of the steppe. Others are strongly suppressed, the least numerous being animals of the tundra. Chief species found.

● *Sus scrofa.*
● ○ *Cervus elaphus.*
▲ *Saiga tatarica, Equus* sp., *Equus (A.) hydruntinus, Bison priscus.*
▲ ○ *Megaloceros giganteus.*
■ ▲ ○ *RANGIFER TARANDUS.*

The community pattern indicates relatively warm climate.

Region 18: Steppe elements prevail, comparatively frequent are also animals of the other environments. Main species found.

● *Capreolus capreolus.*
▲ ○ *Alces alces.*
● ○ *Bos primigenius.*
▲ *EQUUS* sp., *Bison priscus.*
■ ▲ *M. PRIMIGENIUS, C. antiquitatis.*

The species pattern indicates a cold region.

Region 19: Animals of the central European forest zone prevail, elements of the taiga being also represented. Steppe elements evidently come from the promontories. Chief species of the community.

● *Hystrix cristata, Martes martes, SUS SCROFA, Capreolus capreolus, Vulpes vulpes.*
● ○ *Castor fiber, Cervus elaphus, Canis lupus, Ursus arctos, BOS PRIMIGENIUS, Lynx lynx.*
▲ ○ *Alces alces.*
▲ *EQUUS* sp., *Bison priscus.*

■ ○ Gulo gulo.
Other species mentioned: *Panthera spelaea, Rupicapra rupicapra, URSUS SPELAEUS, Ovis* sp., *Lepus europaeus, Capra aegagrus, Mustela* sp.
The species pattern indicates very warm climate.

Region 20: Steppe elements prevail, frequently mentioned are also animals of the taiga and of the tundra and, after all, also those of the central European forest. Main species of the community.

● *Capreolus capreolus, Vulpes vulpes.*
● ○ *Castor fiber, Cervus elaphus, Canis lupus.*
▲ ○ *Marmota marmota, Alces alces, Megaloceros giganteus.*
▲ *Ochotona pusilla, Saiga tatarica, Citellus citellus, Equus* sp., *Bison priscus.*
■ ▲ *Lepus timidus, Alopex lagopus, M. primigenius, C. antiquitatis.*
■ ▲ ○ *Rangifer tarandus.*
■ *Gulo gulo.*

Other species mentioned: *Panthera spelaea, Ursus spelaeus.*
The community pattern indicates a mildlly cold region.

Region 21: The dominant factor are animals of the steppe and of the tundra. Despite this northern location not only taiga animals are found, but also those which are typical of the mild zone forest. Main species of the community.

● *Sciurus vulgaris, Capreolus capreolus, Vulpes vulpes.*
● ○ *Castor fiber, Canis lupus.*
▲ *SAIGA TATARICA, Equus* sp., *Bison priscus.*
▲ ○ *Alces alces.*
■ ▲ *Ovibos moschatus, LEPUS TIMIDUS, ALOPEX LAGOPUS, M. primigenius, C. antiquitatis.*
■ ▲ ○ *RANGIFER TARANDUS.*
■ ○ *Gulo gulo.*

Other species mentioned: *Panthera spelaea, URSUS SPELAEUS, Mustela* sp.
The community pattern indicates a mildly cold region.

The prevailing element of this substage is, besides the region of the Caucasus, the steppe. This, however, does not mean that other habitats should not be represented. It is known that in the prevailing steppe formation forests of the taiga character were locally found, as well as forests of the central European type and, in exposed sites, also tundras. The landscape was thus comparatively strongly differentiated, much more than it is today. This fact is reflected in communities rich in species. A certain exception to all regions is the territory of the Caucasus. The species *Hystrix cristata* found here at that time, requires markedly warm climate. It is also described from the territory of Istria (Yugoslavia), but in that case it seems to me that a wrong stratigraphic classification cannot be excluded.

Climatically, the regions studied at that substage can be evaluated as follows:

very warm climate: 19
warm climate: 3, 4, 12, 17
cold climate: 13, 18
mildly cold climate: 5, 9, 11, 20, 21
very cold climate: 10, 14
extremely cold climate: 15, 18

From the outline it follows that the warmest territory at that substage is the region of the Caucasus. Relatively warm climate can be noted in southern and central France, in the region of the Pannonian lowland, on the Crimea and along the coast of the Adriatic Sea, in northern Yugoslavia and Italy. All the other regions exhibit different degrees of cold communities. Mildly cold climate is found in the following regions: Belgium, the central and the southern parts of Poland, the southern part of the Southern Urals, the northern stretch of the Pechora River (the Northern Urals), the slopes of the Alps. Perhaps the most interesting part of this finding is the position of Poland and those of the Southern, but mainly the Northern Urals.

Very cold climate is indicated in the following regions: Czechoslovakia, the environs of the Danube delta. Extremely cold climate is in the region around the Dniester River (USSR) and in the region south of the City of Kiev (USSR). The influence of the north-

wards trending open landscape was here evidently greater than that of the Black Sea.

It is therefore possible to state that the mildering effects of the sea can be observed only in regions about the northern coast of the Mediterranean and partly also on the coast of Belgium. The coldest climate appears in a broad zone of steppes of the Ukraine up to the coast of the Black Sea. Exceptional is the region of the Crimea which is protected from winds from the north and the region of the Caucasus which at that time is the warmest of the regions studied. Quite surprising is the climatic position of the Urals, even in their northernmost parts.

It has been mentioned that steppe elements were greatly spread at that time, but that in all regions also places were found containing other habitats as well. This means that from the point of view of the presence or absence of the individual species in the given region it is impossible to draw detailed biostratigraphical conclusions, that the community patterns can change from place to place, sometimes essentially. For biostratigraphic purposes it is then essential to elaborate local stratigraphic diagrams.

From what has been said it follows that the individual species are distributed almost everywhere, though in different amounts. A great geographical distribution can be observed in all characteristically steppe species, such as *Equus* sp., *Bison priscus,* and others, almost everywhere also species typical of the taiga or of the central European forest are found: *Alces alces, Ursus arctos, Megaloceros giganteus, Cervus elaphus, Bos primigenius, Capreolus capreolus.* Most of the species penetrate from eastern Europe far to the west into southern and central France (*Saiga tatarica, Rangifer tarandus, M. primigenius*) or only to the region of the Alps and in the north to Belgium (*Alopex lagopus, Alactaga jaculus, Marmota marmota, Ochotona pusilla, C. antiquitatis, Dicrostonyx* sp., *Lemmus lemmus*). It is, however, possible that the area of many of them was found still more to the west.

In some species a concentration to the southern parts of Europe can be observed, as well as to the Crimea, to the Caucasus; they do not occur further in the north: *Felis silvestris, Lynx lynx, Sus scrofa* (an exceptional find in the region of Belgium) and *Equus (A.) hydruntinus* (an exceptional find in Bohemia — ČSSR). The whole of central Europe at that time is populated by *Rupicapra rupicapra* and a number of further species.

A number of species have a dominant position in the broad plains of the European part of the USSR. The prevalence of individual species in the communities of the regions studied:

Equus sp.	The Ukraine, southern and central France, Belgium
Rangifer tarandus	the Ukraine, the Northern Urals, Belgium
Ovibos moschatus	the Ukraine
Alopex lagopus	the Ukraine, the region about the Dniester
M. primigenius	the Ukraine
Dicrostonyx sp.	the Ukraine, central Poland
Bison priscus	the Ukraine, southern and central France
Saiga tatarica	the Northern Urals
Bos primigenius	southern and central France, the Caucasus
Sus scrofa	the Caucasus

It follows that cold adapted and steppe animals were spread towards the west in two zones. One reached as far as southern and central France, the other was roughly limited by the meridian the Alps — Belgium. Climatically only the northern coastland of the Mediterranean Sea, the Crimea and the Caucasus were an exception to the other parts (warmer regions) as well as the whole of the Ukraine (the colder region).

The latter half of W_3

Regions with stratigraphically classified fauna into this substage are relatively scanty. It is only the northern part of the Iberian Peninsula, the southern and central parts of the FRG, Czechoslovakia, the Pannonian lowland and the region NW of the Black Sea (around the Dniester River). It is probable that the species of this age will mostly vary between $W_{2/3}$ and W_3, or even to Late Glacial.

Species covering all the above regions are *Equus* sp., *Vulpes vulpes, Canis lupus, Rangifer tarandus.* Relatively widely spread is also the species *Cervus elaphus* (the northern part of the Iberian Peninsula — dominant, the southern and central parts

of the FRG, Czechoslovakia, the Pannonian lowland). From Pannonia are also registered *Alces alces, C. antiquitatis* and *M. primigenius.*

Owing to scanty material it is impossible to draw deep conclusions, the absence of a species can be due to a variety of secondary causes.

The late part of Stadial W_3

The time in question is the very end of the Last Glacial. The possibility cannot, however, be eliminated that in some cases the sediments in question may come from the whole latter half of W_3. Despite the above drawbacks it can be assumed that most of the species described belong to the very end of the Last Würm Stadial.

Let us now approach the community patterns of the individual regions.

Region 1: Dominant elements are animals of the central European forest, relatively strongly are also represented elements of the taiga and of the steppe. Elements of the tundra are situated quite in the background. Chief community species.

● *Sus scrofa, Vulpes vulpes, Capreolus capreolus, Felis silvestris, Panthera leo, Oryctolagus cuniculus.*

○ *Lynx lynx, Ursus arctos, BOS PRIMIGENIUS, Canis lupus, Cervus elaphus.*

▲ *BISON PRISCUS, EQUUS* sp.

■ ▲ ○ *Rangifer tarandus, Alopex lagopus.*

■ ▲ *Lepus timidus.*

Other species mentioned: *RUPICAPRA RUPICAPRA, Ursus spelaeus, Sorex araneus, Putorius putorius, Mustela nivalis, Lepus europaeus, TALPA EUROPAEA, Meles meles.*

The community pattern and the quantitative representation of individual species indicates a warm region.

Region 2: Dominant elements are animals of the central European forest, but elements of the steppe, the taiga and the tundra are also strongly represented. Main species of the community.

● *Sus scrofa, VULPES VULPES, Capreolus capreolus, Panthera leo.*

● ○ *Lynx lynx, Ursus arctos, CERVUS ELAPHUS, Canis lupus.*

▲ *Ochotona pusilla, EQUUS* sp., *Saiga tatarica.*

■ ▲ ○ *RANGIFER TARANDUS.*

■ ▲ *C. antiquitatis, Lepus timidus, Alopex lagopus.*

■ ○ *Gulo gulo.*

Other species described: *Ursus spelaeus, Crocuta crocuta, RUPICAPRA PYRENAICA, Capra pyrenaica, Putorius putorius.*

The community pattern and the quantitative representation of the individual species indicate a warm region.

Region 3: Dominant elements or animals of the central European forest and of the steppe, strongly represented being also elements of the tundra and of the taiga. Main species of the community

● *SUS SCROFA, MARTES MARTES, Vulpes vulpes, Capreolus capreolus, Oryctolagus cuniculus.*

● ○ *Lynx lynx, Ursus arctos, BOS PRIMIGENIUS, CANIS LUPUS, CERVUS ELAPHUS.*

▲ *BISON PRISCUS, EQUUS* sp., *Equus (A.) hemionus, SAIGA TATARICA.*

■ ▲ ○ *RANGIFER TARANDUS.*

■ ▲ *C. antiquitatis, Lepus timidus, Alopex lagopus, M. primigenius, Ovibos moschatus.*

▲ ○ *Alces alces, Marmota marmota, Megaloceros giganteus.*

■ ○ *Gulo gulo.*

Other species mentioned: *Cuon alpinus, Panthera pardus, Panthera spelaea, Ursus spelaeus, Crocuta spelaea, Rupicapra pyrenaica, Ovis* sp., *Capra pyrenaica, Putorius putorius.*

The community pattern and the quantitative representation of the individual species indicate a warm region, alternating areas of forests and steppes.

Region 4: Dominant elements are animals of the central European forest, with elements of the steppe, the taiga and the tundra occurring abundantly. Chief species of the community.

● *Sus scrofa, Lutra lutra, Capreolus capreolus, Vulpes vulpes, Felis silvestris.*
● ○ *Ursus arctos, Castor fiber, Cervus elaphus, Bos primigenius, Canis lupus.*
▲ *Bison priscus, Equus* sp., *EQUUS (A.) HYDRUNTINUS, Cricetus cricetus.*
■ ▲ ○ *Rangifer tarandus.*
■ ▲ *C. antiquitatis, Lepus timidus.*
▲ ○ *Alces alces, Megaloceros giganteus, Alopex lagopus, Marmota marmota.*
■ ○ *Gulo gulo.*

Other species described: *Panthera pardus, Panthera spelaea, Ursus spelaeus, Crocuta spelaea, Rupicapra rupicapra, Lepus europaeus, Meles meles, CAPRA IBEX, Sorex araneus.*

The community pattern and the quantitative representation of the individual species indicate a warm region.

Region 5: In about the same ratio elements of the tundra, the steppe, the taiga and also of the central European forest are represented in the region. Main species of the community.

● *Vulpes vulpes, Capreolus capreolus, Martes martes, Sus scrofa, Lutra lutra, Panthera leo, Felis silvestris, Glis glis.*
● ○ *Lynx lynx, Ursus arctos, Bos primigenius, Cervus elaphus, Castor fiber, Canis lupus.*
■ ▲ ○ *Rangifer tarandus.*
▲ *Bison priscus, Equus* sp., *Equus (A.) hydruntinus, Citellus citellus.*
■ ○ *Gulo gulo.*
▲ ○ *Marmota marmota.*
■ ▲ *C. antiquitatis, Lepus timidus, Alopex lagopus, M. primigenius, Ovibos moschatus*
■ *Dicrostonyx* sp., *Lemmus lemmus.*

Other species described: *Panthera spelaea, Ursus spelaeus, Rupicapra rupicapra, Talpa europaea, Capra ibex, Putorius putorius.*

The community pattern and the quantitative representation indicate rather cold climate.

Region 6: Animals of the central European forest are strongly suppressed, elements of the steppe and of the taiga prevail. Chief species of the community.

● *Dama dama, Vulpes vulpes.*
● ○ *Cervus elaphus, Ursus arctos, Castor fiber.*
■ ▲ ○ *RANGIFER TARANDUS.*
▲ *EQUUS* sp., *Bison priscus, Cricetus cricetus, Spermophilus* sp.
■ ▲ *ALOPEX LAGOPUS, LEPUS TIMIDUS, C. antiquitatis, M. primigenius, Ovibos moschatus.*
▲ ○ *Alces alces.*
■ ○ *Gulo gulo.*

Other species mentioned: *Ursus spelaeus, Crocuta spelaea, Rupicapra rupicapra, Talpa europaea, Capra ibex, Sorex araneus.*

The community pattern and the quantitative representation of the individual species indicate cold region. The species *Dama dama* occurring in two localities will most probably belong to the Holocene and may have been included into the list by mistake.

Region 7: Elements of the tundra and of the steppe prevail strongly. Animals of the central European forest as well as those of the taiga occur in small numbers. Main species of the community.

● *Capreolus capreolus, Vulpes vulpes, Felis silvestris.*
● ○ *Cervus elaphus, Ursus arctos, Lynx lynx, Canis lupus.*
■ ▲ ○ *RANGIFER TARANDUS.*
▲ *Saiga tatarica, EQUUS* sp., *Spermophilus* sp., *Citellus citellus.*
■ ▲ *C. antiquitatis, M. primigenius, ALOPEX LAGOPUS, LEPUS TIMIDUS, Gulo gulo.*
■ *Dicrostonyx* sp., *Lemmus lemmus.*
■ ▲ *Ovibos moschatus.*
▲ ○ *Megaloceros giganteus, Marmota marmota.*

Other species mentioned: *Ursus spelaeus, Crocuta spelaea, Rupicapra rupicapra, Putorius putorius, Capra ibex.*

The community pattern and the quantitative representation indicate a climatically cold region with rather continental climate.

Region 8: Steppe elements dominate; in about the same ratio animals of the central European forest, the tundra and the taiga are found. Main species of the community.

Vulpes vulpes, Sus scrofa, Felis silvestris.
Castor fiber, Bos primigenius, Lynx lynx, Canis lupus.
RANGIFER TARANDUS.
Saiga tatarica, EQUUS sp., *Bison priscus.*
M. primigenius, Gulo gulo, Lepus timidus, C. antiquitatis.
Dicrostonyx sp., *Lemmus lemmus.*
Alces alces, Megaloceros giganteus.

The community pattern and the quantitative representation of the individual species indicate a steppe, mildly cold region (the proximity of the sea evidently resulted in a partial warming of the climate as compared with the central parts of central Europe).

Region 10: Steppe elements prevail, other climatic zones are roughly balanced as for the amounts of animals. Chief species of the community.

Vulpes vulpes, Martes martes, Panthera leo.
Bos primigenius, Cervus elaphus, Ursus arctos, Lynx lynx, Castor fiber, Canis lupus.
RANGIFER TARANDUS.
Saiga tatarica, EQUUS sp., *Cricetus cricetus, OCHOTONA PUSILLA, Citellus citellus.*
C. antiquitatis, M. primigenius, LEPUS TIMIDUS, Gulo gulo, Alopex lagopus.
LEMMUS LEMMUS, Dicrostonyx torquatus.
Alces alces.

Other species mentioned: *Ursus spelaeus, Crocuta spelaea, Rupicapra rupicapra, Talpa europaea, Mustela nivalis, Sorex araneus.*

The community pattern and the quantitative representation of the individual species indicate a cold region, a loess and an arctic steppes.

Region 11: Steppe and tundra elements prevail, animals of the other climatic zones are represented to a smaller extent. Main species of the community.

Capreolus capreolus, Vulpes vulpes, Martes martes, Glis glis.
Bos primigenius, Ursus arctos, Canis lupus.
Rangifer tarandus.
Saiga tatarica, Equus sp., *Bison priscus, Ochotona pusilla, Cricetus cricetus.*
C. antiquitatis, Alopex lagopus, Lepus timidus.
Dicrostonyx sp., *Lemmus lemmus.*
Alces alces.

Other species mentioned: *Ursus spelaeus, Crocuta spelaea, Talpa europaea, Sorex araneus.*

The community pattern and the quantitative representation of the individual species indicate a cold region, a loess steppe and an arctic steppe.

Region 12: Tundra elements are highly dominant, animals of the tundra and of the steppe being also represented. Animals of the central European forest zone are missing. Main species of the community.

Rangifer tarandus.
OCHOTONA PUSILLA.
DICROSTONYX sp., *Lemmus lemmus.*
Gulo gulo.
Alopex lagopus.

Other species mentioned: *TALPA EUROPAEA, Ursus spelaeus.*

The community pattern and the quantitative representation of the individual species indicate an extremely cold region of the steppe character, with possible isolated forests of the taiga type.

Region 14: Animals of the central European forest are quite suppressed, elements of the arctic steppe and the tundra dominate. Main species of the community.

■ ▲ ○ *RANGIFER TARANDUS.*
▲ *Bison priscus, Saiga tatarica.*
■ ▲ *ALOPEX LAGOPUS.*
Other species mentioned: *Ursus spelaeus, Crocuta spelaea, Ovis* sp.

The community pattern and the quantitative representation of the individual species indicate an extremely cold region of the steppe character.

Region 17: Steppe elements dominate, animals of the other climatic zones occurring in lower numbers. Chief species of the community.
● *Vulpes vulpes.*
● ○ *Cervus elaphus, Lynx lynx, Bos primigenius, Canis lupus.*
■ ▲ ○ *Rangifer tarandus.*
▲ *Cricetus cricetus, OCHOTONA PUSILLA, Bison priscus, Equus* sp., *Equus (A.) hydruntinus, SAIGA TATARICA, Alactaga jaculus.*
■ ▲ *C. antiquitatis, Alopex lagopus.*
▲ ○ *Marmota marmota.*
Other species mentioned: Capra ibex, *RUPICAPRA RUPICAPRA, Crocuta spelaea, Ursus spelaeus, Panthera spelaea.*

The community pattern and the quantitative representation of the individual species point to a relatively warm region of the steppe character.

Region 19: Dominant are animals of the central European forest zone, but also steppe and taiga elements are represented. Tundra elements occur in negligible numbers. Main species of the community.
● *SUS SCROFA, Martes martes, Lutra lutra, Capreolus capreolus, Vulpes vulpes, Felis silvestris, Sciurus vulgaris.*
● ○ *Castor fiber, Cervus elaphus, Lynx lynx, Ursus arctos, BOS PRIMIGENIUS, Canis lupus.*
▲ *Cricetus cricetus, BISON PRISCUS, EQUUS* sp., *Equus (A.) hydruntinus, Alactaga jaculus.*
■ ○ *Gulo gulo.*
■ ▲ *Lepus timidus.*
■ ○ *Alces alces.*
Other species mentioned: *Panthera pardus, Panthera spelaea, URSUS SPELAEUS, Rupicapra rupicapra, Ovis* sp., *Erinaceus* sp., *Talpa europaea, CAPRA IBEX.*

The community pattern and the quantitative representation of the individual species indicate a very warm region, for the most part covered with forests.

Region 20: Both steppe elements and those of the forest are found in the region. Chief species of the community.
● *Capreolus capreolus.*
● ○ *Cervus elaphus.*
■ *Bison priscus, Equus* sp.
■ ▲ *M. primigenius, C. antiquitatis.*
The community pattern and the quantitative representation of the individual species indicate a region not too cold, with interchanging areas of steppes and forests.

The above outline shows that the habitats in Europe were not uniform throught this Late Würm substage on a major area, although the prevailing animals were mostly those of the steppe. There were local developments in relatively small areas of one major region. This means that only on small surfaces it is possible to distinguish the onsets and peterings out of the individual communities; utilizing them for the stratigraphic comparison will thus be very difficult. It also means that it will be necessary to build up local stratigraphic scales.

The communities are essentially richer in the number of species than at any time during the Holocene. Species requiring explicitly warm climate are missing. Climatically the regions studied can be evaluated as follows:

very warm climate: regions 1, 19
warm climate: regions 2, 3, 4, 17
cold climate: regions 5, 7, 10, 11
mildly cold climate: regions 8, 20

very cold climate: region 6
extremely cold climate: regions 12, 14

From the above outline there follows an interesting and unexpected conclusion. The warmest region at that time was the territory of the Caucasus and the NW part of Spain, the coldest was the zone stretching from south Germany across the Pannonian lowland to the Black Sea. The climate north of this zone was milder, south of it essentially warmer. Of interest is the anomaly in the northern part of Europe (FRG, Denmark, Belgium), where the climate becomes warmer, probably due to the effect of the sea.

The communities of that time thus exhibit a strong climatic differentiation from the point of view of the whole of Europe together with a deep local differentiation in the individual regions.

What does the distribution of at least the main species in Europe look like? Considerations of this kind can be divided into two parts, i.e. the distribution proved and the distribution assumed. On the basis of the analysis of the community it is necessary to realize that the data obtained concern every large region as a whole, but can differ essentially in the individual small areas of that region. The objective then remains to elaborate the development of the distribution of the individual species in minor partial independent geographic units, which, unfortunately, is not yet available.

The analysis of the distribution of the individual species yields several main variants independent of each other. A number of species has at that time an unexpectedly large geographical distribution; this distribution has a permanently dynamical character and continues also into the following Holocene. The difference among the indivvidual regions consists only in the number of individuals.

Another group is constituted by species of a similarly large geographical distribution, of which we, however, know that due to a relatively quick change in climatic conditions and thus also in the plant cover they disappear quickly from some or all regions very rapidly.

The last group is constituted by species which take up a limited area for the reason that the conditions of the environment were for them parmenantly disadvantageous, so that their major distribution is ruled out or due to the fact that the disadvantage of the life conditions results in the existence of the species only in regions still suitable for their life, essentially in the formation of endemitic local populations.

Examples of the first variant are the species: *Capreolus capreolus, Ursus arctos, Felis silvestris, Alces alces, Lynx lynx, Bos primigenius, Vulpes vulpes, Cervus elaphus, Bison priscus.*

The second variant, not sharply distinquished from the first one, includes the following species: *Gulo gulo, Lepus timidus, Equus* sp., *Rangifer tarandus, Alopex lagopus, Ursus spelaeus, Capra ibex, Crocuta spelaea, C. antiquitatis, M. primigenius.*

All those species enumerated are almost always found in the following regions: the northern part of the Iberian Peninsula, in the Pyrenees, south and central France, slopes of the Alps, northern Italy, northern Yugoslavia, central Europe, the northern part of the FRG, the Crimea, the Caucasus, the South Urals. They indicate quite clearly the presence of forest areas, both of the taiga type or the forest of the mild zone of central Europe, interchanging with areas of steppes. It is a landscape which, from the ecological point of view, was higly suitable for a great number of species and therefore the given communities are very rich in species. Purely steppe landscapes on major areas had only a subordinate position. The same holds for those which were completely covered with continuous forests.

Dominant positions, as for the amount of individuals, can be seen in the species:

Bos primigenius (the northern part of the Iberian Peninsula, southern and central France, the Caucasus)

Cervus elaphus (the northern part of the Iberian Peninsula, the Pyrenees)

Rangifer tarandus (the Pyrenees, southern and central France, the western coast of the Black Sea)

Bison priscus (the northern part of the Iberian Peninsula, southern France, the Caucasus)

Lepus timidus (central Europe)

Equus sp. (the northern part of the Iberian Peninsula, the Pyrenees, central France, central Europe, promontories of the Caucasus)

Alopex lagopus (central Europe, the western coast of the Black Sea)

Capra ibex (the northern part of the Iberian Peninsula, the Caucasus)

An example of the third variant is the species *Oryctolagus cuniculus*. At that it is limited only to the Iberian Peninsula and to the southern part of France. The same situation can be seen in the species *Equus (A.) hydruntinus,* occupying at that time only the southern parts of the regions studied (southern France, Italy; dominant in northern Yugoslavia, the Crimea and the promontories of the Caucasus. The same holds for the species *Sus scrofa* (dominant in southern and central France) which appears quite isolated also in the space of the northern part of the FRG.

The second part of the third variant continues more or less without any transition in the second one, but preceding it in time. Relatively large areas are occupid by *Rupicapra rupicapra,* but its split into several independent region can be seen:

a) the northern part of the Iberian Peninsula (dominant), the Pyrenees (dominant), the southwestern part of France.

b) the Alps and their slopes, central Europe (essentially the most extensive region).

c) the Crimea (dominant).

d) the Caucasus.

The species *Ovibos moschatus* is limited mainly to the Alps and their slopes. Thus an isolated local population is formed which, in a very short time, disappears from the region.

Of interest is a relatively broad distribution of the saiga. Split local populations are found in a number of regions, the species being quantitatively evidently still very frequent.

a) the Pyrenees, southern (dominant) and central France.

b) NE France, the coastland of the FRG, Denmark, England. The connection of the two latter regions cannot be excluded.

c) central Europe.

d) the western coast of the Black Sea, the Crimea (dominant).

Interesting is also the distribution of explicitly cold steppe elements, such as the genera *Dicrostonyx* and *Lemmus*. Their western limit is the mountain range of the Alps extended to the north to the mouth of the Elbe River, and then the whole of central Europe and the Pannonian lowland. A different situation can be observed in the steppe species *Ochotona pusilla*. Three separated regions can be seen. They are:

a) the region of the Pyrenees

b) central Europe, the northern slopes of the Alps (dominant), the Pannonian lowland (dominant, the most extensive area).

c) the Crimea (dominant).

The above outline of communities and of individual species indicates a high species diversity almost all over Europe, much larger than at any time during the Holocene. Despite the cold climate predominanting at that time continuous forests, with the exception of some regions, did not disappear altogether. On the contrary, alternating areas of steppes and forests, though of the most varied types, were characteristic of that time, creating ideal conditions for the existence of a number of big mammals which, with the onset of the Holocene and the formation of a monotonous plant cover on vast areas, cease to exist there. If we add also species which die out for good, the community of the Holocene appears to be very limited in comparison with the preceding glacial, both in the individual regions and in Europe as a whole.

ANALYSIS OF THE SPECIES

Communities of mammals found at the time studied are relatively quite varied as for species. This also holds even if one takes into consideration only big mammals. In this analysis I shall only mention the most frequently occurring and the most important species from the point of view their distribution in the course of the Last Glacial.

Order: *Lagomorpha*

Lepus timidus Linné, 1758

Characteristics: lives in forest areas both in plains and in the mountains, but also in small forest patches and in forest-steppes.

Distribution: throughout the Last Glacial it occupies the whole area studied. In central Europe dominating towards the end of the Glacial. Evidently always quite

a common animal which had no difficulties with climatic variations and subsequent changes in plants. It is probable that the determined finds of hares will belong to several species.

Oryctolagus cuniculus (Linné, 1758)

Characteristics: living on margins of forests, preferring warm climate.

Distribution: during the Last Glacial occupying always the same regions, i.e. northern Spain and southern France. Those regions are evidently the northern limit of ist continuous more southern distribution. From there it is mentioned in Early Würm as a dominating animal, further described from substage W_1 (in southern France as dominating), then always up to the end of the Glacial. Never extended from the region described.

Ochotona pusilla Pallas, 1768

Characteristics: looking for the environment of steppes or border zones. Typical steppe and forest-steppe animal.

Distribution: from its original area in eastern Europe it penetrates with the changes in the plant cover far west as far as the Pyrenees which, as it seems, it never crosses. The same goes for the north of Italy. In the course of W_1 it inhabits southern France and in central Europe its southern limit of penetration is the Pannonian lowland. From that region only at the end of the Glacial it penetrates still further to the south, to northern Yugoslavia, to Istria. Its extensive distribution throughout the Glacial indicates a great extension of steppes to which this animal was fully bound, and at the same time its full adaptation to different temperatures.

Order: *Rodentia*

Sciurus vulgaris Linné, 1758

Characteristics: living in forests, both continuous and in small forest patches, but also found in the forest-steppe and in the forest-tundra.

Distribution: its finds were always isolated, which, however, is not connected with its distribution and amount, but rather with its way of life under conditions little suitable for fossilization. In Early Glacial it is described from the Alps and from the Pannonian lowland, in W_1 from the Alps and northern Yugoslavia, in $W_{1/2}$ from northern Yugoslavia, from the very end of W_3 from the Caucasus. All finds originate rather from regions with warmer climate and end with Interstadial $W_{1/2}$; after it there is a total cooling of the climate over a large part of Europe.

Towards the end of Würm its find is described from the upper stretch of the Pechora River (the Northern Urals).

Citellus citellus (Linné, 1758)

Characteristic: typical animal of the forest-steppe. Possibly this determinantion covers several species.

Distribution: isolated finds are described from the beginning of the Last Glacial. Their number increases rapidly starting with Interstadial $W_{1/2}$, this increase, however, not at all reflecting its earlier occurrence and being probably due to other reasons. No conclusions can be drawn from it.

Marmota marmota (Linné, 1758)
Marmota bobak (Müller, 1776)

Characteristics: open steppes and forest-steppe regions, mountain meadows.

Distribution: the above species occur all over the territory investigated, throughout the Last Glacial. The then climatic variations had not the slightes effect on their distribution.

Castor fiber Linné, 1758

Characteristics: presence of water streams in a forest or a forest-steppe region necessary. Well adapted also for life on freezing water surfaces.

Distribution: from the beginning of the Last Glacial up to its end all over the territory. A small number of finds does not allow drawing detailed conclusions, but anyway, the end of the Glacial means an increase in its number as against the preceding substages.

Glis glis (Linné, 1766)

Characteristics: seeking above all deciduous forests, also of park character.

Distribution: in W_1 the whole of southern Europe, the northernmost finds from southern Germany, east of the Alps its presence hat not been noticed. In $W_{1/2}$ only northern Yugoslavia, in substages $W_{2/3}$—W_3 and at the very end of W_3 a surprizing

find from central Poland. Its finds are generally too exceptional to allow major conclusions. Its presence towards the end of the Glacial high in the north nevertheless provokes ideas as far as the plant cover present is concerned.

Hystrix cristata Linné, 1758

Characteristics: a steppe species requiring explicitly warm to Maditerranean climate.

Distribution: in Early Würm a find is described from the Pannonian lowland. It indicates warm climate there, but of continental character, so that only steppes were developed there. That is why species requiring warm but oceanic climate and corresponding plants did not penetrate there. On the other hand, mammoths and woolly rhinoceroses did not mind those conditions.

A long hiatus exists after that time. It is, however, not excluded that it means rather lack in fossil records than its complete disappearance from the southern regions. In the substages $W_{2/3}$—W_3 two finds of the species have been recorded, in the region of northern Yugoslavia and in the Caucasus.

Cricetus cricetus (Linné, 1758)

Characteristics: its original region is located in the eastern part of Europe, from where it extended westwards. Its existence depends also on the type of soil, it prefers solid and dry soils. Typical inhabitant of steppes and forest-steppes. Found, however, also in the forest zone in dry meadows.

Distribution: in Early Würm and in W_1 it is mentioned from almost the whole of Europe, westernmost roughly from the region of the Alps and the Rhine, southernmost, however, in northern Yugoslavia. This distribution remains unchanged throughout the Last Glacial.

Lemmus lemmus (Linné, 1758)

Characteristics: a typical inhabitant of the tundra zone, both in the plains and in the mountains.

Distribution: already in W_1 it is found all over the area of central Europe, as far as roughly to the Rhine River. In Early Pleistocene it is recorded in Poland. This region does not change throughout the Glacial, only towards the end of Würm it penetrates farther to the south, to the Pannonian lowland (the southernmost region of its distribution in central Europe) and intensely populates the Alps.

In the broad space of central Europe it is recorded from all climatic variations, though in different numbers and in different habitats.

Dicrostonyx torquatus (Pallas, 1779)

Characteristics: an inhabitant the tundra and the forest-tundra.

Distribution: the distribution of this species essentially overlaps that of the preceding species — *Lemmus lemmus*. Throughout the Glacial it inhabits the extensive areas of central and eastern Europe, in the west it penetrates up to the Rhine River and to the Alps, in the south to northern Yugoslavia. It becomes a dominant element towards the end of the Last Glacial.

Alactaga jaculus Pallas, 1778

Characteristics: an open landscape of the steppe character, but also penetrates to forest-steppes and the desert. In the mountains up to 1500 m.

Distribution: in W_1 only one find from southern Germany, in W_2 from Moravia (CSSR). From the substage $W_{2/3}$—W_3 a find is surprizingly reported from northern Yugoslavia and from a number of places in the European part of the USSR. Towards the end of Würm only Russian finding places.

A low number of finds has evidently a number of reasons. In any case it is a species which in the course of the Last Glacial inhabited the whole of central Europe up to the Rhine and in the south it penetrated to northern Yugoslavia. However, it seems to have disappeared from those regions before the end of Würm, being then limited to only the European part of the USSR.

Order: *Carnivora*

Felis silvestris Schreber, 1777

Characteristics: seeks forest regions, being found both in desiduous and in mixed forests, relatively rare in coniferous monocultures. Not adapted to high snow and strong frosts.

Distribution: isolated finds, rather due to difficulties in preservation. All over

the south of Europe, in Early Würm to the north up to the Alps and the Pannonian lowland, in W_1 registered in south Germany. In $W_{1/2}$ already in Moravia (CSSR). No find from central Europe from the substage W_2. A quick change in climate in this part of Europe made it retreat to the south. But already from $W_{2/3}$—W_3 isolated finds are described both from Austria and from the Pannonian lowland, at the very end of the Glacial from the whole of central Europe up to Jutland. It is interesting to note that its finds from the highest number of localities were recorded from the last substage.

Panthera pardus (Linné, 1758)

Characteristics: forest regions, partly forest-steppes, optimum deciduous forests. In the mountains (in the Caucasus up to the height of 3500 m) also in subalpine meadows. Requires a thin snow blanket in the winter.

Distribution: finds of this species are registered all over Europe. In Early Würm from the southern part of Europe to the north as far as Poland, in W_1 from the south up to the region of the Alps, in $W_{1/2}$ up to the region of the CSSR. The substage W_2—W_3 means evidently some withdrawal to the south, an isolated find from that substage comes only from the territory of Moravia (CSSR). This is another proof that the change in climate at the beginning of the Stadial W_2 on the territory of central Europe must have been quick and intense, so that it resulted in rapid changes in the fauna.

Panthera leo (Linné, 1758)

Characteristics: a species adapted to a very broad spectrum of different environments, mostly, however, to forests, meadows and water.

Distribution: this species is described relatively late from the Last Glacial. The first finds come from $W_{1/2}$ from the region of southern France. Evidently it also existed in northern Spain, as documented by finds dated as W_2. Only towards the end of the Last Glacial ($W_{2/3}$—W_3) is it also found on the territory of Moravia (CSSR). In all these cases they were more or less isolated finds. Only towards the end of W_3 it suddenly becomes very numerous and its localities are scattered all over western and central Europe, only, however, up to 50° northern latitude; in eastern Europe it is missing. Its distribution and different quantitative development is probably connected with the development of the environment.

Panthera spelaea (Goldfuss, 1810)

Characteristics: inhabiting mostly cold forest-steppes, penetrated also high into the mountains. A very broad area inhabited, reaching from western Europe up to eastern Asia, possibly also in North America.

Distribution: found in the region studied throughout the Last Glacial. It is possible to state that as for the number of localities, the optimum substage it is $W_{1/2}$ at the beginning of W_2 its number is reduced, which reduction continues up to the end of the Glacial. It seems to occurat that time chiefly in the southern regions with warmer climate (at the end of W_3 only south of the Alps, in the Crimea and in the Caucasus).

Lynx lynx (Linné, 1758)

Characteristics: looking above all for extensive continuous forests, in coniferous forests found up to the northern limit of their distribution. Very rarely occurring also in the forest-tundra. In the mountains occurring in the rocky zone not covered with the forest, also adapted to move about thick snow cover. Known for major migrations.

Distribution: in Early Würm it is recorded from the whole of western Europe up to southern Germany and northern Yugoslavia (including these regions), further from the Caucasus. In W_1 its area is extended still more, up to central Poland. In the substages $W_{1/2}$ and W_2 the number of its localities is reduced, difficult to say whether it is in full accord with its then distribution. Again in Late Würm 3 its finds become very frequent, at least in central Europe, reaching far to the north up to Jutland.

Crocuta spelaea (Goldfuss, 1823)

Characteristics: an animal with a typical broad range of toleration, occurring therefore in different types of climate and environment.

Distribution: throughout the Last Glacial it takes up tho whole region studied in ample numbers. Only at the beginning of $W_{2/3}$ the number of its localities becomes reduced together with its number which remains unchanged up to the end of W_3.

Canis lupus Linné, 1758

Characteristics: the animal exhibits a broad range of toleration together with a great geographical variability. It is found in all types of landscape. In the tundra it seeks mostly river valleys, in the forest tundra it stays in birch stands, in the taiga chiefly in regions of forests interchanging with open areas. It avoids continuous forest. It occurs further in steppes and even in semideserts and deserts. In the mountains it is found up to the height of 4000 m. In Transcaucasia it lives even in warm subtropics.

Distribution: the above great adaptability indicates in advance that it will occur throughout the region studied in the course of the whole Last Glacial. The number of its localities remains the same all through the stage.

Canis aureus Linné, 1758

Characteristics: open steppe areas both in lowlands and in the mountains. Missing completely in the arctic tundra. As far as found in the forest zone, then above all in open habitats. Warm climate preferred.

Distribution: only isolated finds from the beginning of the Last Glacial. From Early Würm described from the Danube delta and from the Caucasus. Deteriorated climate in the subsequent part of Glacial results in its disappearance.

Cuon alpinus Pallas, 1811

Characteristics: inhabitant of mountain forests, also found in taiga or mixed forest covered hills. Great geographical variability, great seasonal migration.

Distribution: very rare finds. In Early Pleistocene the Alps and the Pyrenees, in W_1 the Alps and southern Germany, in $W_{1/2}$ southern France and northern Italy, in W_2 the Pyrenees, in $W_{2/3}$—W_3 northern Yugoslavia, at the very end of W_3 the Alps. There are more regions with finds of this species, but the localities are not exactly dated. Everything points to the fact that the species takes up a relatively large region during the Last Glacial and persists in it all the time, irrespective of climatic changes.

Vulpes vulpes (Linné, 1758)

Characteristics: prefers open and half-open areas. From the point of view of environment in all types of landscape. In the tundra, the forest tundra, in gallery forests, in the taiga and deep forests. Everywhere in the forest-steppe and the steppe, even in the semidesert and in the desert. In the Pamir up to 4000 m. Optimum for it are mixed forests interchanging with open landscape, meadows, swamps and river valleys. A great geographical variability.

Distribution: throughout the Last Glacial everywhere in the area studied. Numbers of localities and thus probably its amounts principally unchanged.

Alopex lagopus (Linné, 1758)

Characteristics: in the tundra the most frequent and the most common species. Its southern limit identical with the northern limit of forest distribution. Through river valleys it penetrates even into the taiga. Annual migration to long distances (up to 2000 km) is characteristic of it. Small geographical variability.

Distribution: in Early Glacial it does not penetrate to the territory west of the Rhine, in W_1 its westernmost occurrence is only in central Europe (ČSSR, Poland). In $W_{1/2}$ for the first time in northern Yugoslavia and southern France. In W_2 already in the Pyrenees. The highest number of localities appear at the very end of W_3, when it penetrates in the west as far as to northern Spain and takes up the whole extensive area of western, central and eastern Europe.

From the above data it follows that optimum conditions for it set on only during the middle part of the Würm and culminate at its end.

Martes martes (Linné, 1758)
Martes foina (Erxleben, 1777)

Characteristics: the species *Martes martes* is closely connected with forests. It is found from the light pine forests of the Kola peninsula and the taiga type forests up to Mediterranean oak forests.

The species *Martes foina* is a typical inhabitant of the forest to the forest-steppe, requiring rather mild climate. In mountains and hills, as well as in areas without forests or almost without forests.

Distribution: throughout the Last Glacial all over the territory. Particularly numerous finds from the beginnnig of the Glacial up to $W_{1/2}$ including. Starting with W_2 a sharp

drop in the number of localities and their concentration mainly in the southern part of the area studied. Only at the end of W_3 it again penetrates further to the north (up to the territory of Poland), but the number of localities remains unchanged and relatively small.

Putorius putorius (Linné, 1758)
Putorius eversmanni (Lesson, 1827)

Characteristics: *Putorius putorius* is an inhabitant of the forest, the forest-steppe and the steppe. It avoids continuous forests. Optimum are minor forest units alternating with meadows. Relatively little found in the taiga.

Putorius eversmanni prefers open landscape, steppes to semideserts. Ecological requirements, primarily depending on food, are hard to define.

Distribution: isolated finds throughout the Last Glacial. A low number of finds does not permit a more detailed evaluation.

Mustela erminea Linné, 1766
Mustela nivalis Linné, 1766

Characteristics: *Mustela erminea* inhabits a territory reaching from the arctic and boreal zones up to the southern limits of the steppe, semidesert and, sometimes even the desert. Thus it lives in very different environment: the tundra, the forest-tundra, the forest, the forest-steppe and the steppe. It avoids completely open areas.

Mustela nivalis inhabits the territory from the arctic zone up to the subtropic region. Without demands to the environment it is easily adapted to different conditions (the tundra, the taiga, the forest-steppe, the steppe, the semidesert). It is rather an indicator of the amount of voles. Extremely great geographical variability.

Distribution: isolated finds throughout the Last Glacial independent on climatic oscilations.

Gulo gulo (Linné, 1758)

Characteristics: essentially a forest animal typical chiefly of the coniferous taiga, penetrating, however, hundreds of kilometers into the tundra. Its southern limit is the forest-steppe, in isolated cases it can be found in the steppe. It is directly bound to the presence of the reindeer. When they disappear, the wolverine disappears as well. An advantage for it is a deep snow blanket (50—70 cm) lasting for a long time. Such regions constitute a major part of its area, even though it does not limit itself to it only. Both in lowlands and in the mountains. Slight geographical variability of clinal character.

Distribution: in Early Würm it is registered only in Moravia (CSSR), from W_1 also in the Alps. In both cases they are only isolated finds. Only in $W_{1/2}$ do its finding places become slightly more numerous and at that time it penetrates to the Rhine River and to northern Yugoslavia. In all those regions it persists also during W_2. The very end of W_3 is optimum for it. The number of its finding places increases rapidly and its area extends. It penetrates far to the west, up to the Pyrenees, into the southern and western parts of France and into northern Italy.

Lutra lutra (Linné, 1758)

Characteristics: a species bound to water and independent on climate, geographical latitude and the landscape relief. Adverse for its existence is only a long-lasting ice cover on the water. Small geographical variability.

Distribution: isolated finds evidently due to unsuitability from the point of view of fossilization. From Early Würm the region of the Caucasus, in $W_{1/2}$ the Pannonian lowland and Moravia (CSSR), in W_2 southern France, at the end of W_3 northern Yugoslavia and the Caucasus.

Meles meles (Linné, 1758)

Characteristics: a very adaptable animal living mostly where minor forest patches interchange with meadows. In darge forests only at their margins. Found, however, on minor steppe areas near water springs, in isolated cases also in semideserts. A great geographical variability.

Distribution: isolated finds throughout the Last Glacial. In Early Würm the northernmost region of its finds is the Pannonian lowland, in W_1 northern Yugoslavia and central France, in $W_{1/2}$ it is recorded — besides regions situated farthern to the south — also from the Alps, Rhineland, Moravia (CSSR), in W_2 it occupies probably the same regions again, in $W_{2/3}$—W_3 it is found in Belgium, towards the end of W_3 the number

of its localities is again reduced. From the above list no conclusions can, however, be drawn, it is evidently affected by other circumstances.

Ursus spelaeus Rosenmeyer et Heinroth, 1794

Characteristics: its remnants are typical of all karst regions. A species with a broad range of toleration. Geographical and individual variabilities extremely great.

Distribution: throughout the Last Glacial in the broad area of Europe. Its southern limit goes across Spain, Italy, Yugoslavia and the Caucasus. From Early Würm onwards numerous, in karst regions the dominating species. Its number increases particularly in $W_{1/2}$ almost all over the territory of Europe, at the beginning of W_2 a reduction sets on which continues up to the end of the Glacial. At the very end of W_3 only isolated finds, besides the region of the Caucasus, where at that time it still constitutes the dominant component in the faunistic community.

Ursus arctos Linné, 1758
Ursus priscus Goldfuss, 1810

Characteristics: a typical inhabitant of extensive forests, in the north, however, looking periodically for open tundras as well. Prefers coniferous forests to deciduous ones. A great geographical and an individual variabilities. Migration negligible.

Distribution: in Early Würm a number of localities, mainly in southern and western parts of Europe. This is repeated throughout the whole W_1. The substage $W_{1/2}$ means a drop in the number of localities, which is still deepened in W_2, when the species retires more or less to the southern regions. Only the very end of W_3 means again its great extension evidently all over Europe, irrespective of geographical latitude.

Order: *Proboscidea*
Mammonteus primigenius (Blumenbach, 1799)

Characteristics: an animal adapted to cold climate, living, nowever, also in mild and relatively warm climate. Avoided continuous forests, dominated in open landscape of the tundra character, of the arctic steppe, the loess steppe or the steppe. Possibility of living in a landscape of park character in which open areas interchanged with minor patches of forests. Avoided hills with major differences in height and mountains with steep slopes.

Distribution: the above species inhabited extensive spaces of chiefly central and eastern Europe all the time. At that time only its western and southern limits oscillated. The substage of Early Würm reflects to a certain extent its distribution towards the end of the Last Interglacial. The westernmost localities at that time are found in the area of the Rhine, the southernmost ones in the Pannonian lowland and in the region about the Danube mouth. But as early as in W_1 it penetrates to southern France and its finds in the course of the Last Glacial are recorded both in the south of France and in the north of Italy, northern Yugoslavia and the whole of Rumania. That is the situation up to late W_3 when, in a relatively short time, the species disappears completely from the whole territory investigated.

The problems of its extinction on the given territory are most probably connected with an overall change in the climate resulting in the formation of continuous forests which wore quite unfavourable for its existence. Small areas of steppes which must have existed in places were not sufficiently large for its life. The disappearance was relatively quick, because in the course of $W_{2/3}$ and at the beginning of W_3 it was the dominant animal all over the Ukraine and at the beginning also in central Europe.

Palaeoloxodon antiquus Falconer and Cautley, 1847

Characteristics: a species occurring only in explicitly warm and oceanic climate, in a landscape where there are forests, meadows and streams. It avoids dry steppes, continental and cold climates.

Distribution: as early as in W_1 it occurs in northern Spain, southern France and northern Italy, i.e. in regions with warm climate. Its existence in the Last Glacial, of course, does not end with this. In southern France it is recorded in $W_{1/2}$. It lives there together with another elephant species, the mammoth, and also with the woolly rhinoceros, i.e. with species to which cold climate suits better and whose ecological requirements were different. All this indicates that most important for the mammoths were not so much seasonal temperatures, but reather the average annual temperature and the presence of alternating areas of continuous forests and open steppes.

Order: *Perissodactyla*

Coelodonta antiquitatis Blumenbach, 1799

Characteristics: an animal of similar distribution and similar ecological requirements as those of the mammoth.

Distribution: the stage of Early Würm finds it evidently in the same areas as the mammoth. Also in this case the conditions from the end of the Last Interglacial are reflected here. In W_1 it is recorded in southern France where it has even the dominating position, in W_2 it is recorded also in northern Spain. The extent of its distribution remains practically unchanged up to late W_3 when, like the mammoth, it quickly dies out all over the area of its distribution.

The reasons of its extinction are evidently the same as in the mammoth. It is of extreme interest to see how its distribution in the individual time spaces overlaps completely with that of the mammoths.

Dicerorhinus kirchbergensis (Jaeger, 1839)

Characteristics: a species with similar ecological requirements as those of *P. antiquus*. From the point of view of its time distribution it seems, however, that unlike that species it was able to live even in not explicitly warm climate.

Distribution: in Early Würm it is found not only in the Iberian and Italian peninsulas, but also in northern Yugoslavia, in the south-eastern part of France and in isolated cases elsewhere. This situation does not change in the course of W_1, its finds are, however — besides the above areas — also recorded in the Crimea and in the Caucasus. As late as in $W_{1/2}$ it occurs in the southern part of France, northern Italy and in Yugoslavia. This is also the last time of its existence in those regions. Only in northern Spain it survives into the stadial W_2, but with that its existence in the area investigated ends.

From what has been said it follows that in comparison with the ecological requirements of *P. antiquus* this species had a broader range of toleration.

Equus sp.

Characteristics: a typically steppe species, partly also the forest-steppe, in isolated cases semidesert. Plains. In the Last Glacial different species with early the same ecological requirements.

Distribution: throughout the Last Glacial very numerous all over the territory investigated.

Equus (A.) hydruntinus Regalia, 1907

Characteristics: steppe to forest-steppe regions with warmer climate.

Distribution: geographical situation of its finds is very surprising. In Early Würm and in W_1 the finds are spread from the Caucasus over the Crimea and the Danube delta to central Yugoslavia, the Pannonian lowland and Moravia (CSSR). The last mentioned regions are also the westernmost sites of its occurrence. They clearly indicate the eastern origin of this species. In $W_{1/2}$ it is found also in southern and central France, it populates the whole European continent, of course avoiding the northernmost parts (the northern limit being the central part of the Rhineland and the CSSR). In $W_{2/3}$—W_3 it retreats to the south, evidently the deteriorated climatic conditions do not agree with it. However, due to the fact that at that time they are only isolated finds, this statement must be considered rather a working hypothesis. The same can be observed at the very end of W_3.

Order: *Artiodactyla*

Sus scrofa Linné, 1758

Characteristicc: a typical inhabitant of forests, chiefly in river valleys. It is an ecologically very adaptable species which, though warm climate is optimum for it, can stand even very low temperatures (the mean January temperature up to —25 °C). It is, however, tied to a certain thickness of snow only, in no case does it live in regions where the snow blanket is thicker than 0.5 m for a long time. Great variations in quantitative numbers in individual years. Nowadays it exhibits great eurytopy — from the taiga up to steppes, in the mountains up to Alpine zone. Mostly no migration.

Distribution: in Early Würm and in W_1 it is found all over the southern part of central Europe, in the north it is found as arears in central Germany and central Poland. In the substage $W_{1/2}$ and mainly in the course of W_2 its concentration prevailingly to southern parts of Europe can be observed. In only isolated cases it can be found north of the Alps. The same pattern of distribution can be seen in the latter

half of Würm and it its very end, when they start appearing in Belgium and in Jutland; those parts had evidently their own oceanic climate. On the other hand, the regions of the northern part of central Europe and those farther to the east remain without its finds all the time. Despite its great eurytopy of today, in the Last Glacial its great dependence on climate in connection with the plant cover can safely be observed.

Hippopotamus amphibius Linné, 1758

Characteristics: a species of markedly warm climate with the existence of major water streams with forests.

Distribution. in Early Würm its finds are recorded in northern Spain and Italy. In W_1 it is still found in northern Italy and southern France. That is the last time of its occurrence. Later conditions were no longer suitable for its life in those regions.

Cervus elaphus Linné, 1758

Characteristics: a species found in most environment with warm climate — forest, forest-steppe, steppe and in isolated cases also the region of deserts. It stays in one place, concentrating where the snow blanket does not exceed 40—60 cm. The subspecies *C elaphus maral* lives in gallery woods or in small forest patches.

Distribution: Early Würm and W_1 finds it almost all over Europe with the exception of its easternmost part. About the same distribution can still be observed in $W_{1/2}$, when in central Europe it is mostly the subspecies *C. elaphus maral.* The substage W_2 means its intense retreat. Cold and rough climate reduces the number of its finding places and its optimum region at that time is Spain, France, northern Yugoslavia, and in only isolated cases it is found north of these positions. This situation remains unchanged up to the end of W_3, when, however, it takes up not only its former regions, but also the eastern part of the European USSR in the catchment area of the Volga and the region of the South Urals.

Dama dama (Linné, 1758)

Characteristics: an animal adapted rather to warmer climate in a landscape where small deciduous forests alternate with areas cavered with only grass or even bushes. Many times it is found in dry spruce and pine forests.

Distribution: only isolated finds. From $W_{1/2}$ and W_2 localities in central and southern France are recorded. Surprising are finds from the very end of W_3 from southern Germany, as far as the dating was correct and those finds do not belong to Early Holocene.

Capreolus capreolus (Linné, 1758)

Characteristics: populating regions with different climate, from most oceanic climate to dry continental climate. Living both in different forests (deciduous, coniferous, mixed) and in forest-steppes, steppes, and often also in semideserts on the banks of lakes. Avoiding continuous coniferous forests of the taiga type, optimum for this species are forests alternating with meadows. Its northern limit is determined climatically as well as by the amount of snow in the winter (maximum 50 cm).

Distribution: in Early Würm it inhabits the whole of southern and central Europe with the exception of its northern regions. In the east it is recorded only from the region of the Caucasus. During W_1 its northern limit shifts clearly southwards, which continues all the time up to W_2. At that time it evidently inhabits only the southern parts of the area investigated. Only the W_3 substage signifies again its gradual penetration to the north, but not only in the region of central Europe, but also in the east of Europe, surprisingly far (the catchment areas of the Volga and the Pechora Rivers, the South Urals). Up to the end of W_3 there are no more essential changes.

Alces alces (Linné, 1758)

Characteristics: an inhabitant of forests, the forest-tundra, forest-steppes or marginal regions of the steppe zone. Optimum habitat is the light taiga changing in places into forest-steppes. Adapted for life in regions with high snow blanket. Great migration.

Distribution: in the course of the Last Glacial the area of its distribution changes essentially. In Early Würm and in W_1 it is found westernmost in central Europe (Poland, CSSR, Hungary), in northern Yugoslavia and northern Italy. About the same region is populated by it also in $W_{1/2}$. In the substage $W_{2/3}$ and particularly during and at the end of W_3 its great expansion sets on. It penetrates up to central Yugoslavia and central France, inhabiting at that time a great part of Europe. However, it never penetrated to the Pyrenees or across them.

Megaloceros giganteus (Blumenbach, 1803)

Characteristics: an inhabitant of forest-steppe and steppe habitats. Mild climate seems to have been optimum for it.

Distribution: in Early Würm and in W_1 it is found in a broad zone stretching from northern Spain across central France, southern Germany, northern Yugoslavia, the Pannonian lowland, the Danube delta, the Crimea and the Caucasus, i.e. in the southern part of the area studied. Throughout the following substage the area of its distribution remains unchanged, in W_3 and particularly at its end the number of localities increases, at the same time it shifts northwards and appears north of the Black Sea, in the region of the South Urals and in the catchment area of the Pechora. Due to isolated finds it is difficult to decide, whether in the latter case (the USSR) they are newly inhabited regions.

Rangifer tarandus (Linné, 1758)

Characteristics: the tundra, the forest-tundra, the taiga. It does not enter mixed forests. Well adapted to life in plains as well as in the mountains (up to 2500 m). Not inhabiting closed forests, only their margins or places where thick forests interchange with open areas, often of swamp character. An inhabitant of both mild and cold climate. Great migration of animals in big herds (up to 500 km).

Distribution: inhabits the area studied throughout the Last Glacial, from Spain to the Urals. In the course of the Glacial only the number of localities changes (the highest number in W_3, chiefly towards the end) and the amount of individuals. It begins to be the dominating animal in thanatocenoses in W_2, then it appears permanently up to the end of Würm. A particularly high number of localities in which it dominates are found at the very end of W_3 not only in central Europe, but also in central and southern France and in the Pyrenees. At that time its finds are recorded also from central Yugoslavia and from northern Spain.

Bos primigenius Bojanus, 1827.

Characteristics: an animal inhabiting both the steppe and the forest-steppe, as well as light forests. In the mountains up to the Alpine zone. Maximum thickness of snow in the winter 50 cm.

Distribution: in Europe throughout the Last Glacial. Dominating animal at the beginning of Würm in Spain, in $W_{1/2}$ in central Europe towards, the end of Würm it is the most frequent in southern and central France and in the Caucasus. From eastern Europe the finds are described only from Middle Würm onwards, but this may be due to the insufficient number of localities of the preceding stage.

Bison priscus Bojanus, 1827

Characteristics: forest-steppes, steppes, partly also the forest. Indifferent to temperature, able to live both in arctic conditions and in warm climate. As far as it lived in forests, they were deciduous forests with open patches. Former theories concerning living in large closed forest areas are now considered wrong.

Distribution: throughout the Last Glacial all over the area of Europe studied. A high number of localities, but for the most part it was not the dominating animal of the community. Abundant in Interstadial $W_{1/2}$ in central Europe. Conspicuously great is, however, its distribution towards the end of the Last Glacial ($W_{2/3}$ to the very end of W_3), of course in some regions only.

Saiga tatarica (Linné, 1766)

Characteristics: a typical inhabitant of steppes and semideserts, in summer penetrating also into forest-steppes, but not living there the whole year. Preferring plains, avoiding mountains or rolling mountain ranges. Great migrations, up to 250 km in a few days, depending on food, the same as the size of the herds (maximum 150—200 thousand individuals, as a rule, however, 100 to 1000). Snow layer maximum 10 cm. Geographical variability very small.

Distribution: in Early Würm and in W_1 their finds are recorded only in the European part of the USSR, in the Danube delta, and on the territory of Moravia (CSSR). They are isolated finds, but a continuous population can be assumed in the east; penetration to central Europe only in certain time. The species did not penetrate farther west. Thus was the situation also in the course of $W_{1/2}$. Only the W_2 Stadial with an essential change in climate results in further penetration to the west when the whole of western Europe is inhabited, including the Pyrenees. That situation persists up to the very end of W_3. At the time of the greatest expansion the species populates continuously

the whole above territory and in southern France it becomes even the dominating animal of the community.

Rupicapra rupicapra (Linné, 1758)

Characteristics: an animal at present ousted only to high mountains, formerly, however, populating not only mountains, but also highlands and even plains. Minor forest units interchanging with open areas.

Distribution: the species is recorded all over the territory investigated throughout the Last Glacial. It is even the dominating element in northern Spain, the Pyrenees (W_2, end of W_3), in northern Yugoslavia (W_2) and in the Crimea (end of W_3). Its finds are not described only from broad steppe plains in the European part of the USSR.

Ovibos moschatus (Zimmermann, 1780)

Characteristics: an inhabitant of the tundra and of periglacial steppes. Adapted to cold climate.

Distribution: in all cases they were always only isolated finds, but their geographical scattering is of considerable interest, even though finds without exact stratigraphy (the most numerous) are not registered. In Early Würm and in W_1 it is recorded from the territory of Poland, from the Alps and southern Germany. As finds dating back to the beginning of the Glacial they come from surprisingly southern latitudes. In $W_{1/2}$ it is also recorded from the Alps where it evidently lived throughout the Glacial. From W_2 it is described from the region of the Danube delta where it is even the dominant species. The latter half of the Glacial means at the same time an increase in the number of its localities. It can be found essentially throughout the area investigated, relatively abundant also in southern and central France and in the eastern parts of the European USSR. I think that probably it inhabited central and eastern Europe throughout the Last Glacial, it penetrated to France only after the decrease in the average annual temperatures in the latter half of Würm. It is alien to the Pyrenees, northern Italy and the Caucasus.

Capra ibex Linné, 1758
Capra pyrenaica Schinz, 1838
Capra aegagrus Erxleben, 1777

Characteristics: rocky areas alternating with forest or bush covered areas. Individual regions differ strongly from each other.

Distribution: throughout the Last Glacial all over the regions studied with the exception of the east European plains. Both the number of localities individuals seem to have been the same all the time, without any response to climatic oscillations.

Ovis sp.

Characteristics: inhabitants of open areas. Avoiding extensive plains and continuous forests. Relatively great migration. Very strong geographical variability.

Distribution: only isolated finds. In Early Würm Moravia, the Pannonian lowland, the Crimea, the Caucasus. In $W_{1/2}$ central France, northern Italy, Pannonia. In $W_{2/3}$—W_3 only finds in the Caucasus, towards the end of W_3 central France, the Danube delta and the Caucasus.

The above species may have inhabited always the same territory, but W_2 seems to have reduced its number and may be also its disappearance from some regions.

Conclusion

The species studied represent the main component of fossil communities in the Last Glacial. They are mostly big animals, from small animals only those are added which occur more frequently and are of paleoecologic importance. Only those finds have been described that were stratified. If they constituted a dominant component in the given locality, this fact is mentioned. In the opposite case their number is not recorded. The region studied includes only the territory of northern Spain including the Pyrenees, southern and central France, northern and central Italy and Yugoslavia, and further all territories north and east of the above ones, up to the Urals (the Urals included).

Despite a great number of species studied, with different ecological requirements, some trends of the same kind can be distinguished in the general pattern. From the view-point of the geographical distribution in the Last Glacial two great groups can be specified:

1) species living essentially in the area of the whole region studied. Mostly only their numbers increased or decreased. The following species belong here: *Lepus timidus,*

Marmota sp., *Vulpes vulpes, Martes* sp., *Ursus spelaeus, Equus* sp., *Rangifer tarandus, Bos primigenius, Rupicapra rupicapra, Crocuta spelaea.*

2) species living only in a part of the region studied. This phenomenon was due to different causes:

a) animals tied for different reasons to a certain area where they live all the time. A change in living conditions results in their disappearance: *Hystrix cristata, Canis aureus, Hippopotamus amphibius, Palaeoloxodon antiquus, Dicerorhinus kirchbergensis, Dama dama, Oryctolagus cuniculus.*

b) animals populate only a part of the region, the area of their distribution always changing in the course of Würm: *Cricetus cricetus, Lemmus lemmus, Dicrostonyx torquatus, Alactaga jaculus, Cuon alpinus.*

c) animals inhabiting different areas of the region studied at different times, depending on the changing living conditions: *Ochotona pusilla, Glis glis, Felis silvestris, Panthera pardus, Panthera leo, Lynx lynx, Alopex lagopus, Gulo gulo, Megaloceros giganteus, Ovibos moschatus, Meles meles, Ursus arctos.*

d) isolated finds due most probably to an adverse possibility of preservation: *Lutra lutra, Mustela* sp., *Putorius* sp.,

Despite a relatively short duration of the Last Glacial in some species one can well observe the areas from which they extend to further regions during Würm. They can be roughly divided into two groups:

A) animals at the beginning of Würm taking mostly the western or the southern part of the area investigated, from where they gradually spread with the changes in climatic conditions into more northern or eastern parts of Europe (the region of the Caucasus constituting an independent area not related to eastern or central Europe): *Panthera leo, Felis silvestris, Glis glis, Meles, meles, Ursus arctos, Sus scrofa.*

B) animals at the beginning of Würm taking only the eastern part of Europe from where they gradually extended chiefly in the western direction, less in the southern direction. They reached differently distant regions at different times:

a) the westernmost region is the area of central Europe: *Cricetus cricetus, Dicrostonyx torquatus, Alactaga jaculus.*

b) the westernmost region is the area of southern France: *Mammonteus primigenius, Equus (A.) hydruntinus, Alces alces, Ovibos moschatus.*

c) the westernmost region are the Pyrenees: *Ochotona pusilla, Gulo gulo, Saiga tatarica.*

d) the westernmost region is the area of northern Spain: *Alopex lagopus, Coelodonta antiquitatis, Rangifer tarandus.*

In the course of the existence of species in the Last Glacial, in some of them the number increased, sometimes so that the species became dominant. If those animals are left out in which this phenomenon oscillated in relation with the extending area, the following species remain in the individual substages (irrespective of the areas):

W_1: *Coelodonta antiquitatis, Equus* sp.

From Early Würm to $W_{1/2}$ (including): *Martes sp., Equus* sp.

$W_{1/2}$: *Ursus spelaeus, Equus* sp., *Bovidae.*

$W_{2/3}$—W_3: *Mammonteus primigenius, Rangifer tarandus, Bison priscus, Equus* sp.

End of Würm: *Lepus timidus, Castor fiber, Panthera leo, Lynx lynx, Alopex lagopus, Gulo gulo, Ursus arctos. Megaloceros giganteus, Rangifer tarandus, Saiga tatarica, Equus* sp.

In the latter half of Würm the numbers of *Crocuta spelaea* and *Ursus spelaeus* gradually reduce. before the end of Würm *Alactaga jaculus* disappears.

From the outline it is evident that the number of species in the community increased at the end of Glacial in animals with different ecological requirements.

THE DEVELOPMENT OF FAUNISTIC COMMUNITY

The pattern of the faunistic community of the Last Glacial is the result of a long preceding development. Although the picture recorded renders neither the whole community nor all finds of the individual species, i.e. it does not reflect their maximum extent, but only those that have been stratigraphically classified, relatively great changes of geographical cha-

racter are evident. The reconstruction of the paleoecosystems clearly shows that the communities never achieved the state of optimum balance, a climax stage; before this could be achieved, the environment changed, thus causing also gradual changes in the community. Never does it happen that the community should exist unchanged for a long time or that it should be replaced by quite different communities. It was always a rather slow change, often so frequently interrupted in the trend of its development that it could not call forth the origin of new species and maybe even lower taxonomic units. Evolutional changes can therefore be expected only within the species, they are of only intraspecific character. This points out the necessity of dealing more with the study of paleopopulations in relation to the environmental factors. It cannot be excluded that in many organisms different ecological factors in which they lived are not reflected in morphological and metrical changes even within the populations.

The first assumption of further increasing our knowledge appears to be a detailed study of populations from exactly stratified horizons of the individual biomes and the determination of the community pattern in terms of population sizes.

The essential part of Europe which was studied is sufficiently large to exhibit different climatical zones in the Last Glacial. The study of the individual species and community patterns has shown that the individual regions have their own specific evolution, although it is, of course, subject to the overall development of the climate. Thus they differ from each other, other difference raching a differently great degree.

The following climatic zones can be observed in Europe at that time:

1) moist winter with summer drought
2) warm mild climate of oceanic character
3) mild climate with short periods of frosts (nemoral)

All those climatic zones are typical chiefly of western Europe, regions around the Mediterranean, an extensive region of the slopes of the Caucasus and the Crimea.

4) arid climate with cold winters (continental)
5) cold climate with cold summers (boreal)
6) arctic climate

The last three climatic zones are typical chiefly of the whole extensive region of central and eastern Europe.

From the above it follows that the whole part of Europe studied can be climatically divided into essentialy two large units in which there were only climatic oscillations of the second order in the course of Würm.

The studied communities of the individual localities are defined on the one hand by their taxonomic pattern and/or the quantity of the individual species, on the other hand by their ecological pattern. It is necessary to realize that in no case they can be actual biocenoses, but they are only taphocenoses or, more correctly, oryctocenoses. Dominant species of an oryctocenosis need not quite truly reflect the dominant species of the biocenosis. The deduced paleoecological data thus represent only a certain part of the original community. Despite these drawbacks which are hard to remove it is possible to maintain on the basis of present-day actuopaleontological studies that a certain level of overall know-

ledge it is possible to obtain a variety of data nearly identical with those obtained from the study of present-day biocenoses. On the other hand it appears that a reliable conclusion about the original environment cannot be obtained from the study of only one isolated oryctocenosis.

The above two units are divided into regions of different sizes that can be denoted as bioprovinces which are in turn divided into individual biomes. The areas of bioprovinces were different and in the course of Würm they included major faunistic changes. Bioprovinces thus represented stable but dynamically changing ecosystems depending on the changing climate, the extent and length of these changes being different both in the time scale and from the geographical point of view, and, in this case, also at the same time. This in itself points to complicated conditions and particularly mutual relations at that time.

We have shown at the beginning of this paper that it is absolutely out of question to transfer information as to the community pattern, quantity of species, their onset or possible disappearance from one biome to another (even within one province) without certain corrections. From this it follows that the communities of the individual biomes are considerably differentiated within one bioprovince. This is particularly conspicuous in the area of central Europe in the broad sense. This results in the fact that although it is possible to characterize a certain bioprovince or a number of biomes as to the community patterns and their detailed development, the validity of this conclusion is possible only on the general level. In no case can it be applied without any adaptations for detailed biostratigraphy. The differentiation within the individual biomes is so great that detailed biostratigraphy based on these changes assumes the elaboration of local biostratigraphic diagrams. Only on that basis would a relative time comparison of different biomes be possible. The same conclusion has been reached also by a number of other specialists (such as BIBIKOVA, BELAN, 1979).

Local biostratigraphic diagrams have at present been elaborated for only some regions. This means that in the future one will have to concentrate in this direction to be able on the one hand to get acquainted with a detailed development of communities in time in individual minor geographic regions, on the other hand to utilize that information for a detailed relative time comparison and dating.

The first order climatic unit in the Last Glacial is a drop in average annual temperature and its oscillation. This affected the formation of land and mountain glaciers or their melting, the formation of sediments of different type and thickness and towards its end also the character of the plant cover and the pattern of the faunistic community tied to it. This view that appeared and has essentially been formed in the course of this century is generally considered to be correct. But in my opinion it cannot be made quite absolute from the point of view of faunistic communities. A certain incorrectness consists in the fact that this view neglects and does not take into consideration a number of further factors of the same importance, not to speak of the fact that the characteristics of, say, the present taiga and tundra are transferred without correction to more southern regions with always a different length of daylight and

a different amount of solar radiation. All these and many other factors then distort the conclusions drawn.

When studying the individual species and their distribution in the course of Würm it was evident that in most cases a broad range of toleration must be taken into consideration, as well as their adaptability to different temperatures, etc. Species always considered to be cold-adapted, whose names are directly connected with regions of the tundra character or those of loess steppes, currently — not in isolated cases — appear amidst quite a different community, with species tied to warm climate (*D. kirchbergensis, P. antiquus, H. amphibius*) and with a variety of species even today living in explicitly warm climate. This concerns also the reindeer, but also the mammoth, the woolly rhinoceros and a number of others. They are not only habitats in which those animals could live for a limited period of time, but habitats where they not only live, but currently reproduce. This statement in itself makes one think of the correctness of many hitherto assumptions. The analysis shows that there are much fewer stenothermic animals than could be expected. The deep-rooted idea of explicitly cold-adapted species is greatly shaken by the analysis of the community patterns of different bioprovinces.

All this indicates that although average temperature must have played the decisive role both in the flora and in the fauna connected with it, it was not the only factor and for many species it may not have been the most important one. It appears more and more clearly that a factor of the same importance is also the oceanity and the aridity of the climate to which many species of big mammals are even more tied than to cold or heat. This conclusion is also supported by the above mentioned existence of a number of species considered to be typical animals of cold regions, which, however, are so highly eurythermic that they can quite well exist also in regions with very warm climate together with typical thermophile species. Nobody would think of it the other way round and consider these typical thermophile species to be species looking for cold regions.

What is, however, the most decisive, are of course the basic living conditions of the habitats, that means at that time the presence of free open grass-covered areas interchanging with areas of forest units. In the Last Glacial a biome is formed in a great extent of almost the whole of Europe, one that does not exist nowadays. It is a biome of alternating forest and forest-steppes, where there are only oscillations of the individual areas, but mostly never a monotous development in one direction or another. This constitutes assumptions for the possibility of living under the given conditions for a relatively large number of species. The alternation of closed and open areas which was so typical of the Last Glacial in the extensive areas of Europe is at that time due to an increased aridity of the climate or alternation of oceanic and continental climate. That is why at the beginning of Holocene, when there is a conspicuous change in the amount and distribution of precipitation and thus also the formation of continuous forest units there is also a great change in the faunistic community.

Another, by no means less important factor is the fact that the eco-

logical requirements of some species are sometimes judged according to their present-day distribution which, judged by their distribution in Pleistocene, is certainly influenced by a number of most varied, mainly anthropogene factors.

This set of problems is connected with the problem of the so-called mixed faunas. This term, at least in the form as its content is sometimes explained and used, is quite inaccurate. It follows from a non-historic view of previous communities and the type of the then plant cover. It judges these communities from the point of view of closed and sometimes monotonous forest stands on the one hand and with the presence of extensive steppe areas on the other hand. This, of course, was mostly not the case throughout Würm. Besides the region of eastern Europe, open areas alternated with forest units all over the territory studied, of course in dynamic oscillation in the course of the Last Glacial. And the community of the Last Glacial corresponded exactly to the given plant cover, there being no need for any secondary mixing. At the same time this shows that this landscape pattern was much more suitable for most animals than was the case in Holocene and this is the reason why communities at that time were much richer in species than those of Holocene. Species migration and the extension of their areas was not so much due to temperature oscillation as to a more suitable and mainly more varied plant cover. That is why at the beginning of Holocene and with the onset of quite different ecological conditions a number of species disappear from certain regions very quickly and for good.

The oscillation of aridity and the drop in average annual temperatures in the broad spaces of Europe causes the species of the present eastern and northern regions of Europe to become the main migration element. In migration waves they penetrate to different distances westwards and southwards at different times. My study shows that the westward migration across central Europe to France, the Pyrenees and northern Spain was for them always easier than the migration in the southern direction to the Balkan peninsula and to Italy, at that time connected with Yugoslavia by a much wider belt of land than it is today, since the northern part of the Adriatic Sea was land at that time. Besides these migrations at the given time also migrations in the opposite direction, i.e. from the west to the east, can be noticed, even though they are much weaker and concern only a small number of species.

Individual bioprovinces characterized as a whole with a faunistic community changing in species, have areas of different sizes essentially remaining unchanged throughout the Last Glacial. Based on the evaluation of faunistic finds, I divide the studied region of Europe in the Last Glacial into the following bioprovinces:

A) eastern and central Europe

This takes up the most extensive territory with considerable climatic differentiation, but nevertheless with a number of signs indicating its unity.

B) the region of southern and central France and the Pyrenees

These seemingly unconnected regions are subject to the same develop-

ment and throughout Würm they influenced each other strongly, irrespective of great relative differences in height.

C) the region of northern Spain

Essentially the territory lying to the south and to the west of the Pyrenees which, throughout Würm, had an independent development differing both from the Pyrenees proper and from the parts of Spain situated more to the south. At the same time it was always under the influence of the adjacent regions.

D) the region of the Caucasus

Throughout Würm this territory was strongly different in the fauna pattern from regions lying more to the north and had always a substantially different development, specific of that region.

E) the region of the Crimea

Despite a relatively small territory it was necessary to classify it as an independent bioprovince, because throughout Würm it always strongly differed from its surroundings both by the pattern of its faunistic community and by its development. This was due to the configuration of its relief as well as to a certain extent to the underlying rocks.

F) the region of northern Italy and Yugoslavia

It is evidently only a part of the whole bioprovince which extended still further to the south, taking up areas nowadays covered with the sea. Faunistically it was strongly affected by the regions lying more to the south.

The delimitation of the bioprovinces evidently does not include the whole of Europe, but only the part investigated. They are in turn subdivided, as far as central and eastern Europe is concerned, into a number of biomes formed in dependence on the extent of the climatic and plant changes taking place, many times due to chiefly the relief and the distance from the sea.

In the bioprovince of eastern and central Europe (A) the following biomes are distinguished:

the Alps (5)
northern slopes of the Alps, southern part of the FRG (6)
central part of Germany (FRG, GDR) (7)
northern parts of the FRG, Jutland (8)
the region of Belgium (9)
the region of the CSSR (10)
the region of lowland Poland (11)
the region of Hungary (12)
the region of the central part of Rumania (the Carpathians) (13)
the region of the Danube delta (14)
the region of the lower stretch of the Dniester River (USSR) (15)
the region south of the City of Kiev (USSR) (16)
the region between the middle stretches of the Don and the Volga (USSR) (20)
the southern part of the Ural Mountains (USSR) (20)
the upper stretch of the Pechora River (the Northern Urals, USSR) (21)

The division of the biomes is to a certain extent dependent on the present level of knowledge of fossil faunas in the given bioprovince

and also the frequency of the discovered localities plays a certain part here.

In the bioprovince B the following biomes are distinguished:

the Pyrenees (2)

the region of southern and central France (3)

All other bioprovinces are not divided into biomes. This is due not only to a smaller extent of the area, but also to the frequency of localities with fauna, as they are known nowadays.

Before proceeding to the description of the development of the individual biomes, let us imagine a rough picture of changes taking place in the Last Glacial all over the territory studied, the picture being based on the analysis of faunistic communities. It is thus a generalization which will differ from biome to biome. This generalization has been elaborated only on the basis of paleontological finds; there are, however, regions where the finds are not classified into individual time spans. In such a case I omit those regions in my evaluation. The evaluation concerns only the studied parts of Europe.

Early Würm

All over the area of that time relatively great aridity sets in under mildly warm climate. The result are interchanging steppe and forest regions all over Europe, irrespective of the average temperatures in different parts of the European territory. The region of northern Spain appears to be the warmest, being followed by northern Italy and Yugoslavia. This will no doubt also concern the Caucasus, but finds of that time are not differentiated there. A cool zone stretches across the spaces of Germany, Czechoslovakia to the Danube delta.

Substage W_1

The aridity of the climate continues all over the area studied. Although the average temperature is still higher than in the subsequetn substanges — extremely cold climate cannot be observed anywhere — the temperature differentiation is quite great. The coldest regions are found in the central part of Europe (the territories of Czechoslovakia and Poland).

Substage of Interstadial $W_{1/2}$

The aridity of the climate is still the same as in the preceding substages. But the temperature differentiation which set on in the preceding stadial deepens. This concerns mainly the region of central Europe. There are biomes indicating explicitly warm or mild climate by their community patterns, but also cold climate. Extremely cold climate existing at that substage has, however, not been found. The steppes become extended, forest units, however, being still present. The coldest zone of that time stretches from central Germany across Poland, Czechoslovakia and the Pannonian lowland.

Substage of Stadial W_2

A relatively quick onset of cold climate. The dominating element is

the steppe which, at the cost of forest units, began prevailing already in the preceding interstadial. Unlike the preceding substage this is a cold steppe, the forest units either disappearing altogether or strongly retreating, persisting only on optimum sites and changing their species pattern. The coldest regions are found north of the Alps, in Czechoslovakia and on the western coast of the Black Sea. The onset of cold climate place chiefly in the regions of central and eastern Europe; in some territories only an increase in the quantity of steppe species was registered, which evidently reflects the extension of steppe areas.

Substage of oscillation $W_{2/3}$ to W_3

The landscape is climatically very strongly differentiated, the climate being mostly cold to extremely cold; like in the preceding stadial, the cold steppe prevails. Besides regions with the tundra also elements of the taiga can be found and in some regions even those of the central European forest. The warmest climate at that time is in the Caucasus, extremely cold climate registered in eastern Europe is in the catchment area of the Dniester River and in the region south of the City of Kiev.

End of Stadial W_3

Also at that time a strong differentiation of faunistic communities can be noticed, mainly because warmer forest elements start appearing gradually in some biomes. The warmest regions are territories in the north-western part of Spain and the Caucasus. The coldest territory is a zone extending from south Germany across the Pannonian lowland up to the Black Sea.

The above general climatic evolution is in detail influenced by different levels of procession of the individual biomes. It is quite certain that further new information, particularly from the eastern parts of Europe, can complete it substantially. A closer view of the others will be given by the analysis of the development of the individual biomes of central and eastern Europe.

A. Bioprovinces of eastern and central Europe

The Alps

It is not only the mountain range proper, but also extensive slopes, which to a certain extent level the differences due to different absolute heights of that region. In the substage W_1 one still finds in the localities animals from different climatic zones, but major finds of *Sus scrofa* and *Felis silvestris* terminate. In $W_{1/2}$ there is still relatively warm weather, tundra elements are in a subordinate position, animals of the taiga and of the central European forest prevail. In $W_{2/3}$ mildly cold climate prevails, of course besides the highest situated parts. Animals of the individual zones are more or less balanced in the community, but steppe elements prevail. Stadial W_3 indicates cold climate, when approximately to the same extent are represented elements of the individual plant zones (the tundra, the taiga, the steppe, the central European forest).

The above outline of development does, of course, not hold for the high positions of the range and corresponds rather to the western and southern

parts than to the northern part. A relatively great height and geographic differentiation must be assumed. In lower positions, discontinuous forest units never disappeared altogether, even though their strong reduction took place in W_2, $W_{2/3}$ and in the first half of W_3. At the same time it follows from the above that the formation of extensive glaciation must have been influenced by a variety of other factors than by a mere drop in the average annual temperature.

The northern slopes of the Alps and the southern part of the FRG

This region was relatively very cold throughout the whole of Würm. As early as at the beginning of the Last Glacial steppe and tundra elements indicating very cold climate prevail. This pattern is also found in W_1, but in places even small units of the central European forest must have existed. It is interesting that this substage appears to be mildly cold, i.e. relatively warmer than the very beginning of Würm, when it is very cold there. In the stadial W_2 steppe elements dominate, the climate being cold. At the very end of W_3 the climate is very cold, dominant being the elements of the steppe and of the taiga.

From what has been said it follows that the northern territory adjacent to the Alps and the southern region of the FRG had relatively cold climate in the whole Würm, steppes were mostly dominant, even though minor forest units of the taiga type or even those of the type of the central European forest existed in places, chiefly in the first half of the Last Glacial.

The central part of Germany

This region is of utmost importance from the point of view of the migrations of individual species between east and west, and at the same time it is a region in which the dividing line of oceanic and continental climate oscillated influencing the species pattern of the animals. Unfortunately, exactly classified finds as for the time are still relatively very few. The Interstadial $W_{1/2}$ indicates rather cold climate, in the landscape the steppe, the taiga and the central European forest are mixed. Even the presence of the tundra cannot be eliminated. The same situation exists at the end of the Glacial, when tundra and steppe elements prevail, but minor units of the central European forest and the taiga must have existed in isolated cases.

Like in the preceding biome the forests did not disappear altogether in the course of Würm. Evidently they must have existed all the time, even though to different extents at advantageous sites.

The northern regions of the FRG and Jutland

At the very end of W_3 the steppe dominantes, of course the other types of the plant cover are also present. Cold climate.

The region of Belgium

This region is to a certain extent all the time affected by the sea. In stadial W_2 the central European forest interchanging with the steppe must have been greatly extended. The climate was mildly cold. Everything points to a certain climatic difference from central Europe, where the beginning of W_2 means mostly the onset of conspicuously cold

climate. Only in W_3 the steppe begins prevailing intensely in the given region, but despite this forest units must have been relatively large even at that time. Climate was always mildly cold.

The above region had cospicuously different climate and plant cover as against central Europe.

The region of Czechoslovakia

Early Würm is characterized by mildly cold to warm climate. This probably holds also for the whole of W_1. In the Interstadial $W_{1/2}$ the tundra and the steppe prevail, forests of only the taiga type exist, the average temperature being higher and the climate mildly cold. The beginning of W_2 is characterized by the expansion of steppes, the number of tundra elements increases, others are strongly suppressed. The average temperature drops abruptly, the climate becoming extremely cold. Even though the temperature is on the average somewhat higher in $W_{2/3}$—W_3, the climate still remains very cold, only the presence of the taiga type forests increases. Towards the end of W_3 another increase in temperature follows, the climate is only cold, the steppe, however, always dominant.

From the outline it is evident that in the course of Würm the territory of Czechoslovakia was always covered with a steppe and with small forests of the taiga type whose size and distribution evidently oscillated. The climate, in comparison with other regions, was rather cold. Due to a great variability of the relief a great differentiation even to short distances must be assumed.

The region of lowlands in Poland

The beginning of the Last Glacial is characterized by mildly climate with the extension of the steppe, sometimes also of tundra and taiga-type forests. Temperature in W_1 drops constantly, the climate becomes very cold, steppe and tundra elements begin to prevail. A similar situation can be encountered in Interstadial $W_{1/2}$ as well, when the steppe and the tundra still dominate and the elements of the central European forest are quite missing. The climate is still very cold. From W_2 there are not sufficient exactly stratified finds, the substage $W_{2/3}$—W_3 indicates, however, mildly cold climate with the presence of the steppe, the tundra and the taiga. A similar situation exists at the very end of W_3, when elements of the steppe and the tundra prevail, the other elements being in a subordinate position. The climate is still cold.

The broad plains of Poland thus had cold climate throughout Würm, with the presence of the steppe, the tundra, and in different extent with forests of the taiga type. The proportionality of the individual plant covers oscillated.

The region of Hungary

The beginning of the Glacial is different from regions situated more to the north and is characterized by relatively warm climate with the presence of steppes, but also forest units of the taiga type as well as that of the central European forest. In $W_{1/2}$ the climate is mildly cold, one can find elements of the steppe, the taiga and the tundra, very weekly

also of the central European forest. The Stadial W_2 is also substantially different from the northern regions. The climate is warm, the central European forest is strongly developed as well as the taiga, but, of course, steppe regions are abundant. In this case, however, it is due to the aridity of the climate. Warm climate is also found in the substage $W_{2/3}$—W_3, when elements of the central European forest and of the steppe prevail. Only at the very end of W_3 a dramatic climatic change takes place. The climate becomes extremely cold, practically the coldest in the whole of Würm, elements of the tundra begin dominanting, the forest of the mildly cold zone disappears.

The region of Hungary, essentially the Pannonian lowland, has its specific climate in the course of the Glacial, differing from that of the regions located more to the north. It is on the average substantially warmer, the colder onset does not begin at the beginning of W_2 like in other regions, but appears only at the end of the Glacial. For the whole time, besides the end of W_3, the forest of the central European type is present, interchanging with areas of warm steppes.

The region of the central part of Rumania (the Carpathians)

In W_1 the climate there is relatively warm. The same can be said about the Interstadial $W_{1/2}$, when the steppe prevails, forests of the taiga type are present and the central European forest is very weakly represented. From the substage W_2 there is an insufficient number of stratifiable finds, in $W_{2/3}$—W_3 the climate is cold and steppes dominate. It can thus be supposed that the beginning of W_2 means the onset of cold climate also here.

The region of the Danube delta

This region has its specific development different from the Carpathians situated more to the west. Hitherto finds point to the fact that the beginning of the Glacial is characterized by very cold climate with a significant supremacy of steppe elements. Finds from later times, up to W_2, also indicate very cold climate with prevailing elements of the steppe, the tundra and the taiga type forests. The same is evident in the subsequent substage $W_{2/3}$—W_3. Towards the end of W_3 the average temperature drops still more, the climate becomes extremely cold, elements of the steppe and of the tundra dominating.

The above outline shows that throughout the Last Glacial the region had conspicuously cold climate, due to probably its being open in the northern direction. At the same time it appears that the effect of the Black Sea on the mildering of average temperatures must have been minimal and thus quite different from the region of Belgium. This kind of development is thus quite typical of the region.

The region of the lower stretch of the Dniester River

In the substage $W_{1/2}$ the steppe dominates altogether, the climate being cold. In the substage $W_{2/3}$—W_3 the climate there is extremely cold with a clear dominance of the steppe, elements of the taiga being less frequent.

The region south of the City of Kiev

Finds marked as the substage $W_{2/3}$—W_3 indicate extremely cold climate

with the steppe prevailing, but elements of the tundra and those of the taiga being relatively frequent.

The region between the middle stretch of the Don and the Volga Rivers

The substage of W_1 is characterized by the open steppe. In the substage $W_{2/3}$—W_3 the steppe still prevails, but all the other plant covers are also present. In comparison with the preceding biomes a certain improvement of the climate is evident, which is reflected in an increased presence of taiga type forests.

All the above regions of the Soviet Union take up extensive plains of eastern Europe, being characterized for the whole time by a clear dominance of the steppe and of cold climate. In relation with them, quite the same development was that of the region of the Danube delta.

The southern part of the Urals

In the substage $W_{2/3}$—W_3 mildly cold climate prevailed with the steppe dominating. Elements of the central European forest are also present. The region differs essentially from the Russian plains.

The upper stretch of the Pechora River (the Northern Urals)

It is interesting to see that also this region differs from the Russian plains, even though it is located so far in the north. In the substage $W_{2/3}$—W_3 the climate there was mildly cold, elements of the steppe and the tundra being dominant, others represented to a smaller extent.

From the outline of the bioprovince of central and eastern Europe a number of serious facts follow.

1) The average temperature of the individual biomes does not depend on whether they lie more to the north or to the south, but is evidently influenced by a number of other factors which are sometimes more importants than their geographical position. In western Europe it is e.g. the proximity of the sea (such as in Belgium). The coldest regions at all are perhaps the extensive plains of eastern Europe. Quite surprising in relation with them is the behaviour of the region of the Northern and Southern Urals.

The average temperature of the air seems to be influenced chiefly by the circulation of cold air.

2) Most biomes exhibited differently cold climate for the whole time of Würm, warmer climate occurring in only isolated cases. It is, however, necessary to realize that this view follows more or less from the comparison of the individual biomes. A different behaviour was only noticed in the Pannonian lowland which is quite different from all the other biomes.

The beginning of the Stadial W_2 mostly means the deterioration of the climate, as far as the average temperature is concerned. In only isolated cases this deterioration sets on later.

3) All biomes never developed permanently only steppes or only continuous forests, either of the taiga type or of the mild zone forest. Always in different ratios open areas of steppes were present interchanging with forest units of different sizes, mostly of the taiga type.

Forest of the central European type were present only in some places and in subordinate amounts.

4) Even though from the faunistic point of view there is only one bioprovince, its extensive climatic, plant and animal differentiations are evident. Those differentiations can even be seen in the individual biomes. That is why the time comparison from the point of view of the mutual comparison of communities, from the onsets of the individual species and/or their quantitative analysis, is very difficult, sometimes, at the present level of knowledge, even imposible. From this situation there follows the necessity of a through recognition of the development of local communities, their individual populations and — on this basis — the formation of local stratigraphic scales. Only then it will be possible to arrive at further more exact conclusions concerning both development of the fauna and detailed biostratigraphy.

B. The bioprovince of southern and central France and the Pyrenees

The region of southern and central France

In the substage W_1 this region has significantly very warm climate, extensive forests of the mild zone interspersed with open steppe areas. The dominanting element are forest animals, but the number of steppe animals is not negligible. Quite current are species with higher temperature requirements, such as *D. kirchbergensis, H. amphibius, P. antiquus*. Together with them there, however, occur also species living in the tundra and the taiga, such as *Rangifer tarandus, M. primigenius, C. antiquitatis* etc. The same is repeated in the substage $W_{1/2}$; most numerous are again animals characteristic of the central European forest of the mild zone, abundant are also steppe animals. *D. kirchbergensis* and *P. antiquus* are still present, together with *Rangifer tarandus, Alopex lagopus*. The climate is still very warm.

The substage W_2, unlike in bioprovince A, does not mean any substantial change. The climate remains very warm, elements of the mild zone forest prevail, steppe animals are frequently represented, elements of the tundra and of the taiga are relatively few. But species requiring very high average temperatures have disappeared altogether. Only this change can, to a certain extent, remind of much greater changes appearing at that time in central and eastern Europe.

Only the substage $W_{2/3}$—W_3 signifies a certain drop in temperatures. The climate is, however, still warm, evidently highly arid. For the most part there occur animals characteristic of life in the steppe, the number of elements of the central European forest drops. Evidently the areas of steppes extend at the cost of the forest.

A similar situation exists at the very end of W_3. Dominant elements are on the one hand steppe animals, on the other hand forest animals. Also elements of the tundra and of the taiga are relatively strongly represented. [*Ovibos moschatus, Alopex lagopus, Mam. primigenius, Coel. antiquitatis* and others.] The climate is, however, still warm.

From the outline it follows that the biome in question had warm to very warm climate all the time which, however, was evidently differently

arid in the course of time. Only towards the end of the Glacial drop in the average temperature can be noticed which was reflected by the disappearance of highly thermophile species and later on by an increased share of steppe elements together with animals of the tundra and the taiga. Animals typical of the tundra and the taiga have lived there practically without interruption almost since the very beginning of the Glacial irrespective of the average high temperature, only their quantity changes. By its overall development this biome thus essentially differs from all biomes of bioprovince A.

The Pyrenees

The first major number of exactly stratified finds come only from the Stadial W_2. The climate at that substage was warm, most animals are forest and steppe ones, relatively frequently also taiga and tundra elements are found. A similar situation is found at the very end of W_3. The dominant element at that substage are animals of the central European forest, but elements of the steppe, the taiga, and the tundra are also strongly represented.

No changes are apparent in the biome between the Stadial W_2 and the end of W_3. In any case differences following from different relative heights of the mountain range are necessarily to be expected.

This outline itself shows some specificities within the whole bioprovince

1) The climate was warm to very warm throughout Würm. Towards the end of the Glacial average temperature drops, but the drop is not too great and it is rather a matter of increased aridity. Thus this region differs strongly from central and eastern Europe.

2) All the time there existed side by side units of the central European forest (the forest of the mild zone) and open warm steppes, there may have only been oscillations as far as their mutual ratio is concerned. Up to the end of W_2 animals of the forest prevail, from that time onward steppe elements make themselves more felt.

3) From the very beginning of Würm animals requiring explicitly warm climate live side by side with species nowadays living in regions of the tundra and the taiga (*Rangifer tarandus, Alopex lagopus*) and extinct species which, according to some authors, looked only for cold climate (the mammoth, the woolly rhinoceros). The possibility of their coexistence with other animals is rather due to the character of the landscape (open steppes and forest units), i.e. certain aridity of the climate and in no case to only the average annual temperature, as some still think.

C. The bioprovince of northern Spain

This is the northernmost part of the Iberian Peninsula besides the Pyrenees. In Early Würm forest species prevail, but steppe elements are also frequently represented. The climate was very warm, *H. amphibius* and *D. kirchbergensis* occur quite commonly. An analogical situation can also be seen in the course of W_1, both as regards the temperature and the species pattern. Only W_2 means a certain change consisting in *H. amphibius* being missing, but *D. kirchbergensis* still being present.

Most species are still characteristic of the forest zone, tundra elements are relatively few (*Rangifer tarandus*, *Coel. antiquitatis*). The climate was always very warm. The same is repeated at the end of W_3 with only one difference, viz. that species bound explicitly to very warm climate are missing.

From the outline it is evident that for the whole time of Würm the climate was very warm. If in the preceding bioprovince, B, there were evident changes reflected chiefly in the ratio of forest and steppe animals, in this case it is not like that. The species pattern of the community does not change essentially in the course of the Glacial, besides species that die out. That means that the effect of climatic oscillations of the Last Glacial which were particularly strong in central and eastern Europe and which were still felt in southern and central France, even though rather in a different degree of aridity, are not reflected even in that way. It is possible to except the fauna to be more monotonous and changes due to extinction and migration.

D. The bioprovince of the Caucasus

The substage W_1 is characterized by very warm climate, forest elements dominate, but steppe elements are quite frequent as well. From among extinct climatically requiring species *D. kirchbergensis* is present.

In the substage $W_{2/3}$—W_3 the situation is similar. Forest animals still dominate, but the number of steppe elements decreases, while the number of animals found in the taiga grows. The climate is still very warm. Essentially the same is repeated at the end of W_3. Conspicuous is the prevalence of animals of the mild zone forest, the climate, however, remaining very warm.

Throughout Würm the region of the Caucasus differs conspicuously from the region lying north of it. Throughout the Glacial the climate is very warm, species of the mild zone forest prevailing. No dependences can be seen from the presence of species of the steppe, the taiga and the tundra and mainly from their oscillations. It can, therefore, be assumed that the climatic oscillation of Würm were not much reflected there, of course neglecting again the height factors which must have resulted in certain differentiation.

E. The bioprovince of the Crimea

The climate in W_1 was very warm, as indicated by the presence of *D. kirchbergensis*. Steppe forms are highly predominant, animals of the mild zone forest and those of the taiga are present to a lesser extent.

Of interest is the community pattern in the Interstadial $W_{1/2}$. Steppe forms stil predominate, which, after all, is due to the underlying rocks in the region. But animals of the mild zone forest and of the taiga are relatively abundantly represented. A relatively high presence of tundra elements is explained by their continuous penetration from the region lying to the north of the Crimea. Therefore I think that the climate was still warm.

A similar situation is repeated in the substage $W_{2/3}$—W_3 and, after all, also at the very of W_3. It cannot be excluded that percentual rations

might indicate certain cooling in $W_{2/3}$—W_3, but then the end of W_3 would again mean a change towards warmer climate. The climate was, however, always warm.

The bioprovince of the Crimea is characterized by certain specificity by which it differs from its immediate surroundings:

1) Unlike in the region lying more to the north, the climate was always warm all the time of the Glacial, which is due to the configuration of the terrain, i.e. the terrain is open toward the south and closed towards the north. It is not due to the Black Sea whose presence was not reflected in the Danube delta, and it cannot be assumed that it would operate in the Crimea.

2) Dominance of steppe elements is due to the underlying rocks on the one hand and to the aridity of the climate on the other hand. It is typical of the whole Würm.

3) So far it cannot be safely proved that changes in the representation of species of the individual climatic zones are in relation with the climatic oscillation of Würm.

F. The bioprovince of Northern Italy and Yugoslavia

The northern part of Italy and Yugoslavia has at that time its own development. On the one hand it is fully connected with southern parts influencing it strongly, on the other hand it is relatively well connected to eastern Europe. From this it follows that it is a region influenced by two different aspects, the northeastern influence being subject to oscillation.

In Early Würm the climate is very warm. *D. kirchbergensis* is present there. Despite a low number of finds it can be judged that in the landscape forest stands interchanged with open steppe areas. This conclusion is quite clearly verified by finds coming from W_1. Elements of the mild zone forest dominate, animals of the steppe are relatively frequently represented. Tundra elements are almost altogether suppressed, species of the taiga are somewhat more represented. The climate is very warm, as indicated also by the presence of the species *P. antiquus, D. kirchbergensis*, and *H. amphibius*. This development continues up to the Interstadial $W_{1/2}$, but there is a partial change. Only *D. kirchbergensis* is present, and despite a great prevalence of forest species also those typical of northern regions, for the taiga and the tundra, begin appearing in the greater amounts. This is an analogical phenomenon to that observed in France, which is due to migration from the northern into the region in which areas of forests and those of steppes alternate. The climate, however, remains to be still very warm.

The Stadial W_2 means a certain climatic break. Average temperature drops, the climate is mildly cold. Elements of steppes and those of the taiga begin to mildly prevail, the number of tundra species increases rapidly. At the same time the number of species typical of mild zone forest decreases. This drop in temperature lasts only in this Stadial. Already in the subsequent substage, between $W_{2/3}$—W_3, the number of species of the the central European forest increases, the number of taiga

and tundra species is somewhat reduced. But the steppe still prevails in the region. The climate at that time has changed to warm. A similar situation can be noticed at the end of the Glacial, when there is no essential change in comparison with the preceding substage.

It follows from the outline that up to W_2 the climate was very warm. The Stadial W_2 means cooling which, however, changed into warm climate from $W_{2/3}$. Irrespective of the average temperature there still exist forests and steppes all the time, starting with W_2 steppes spread at the cost of forests.

CONCLUSION

The present paper is based on hitherto published exactly stratified paleontological finds of mammals from the substantial part of Europe. It concerns only the Last Glacial, a stage most important from the point of view of the formation of present-day fauna. The region under investigation is divided into a number of bioprovinces, some of which are subdivided into biomes.

The analysis of the communities of the individual time sectors shows the complex character of their development, that most of the species are neither warm nor cold adapted, but not even stenothermic, but rather eurythermic. Therefore our ideas concerning some present, but mostly exctinct animals had to be changed in this respect.

The changes in the Würm macroclimate are well known in the general level. Although they are important from the point of view of the communities, much more important is the mesoclimate of the individual minor territories. This local climate is very strongly differentiated chiefly in the area of central Europe. The consequence thereof is that in this area local stratigraphic diagrams will have to be elaborated from the point of view of biostratigraphy, and only on this basis it will be possible to compare the localities of individual territories.

In the Last Glacial there was a biome in the whole of Europe which in this extent does not exist nowadays, i.e. the biome of interchanging forests and steppes, ending by the onset of Holocene. The analysis of the fauna shows that the majority of species were tied rather to this plant cover than to average annual temperature, which means that the aridity or the oceanity of the climate were often more important than the drop or the increase in the average annual temperature. Differences in temperature in many mammal species were thus not the chief factor of their distribution in the region studied. At the same time it appears that the primary effect of temperature was not always due to the degree of latitude in the given area.

In the conclusion it can be said that the Last Glacial under all above conditions had faunistic communities much richer than ever the case in Holocene which means their essential reduction. And the main role in this reduction — at least at the beginning — is not the presence of man. From this point of view that stage appears much more favourable for the existence of the fauna than has been considered so far under the influence of purely geologic information.

Distribution of some mammal species in the Last Glacial in the studied region of Europe. It does not concern the maximum distribution, but only finds stratified in detail. That means that the areas of distribution of the individual species are larger. Explanations to all the maps: empty and full signs without stroke denote the presence of the species in a locality, empty and full sings with stroke the dominance in the community.

Full circles — Early Würm
Empty circles — substage W_1
Full triangles — Interstadial $W_{1/2}$
Empty triangles — Stadial W_2
Full squares — substage $W_{2/3}$ to W_3 (included)
Empty squares — end of W_3

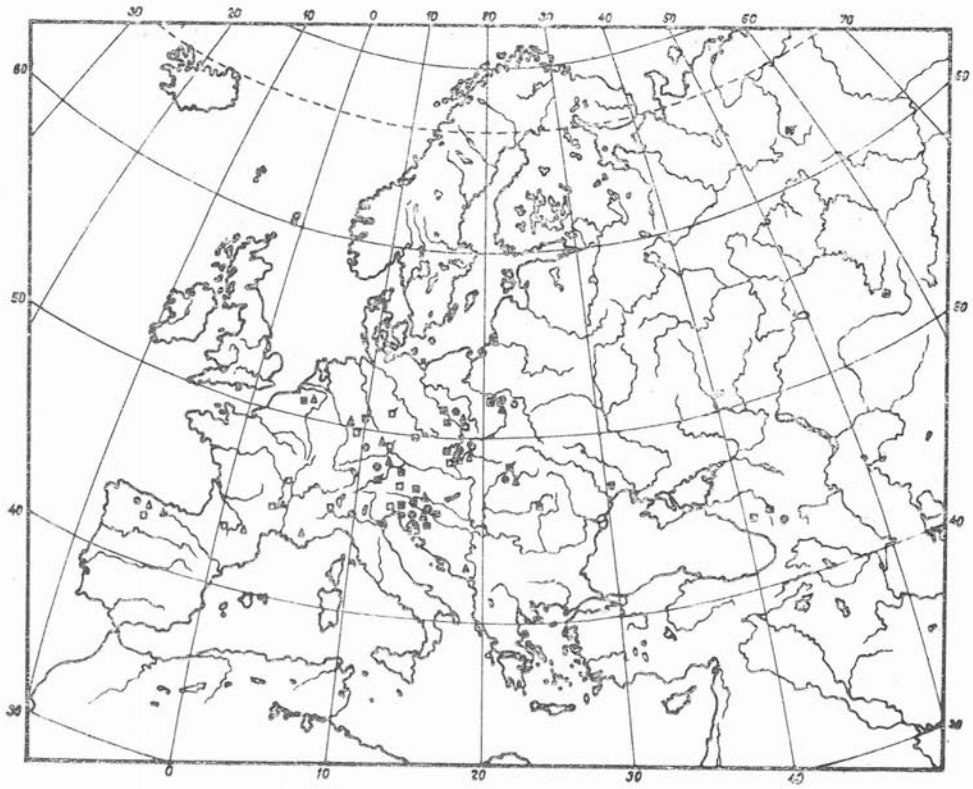

Fig. 1 *Lepus timidus*

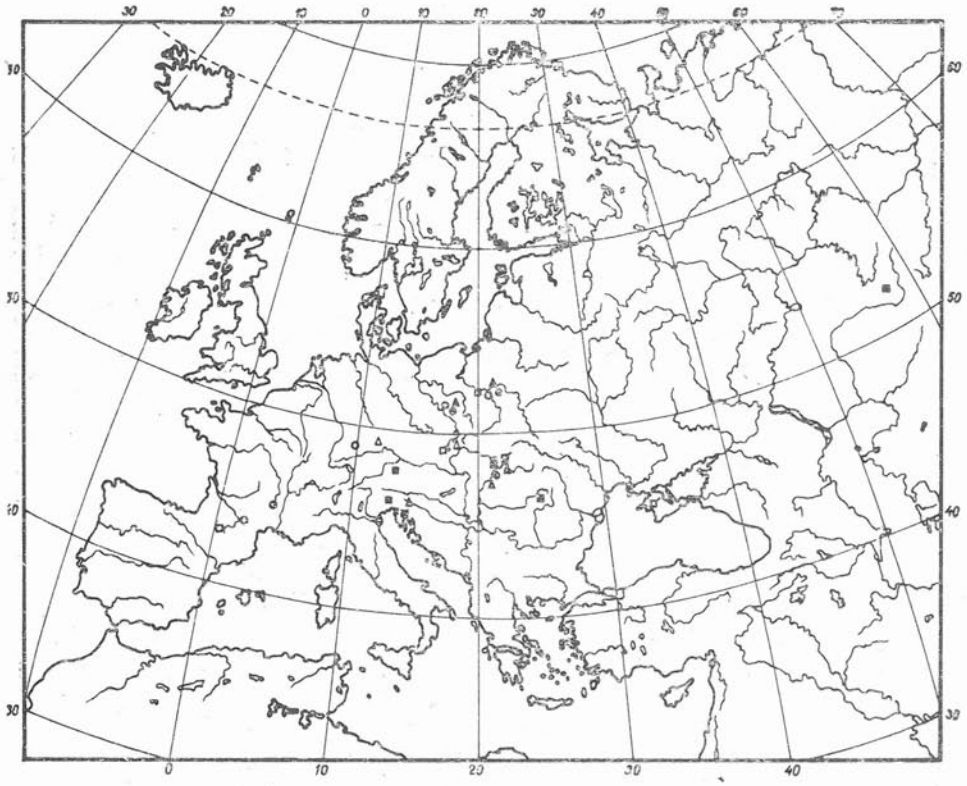

Fig. 2 *Ochotona pusilla*

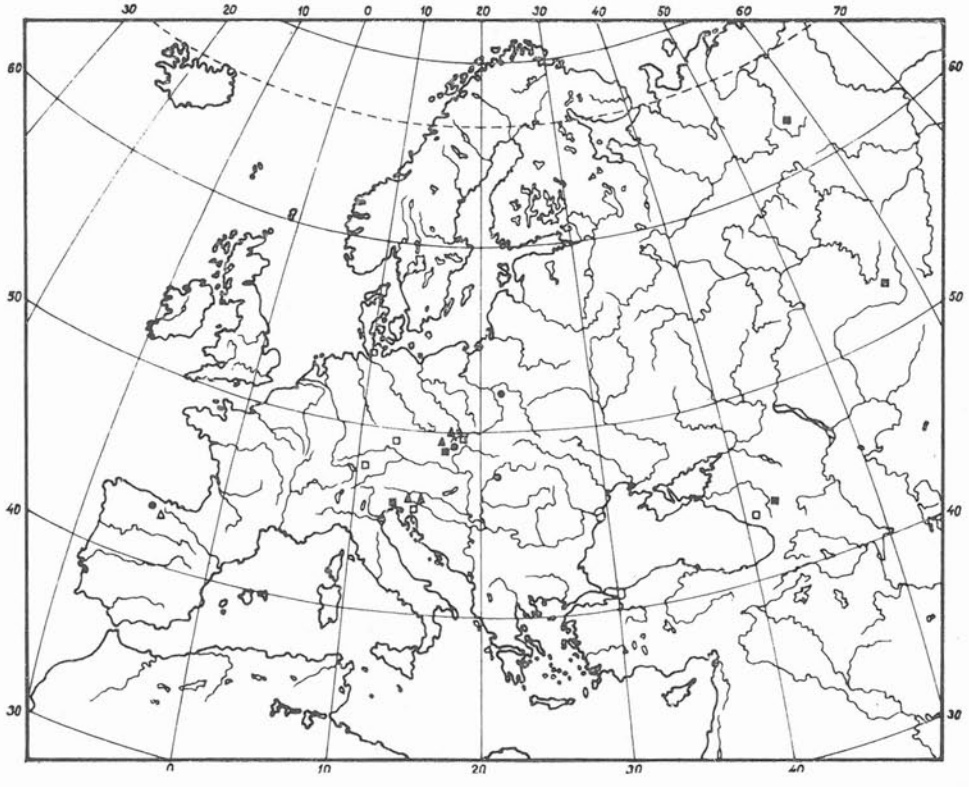

Fig. 3 *Castor fiber*

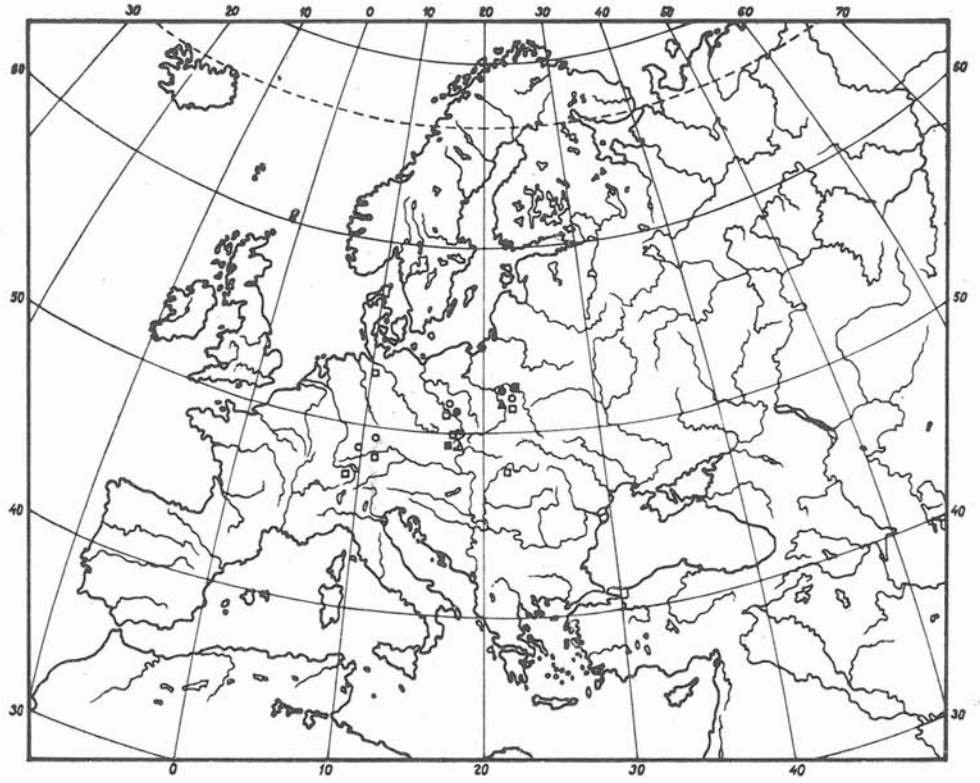

Fig. 4 *Lemmus lemmus*

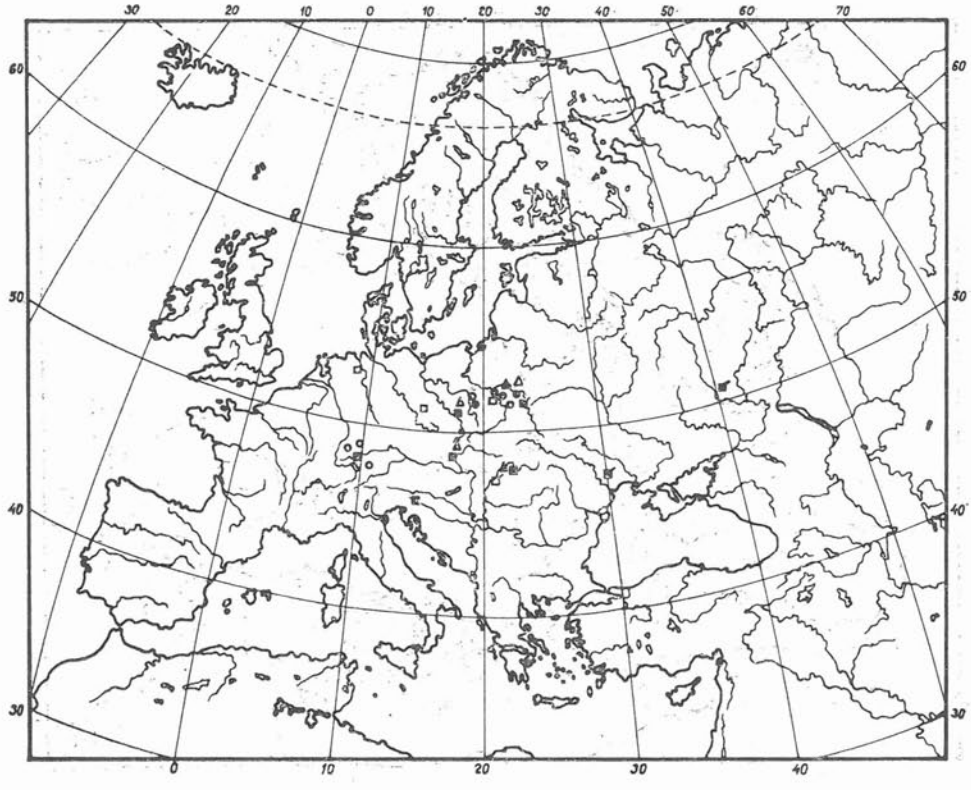

Fig. 5 *Dicrostonyx* sp.

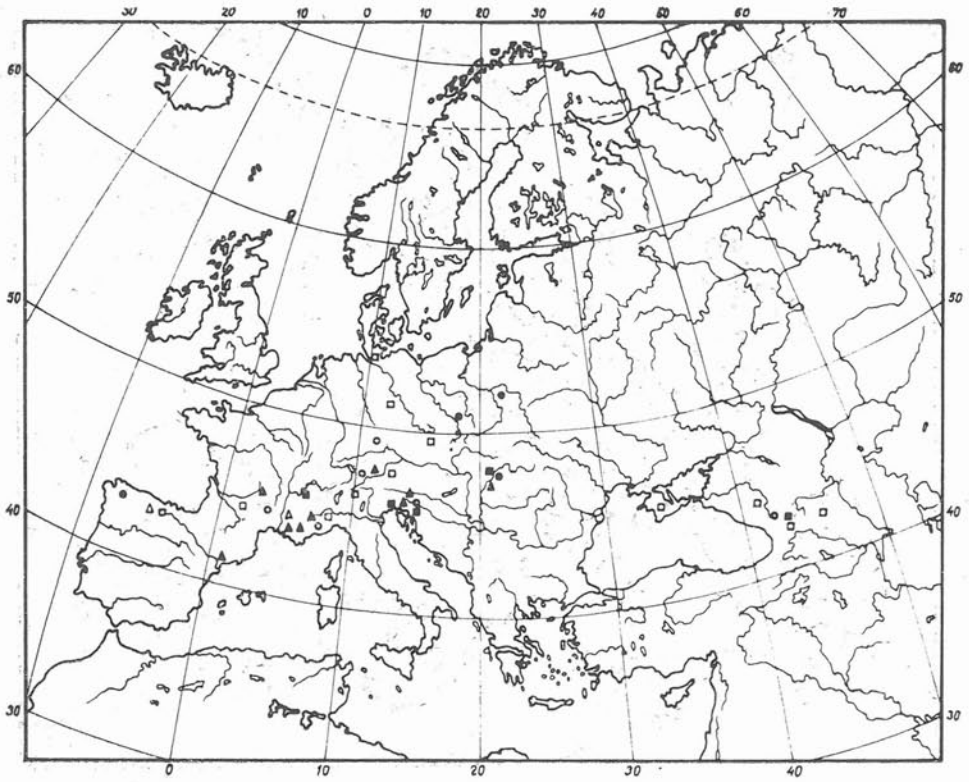

Fig. 6 *Lynx lynx*

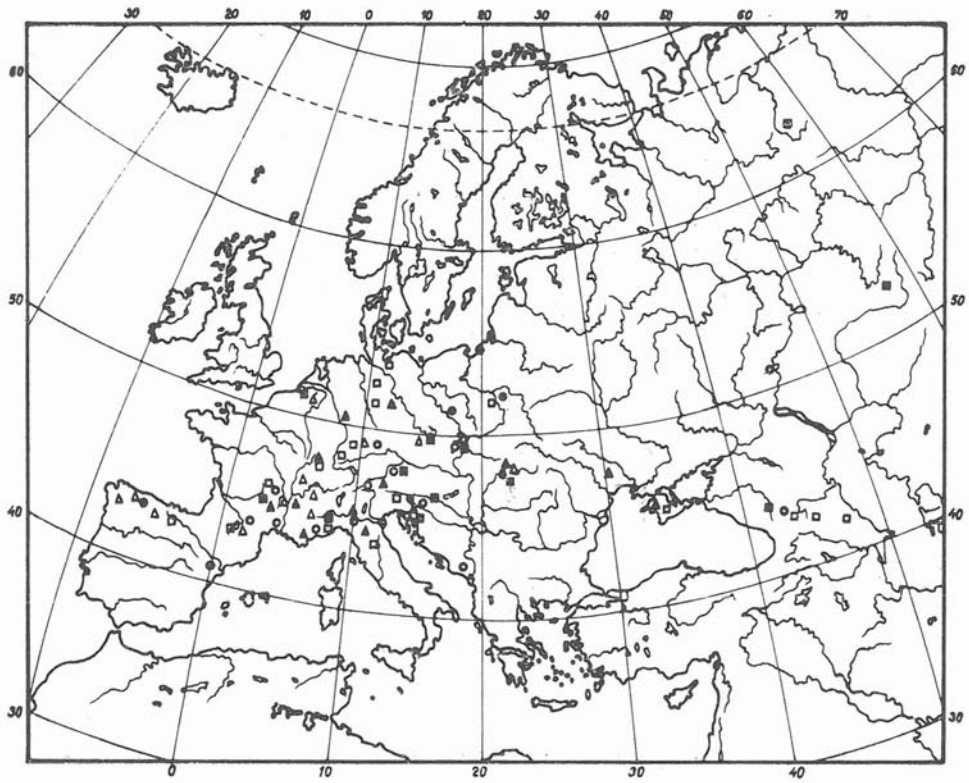

Fig. 7 *Vulpes vulpes*

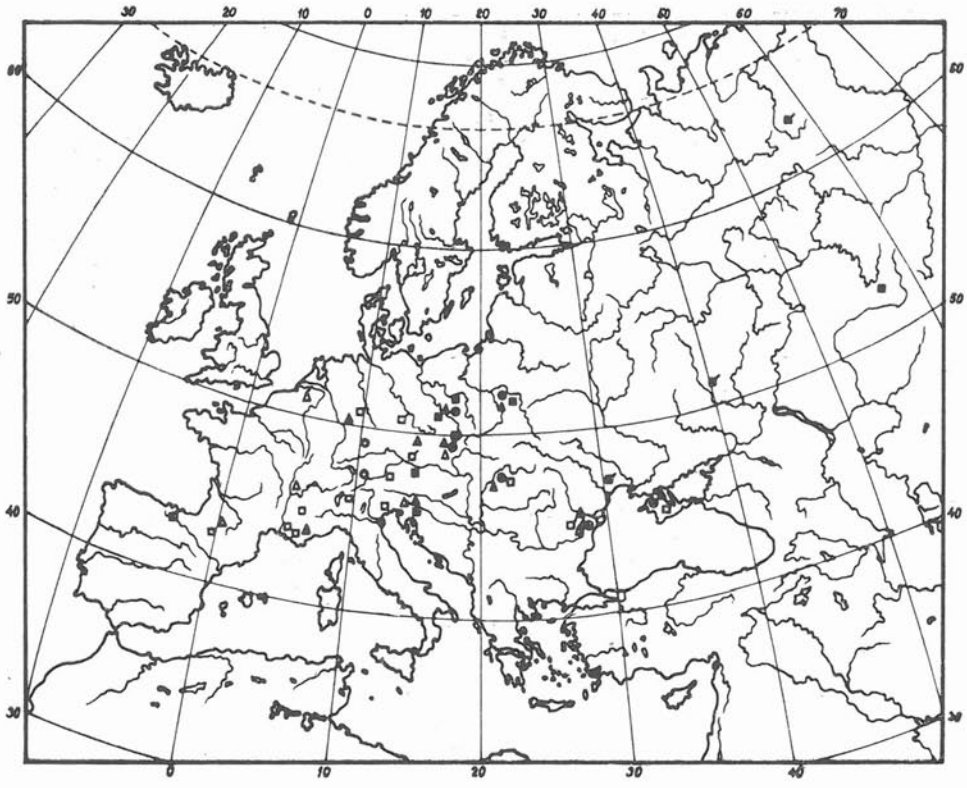

Fig. 8 *Alopex lagopus*

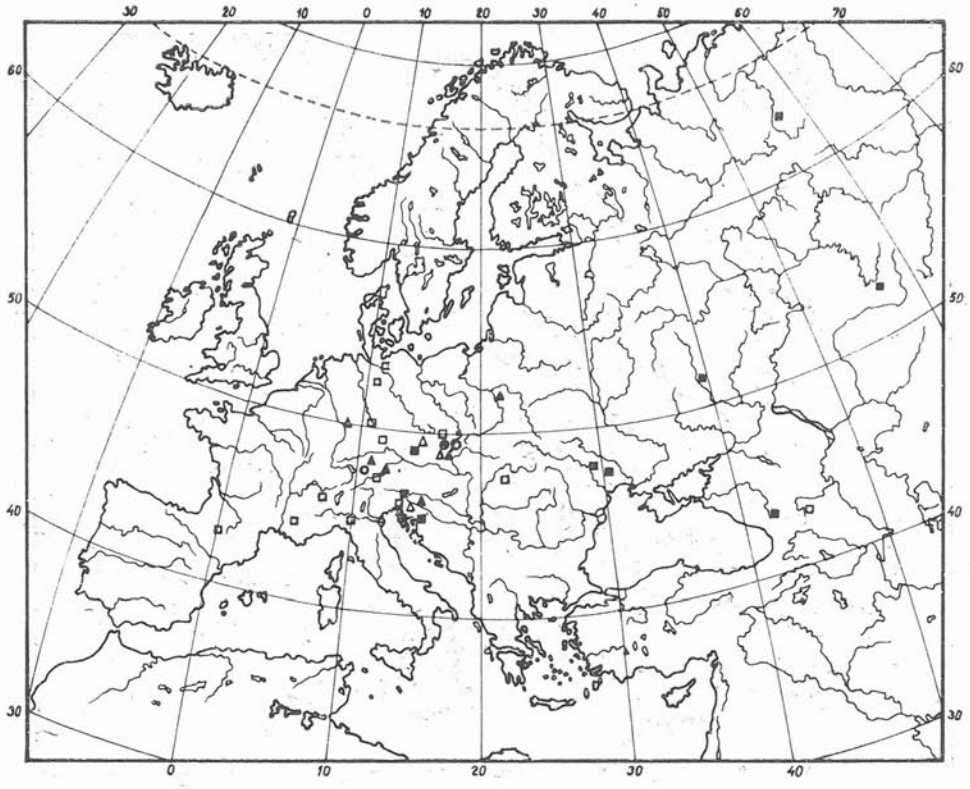

Fig. 9 *Gulo gulo*

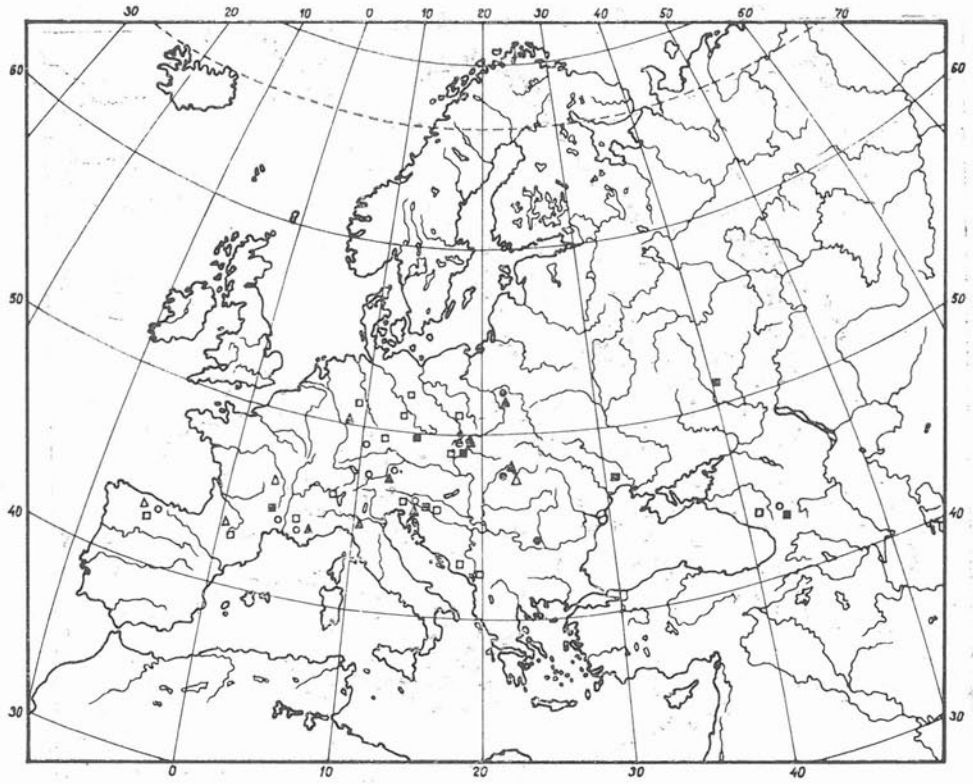

Fig. 10 *Ursus arctos, Ursus priscus*

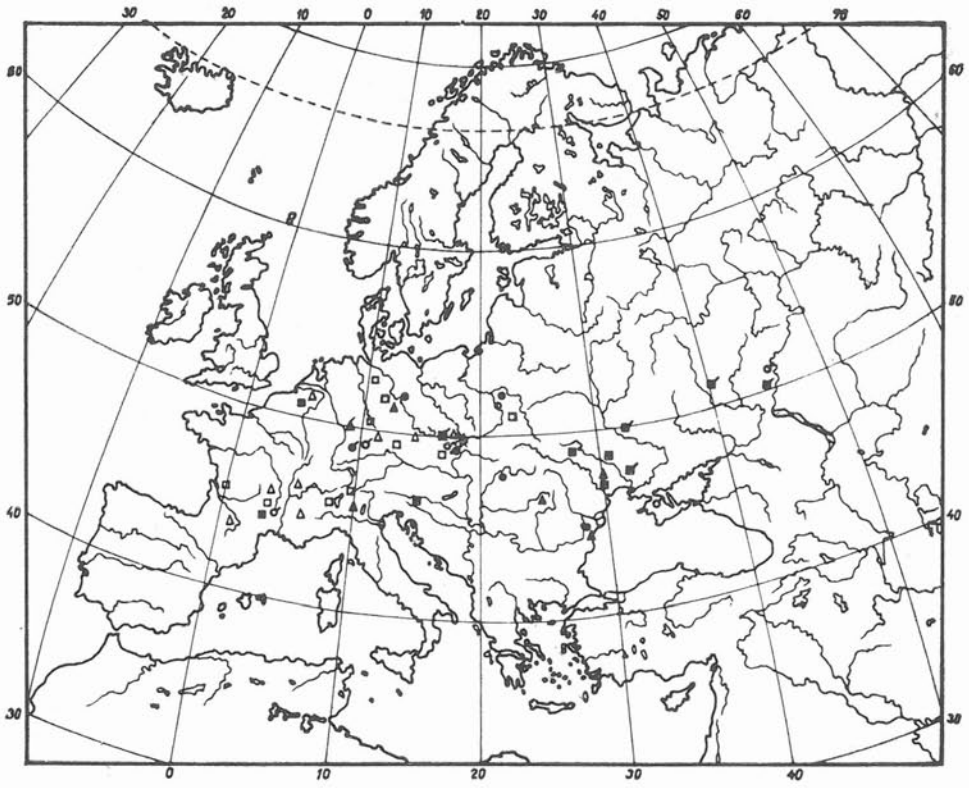

Fig. 11 *Mammonteus primigenius*

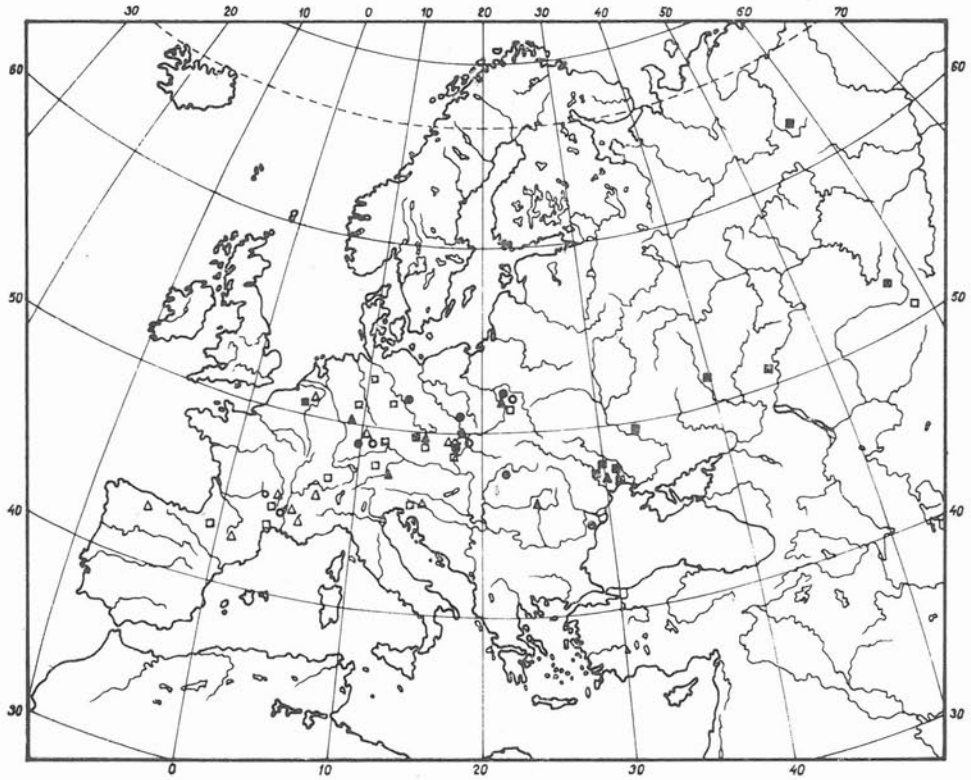

Fig. 12 *Coelodonta antiquitatis*

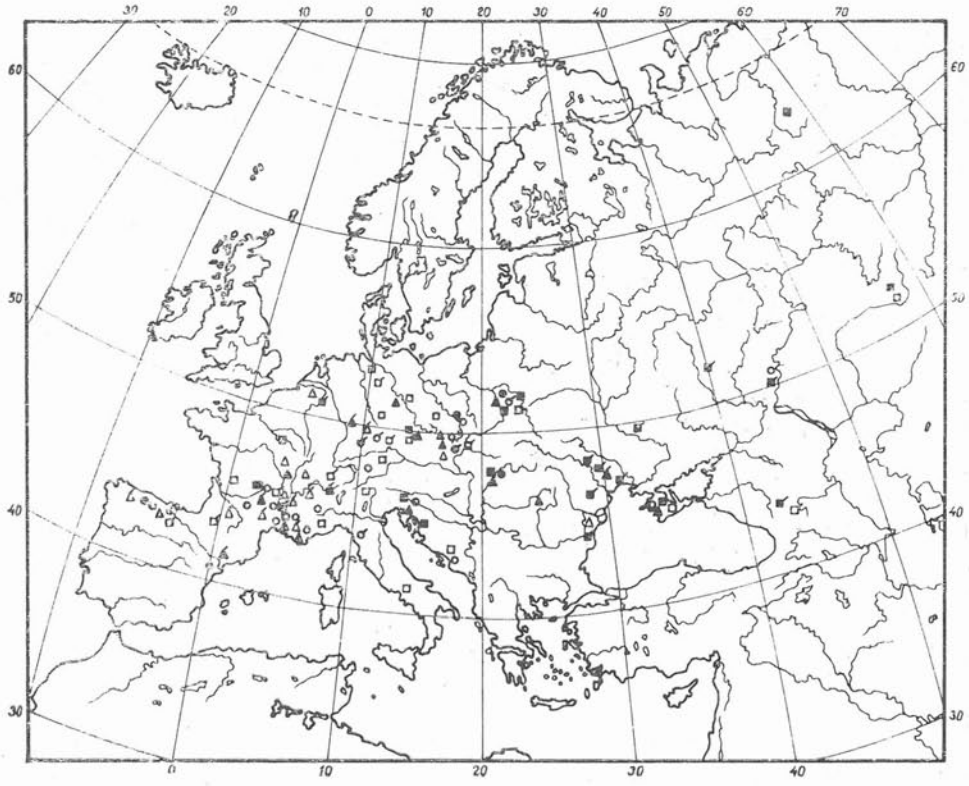

Fig. 13 *Equus* sp.

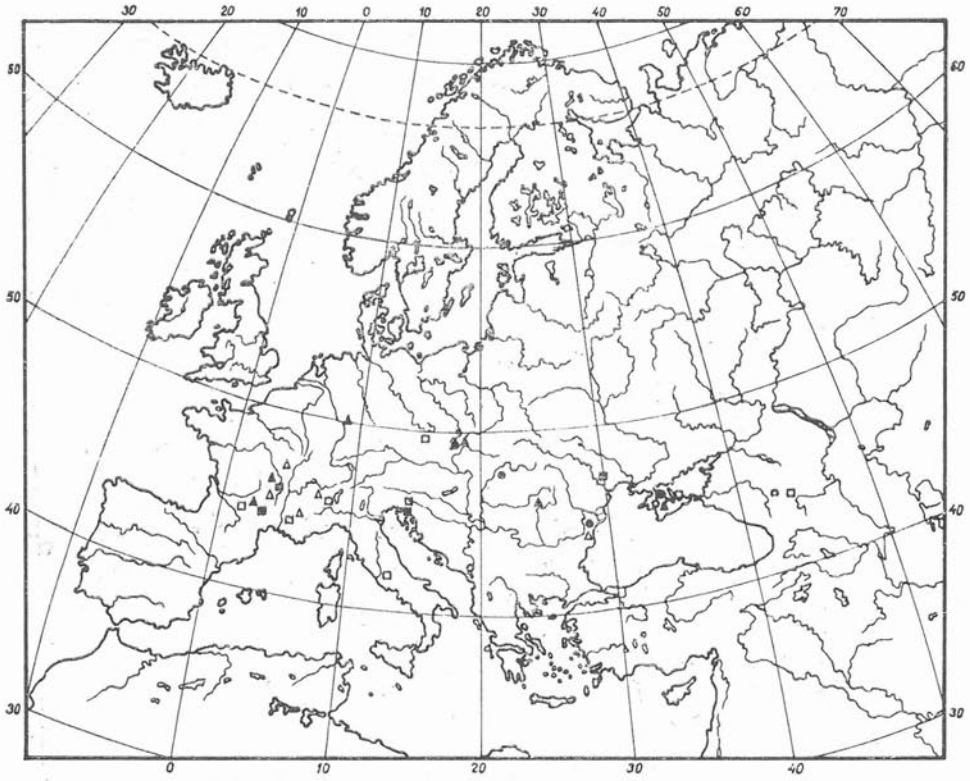

Fig. 14 *Equus (Asinus) hydruntinus*

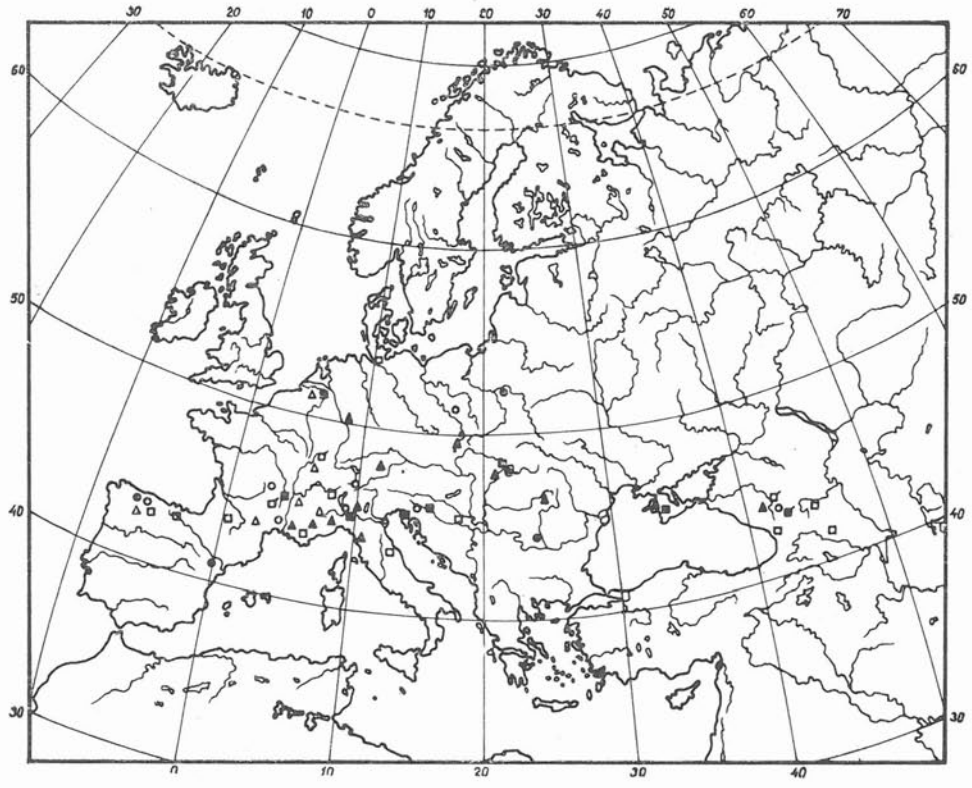

Fig. 15 *Sus scrofa*

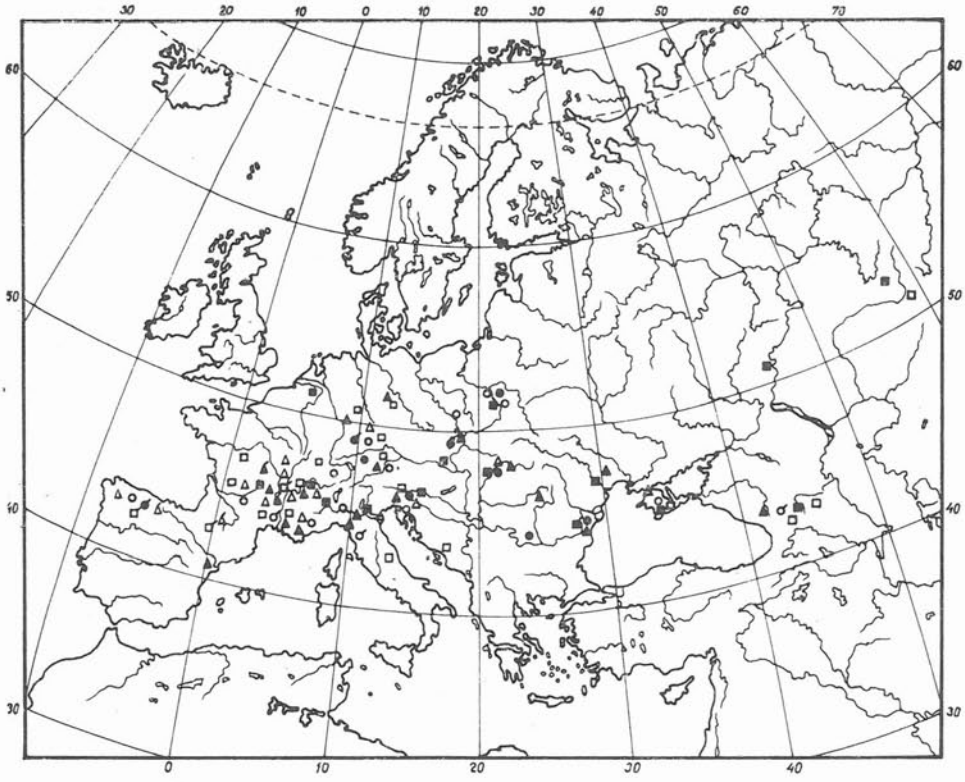

Fig. 16 *Cervus elaphus*

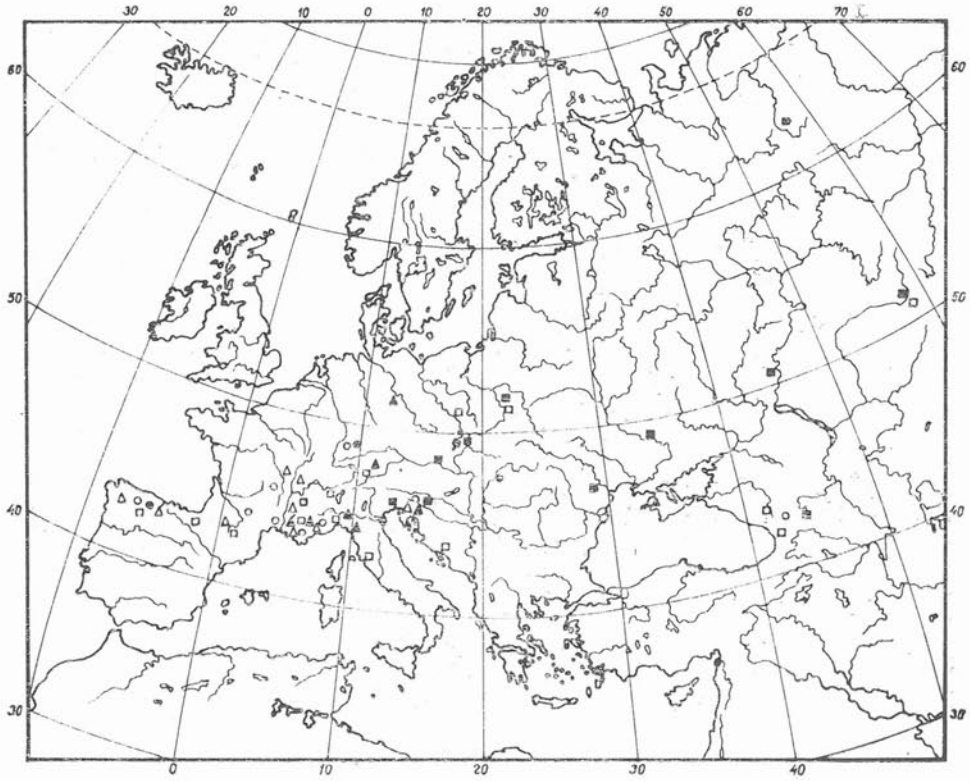

Fig. 17 *Capreolus capreolus*

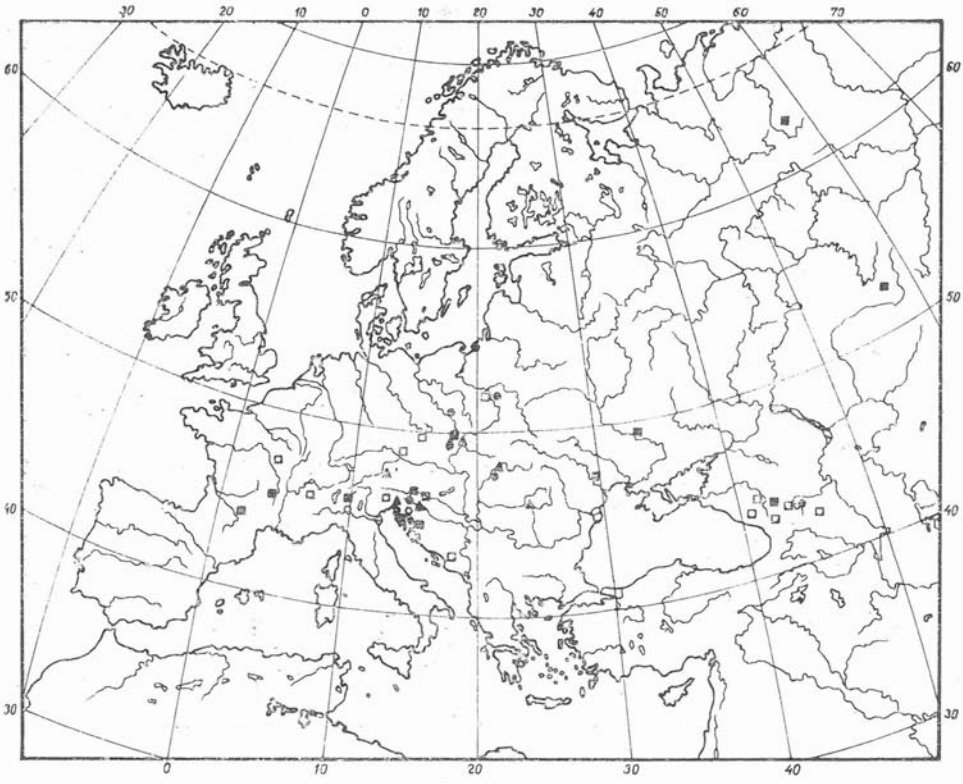

Fig. 18 *Alces alces*

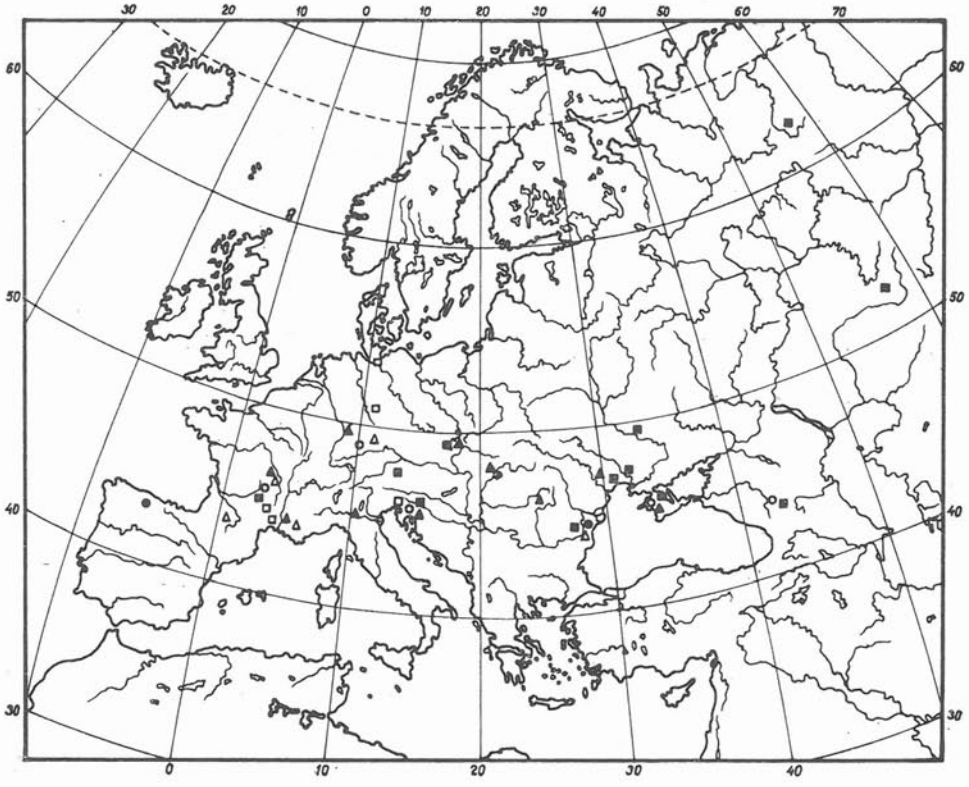

Fig. 19 *Megaloceros giganteus*

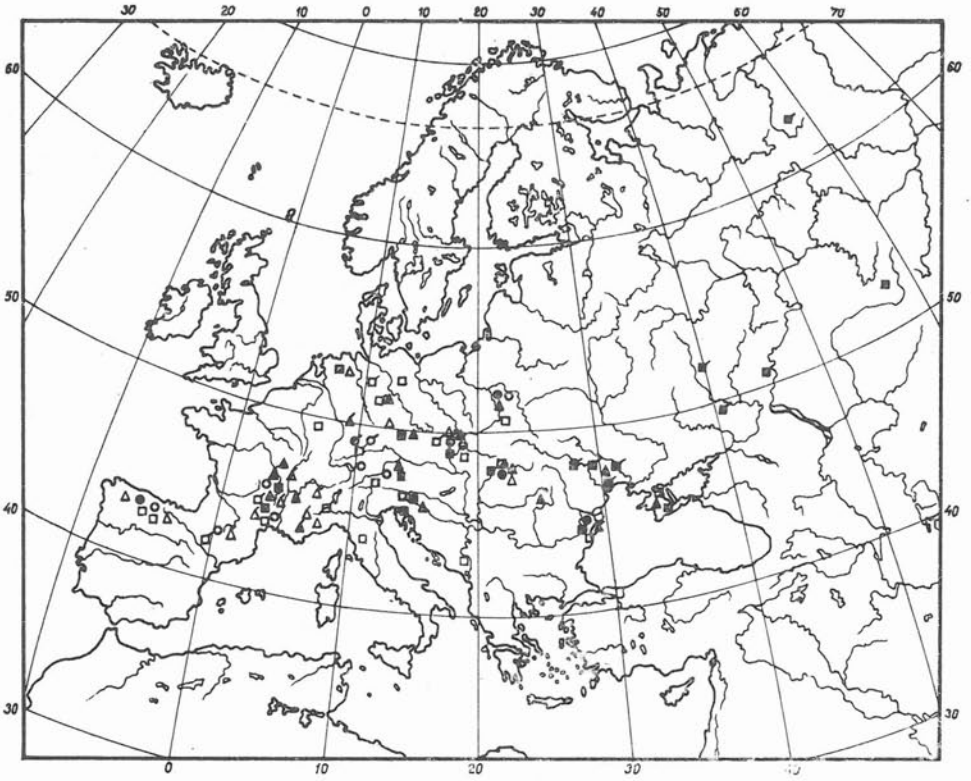

Fig. 20 *Rangifer tarandus*

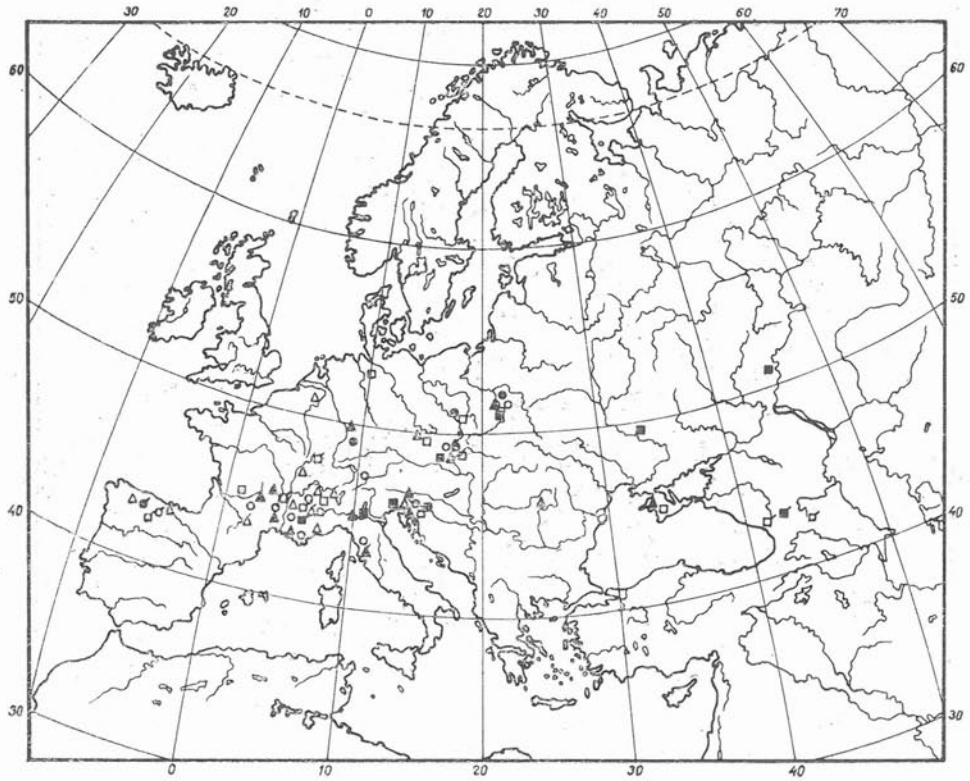

Fig. 21 *Bos primigenius*

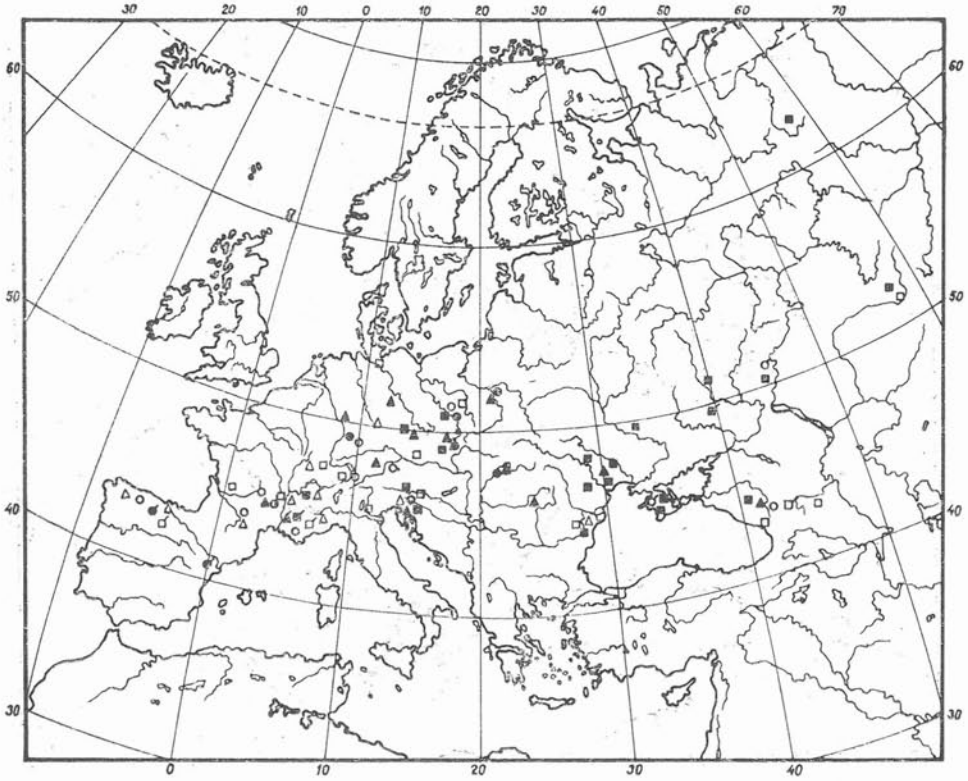

Fig. 22 *Bison priscus*

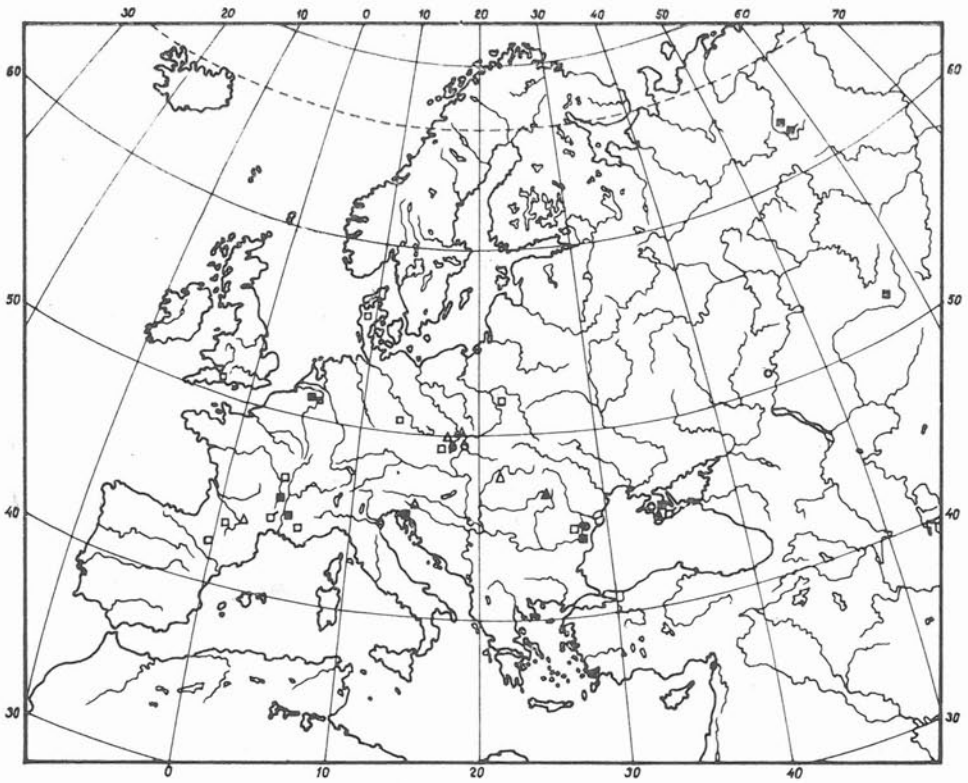

Fig. 23 *Saiga tatarica*

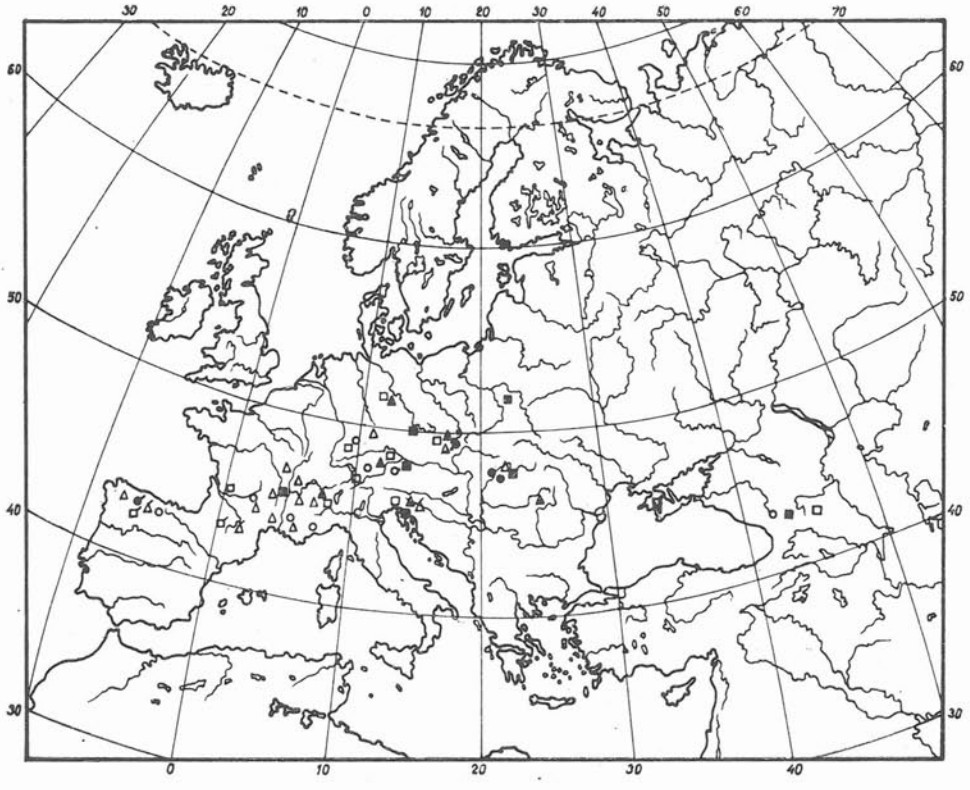

Fig. 24 *Rupicapra rupicapra*

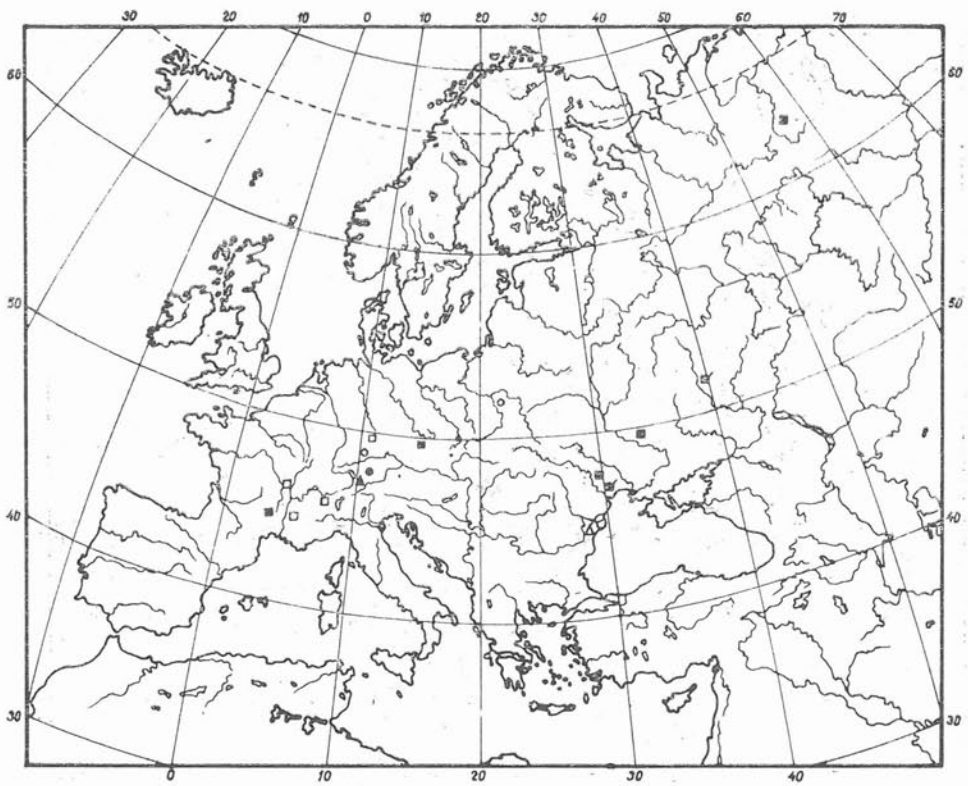

Fig. 25 *Ovibos moschatus*

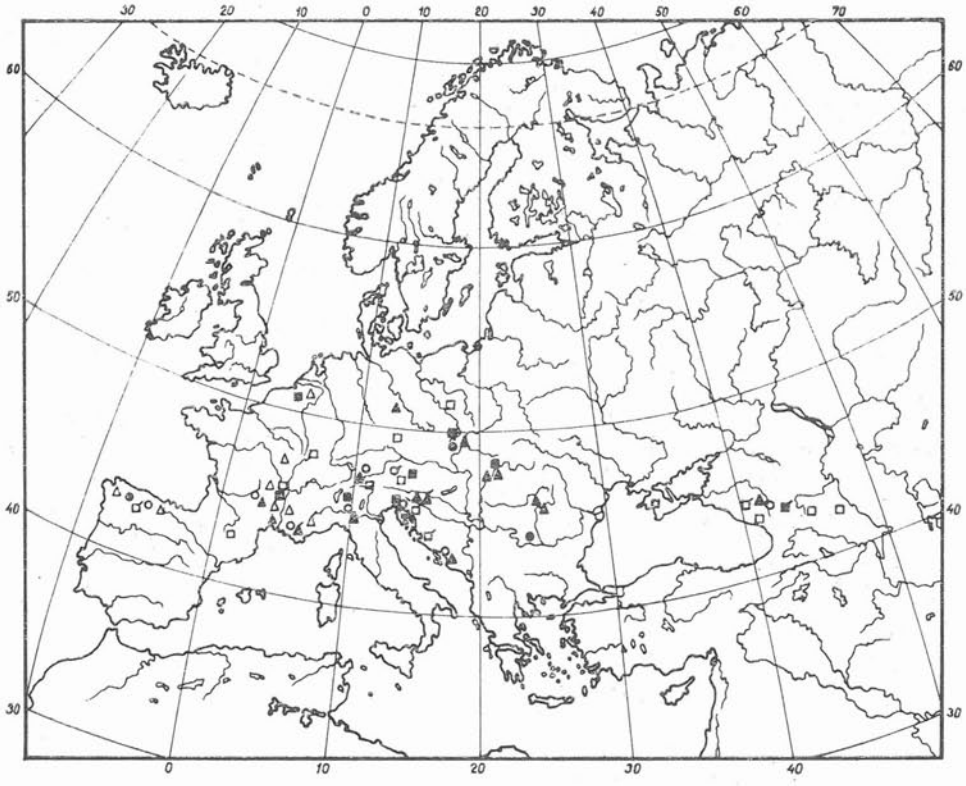

Fig. 26 *Capra ibex, Capra pyrenaica, Capra aegagrus*

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RUDOLF MUSIL

PALEOBIOGRAFIE TERESTICKÝCH SPOLEČENSTEV V EVROPĚ BĚHEM POSLEDNÍHO CLACIÁLU

Když jsem zpracovával monografii o jeskynních medvědech z oblasti celé Evropy (Musil 1980, 1982), shromáždil jsem veškerou mně dostupnou literaturu ze všech evropských států. Jednotlivé články pojednávaly nejen o jeskynních medvědech, ale podávaly i přehled celých faunistických společenstev, mnohdy i velmi detailně a po jednotlivých časově přesně zařazených vrstvách. Z tohoto celkového přehledu, který mám k dispozici, vznikla pak moje snaha podat v této práci vývoj faunistických společenstev Evropy.

Jako nejvhodnější se mně jevilo omezit se pouze na poslední glaciál, a to z toho důvodu, že toto období je nejhojněji zastoupeno nálezy, je po všech stránkách nejlépe známé a vykazuje celou řadu klimatických oscilací. Předchází také bezprostředně holocénu, tedy období, ve kterém se definitivně formovala naše dnešní fauna a již jen z tohoto hlediska je to proto období nesmírně důležité.

Původně jsem chtěl oblast celé Evropy rozdělit rovnoměrně do jednotlivých provincií a tyto zpracovávat samostatně. Již na samém počátku však bylo zřejmé, že to nebude dost dobře možné. Je tomu tak proto, že naleziště fosilní fauny nejsou rozprostřena stejnoměrně, ale koncentrují se pouze do určitých oblastí. Tím pak vznikají jednak místa s velkou kvantitou nálezů, jednak plochy, kde jsou nálezy pouze ojedinělé, případně zcela chybí. K tomu přistupuje samozřejmě i stupeň prozkoumanosti jednotlivých oblastí.

Z výše uvedených důvodů jsem proto vyčlenil oblasti s větším množstvím lokalit a zhruba ve stejnou dobu se stejnými klimatickými podmínkami. Do ostatních okolních ploch je možné pak závěry obecně interpretovat. Jednotlivé samostatně zpracovávané oblasti od západu na východ jsou pak tyto:

Oblast 1 severní část Pyrenejského poloostrova (mimo Pyreneje, převážně sz. část)
2 Pyreneje a jejich podhůří
3 jižní a střední Francie
4 severní a střední část Itálie a Jugoslávie při pobřeží Jaderského moře
5 Alpy a jejich rozsáhlé předhůří
6 jižní část BRD
7 střední Německo (BRD a DDR)
8 severní část BRD, Jutský poloostrov a jeho jižnější okolí
9 oblast Belgie
10 Československo, hlavně Morava, méně Čechy a Slovensko
11 Polsko, převážně jeho střední a jižní polovina
12 Panonská nížina, hlavně její severní část
13 vnitrozemí Rumunska
14 okolí dunajské delty
15 oblast kolem řeky Dněstr (SSSR)
16 oblast jižně od města Kyjev (SSSR)
17 poloostrov Krym (SSSR)
18 oblast mezi řekou Don a Volha (SSSR)
19 Kavkaz se svým podhůřím
20 jižní část pohoří Jižní Ural
21 severní tok řeky Pečory (Severní Ural)

Tyto oblasti vytyčené hlavně z hlediska koncentrace lokalit tvoří tedy opěrnou kostru k řešení problematiky vývoje společenstev Evropy během würmu.

V práci je proveden časový rozbor faunistických společenstev jednotlivých oblastí s paleoekologickým vyhodnocením a s uvedením dominantních druhů. Tohoto vyhodnocení je použito pro rekonstrukci klimatu a rostlinného krytu a jednotlivé oblasti jsou pak ve stejných časových úsecích vzájemně srovnávány.

V další části je pak proveden rozbor jednotlivých druhů z hlediska jejich rozšíření, jejich migrací a kvantity zastoupení.

Poslední kapitola pojednává o vývoji celého faunistického společenstva během posledního glaciálu ve studované oblasti, se závěry týkajícími se dalšího studia. Rozebírá základní faktory tehdejšího prostředí, ekologické požadavky jednotlivých druhů a na tomto základě rozděluje studovanou oblast do jednotlivých bioprovincií a biomů würmu.

Rozbor společenstev jednotlivých časových úseků ukazuje na komplikovanost jejich vývoje, na to, že většina druhů není ani termofilních nebo kryofilních a ani stenotermních, ale spíše eurytermních. Proto naše představy o některých současných, ale hlavně vymřelých zvířectvech by bylo nutné v tomto směru poněkud pozměnit.

Změny makroklimatu würmu jsou v obecné rovině dnes dobře známé. I když jsou z hlediska vývoje společenstev důležité, přesto mnohem důležitější je mezoklima jednotlivých menších území. Toto místní klima je totiž hlavně v prostorách střední Evropy velmi silně diferencované. Důsledkem toho je, že v tomto areálu je nutné z hlediska biostratigrafie přikročit k vytváření lokálních stratigrafických schémat a teprve na tomto podkladě srovnávat lokality jednotlivých území.

Celá Evropa měla v posledním glaciálu biom, který v tomto rozsahu dnes neexistuje, a to biom střídajících se lesů a stepí, který končí nástupem holocénu. Rozbor fauny přitom ukazuje, že vazba většiny druhů existovala spíše na tento rostlinný kryt než na průměrnou roční teplotu, že tedy aridita nebo oceanita klimatu byla mnohdy důležitější než vlastní snížení nebo zvýšení průměrné roční teploty. Rozdíly v teplotě nebyly tedy u mnohých druhů savců hlavním faktorem jejich rozšíření ve studované oblasti. Zároveň se ukazuje, že primární teplotní efekt nebyl vždy vyvolán pouze stupněm šířky v dané oblasti.

Závěrem je možné říci, že poslední glaciál právě ze všech výše uvedených důvodů měl faunistická společenstva počtem druhů mnohem bohatší než tomu kdykoliv bylo v holocénu, který znamená jejich podstatné ochuzení. A hlavní úlohu v tomto ochuzení — aspoň zpočátku — nehraje přítomnost člověka. Z tohoto pohledu se nám pak toto období jeví pro existenci fauny mnohem optimálnější, než se někdy hlavně pod vlivem čistě geologických poznatků dosud uvažovalo.

Table 2. Eastern and Central Europe (bioprovince A) in the course of Würm. Abbreviations in the individual biomes denote the quantitative representation of the individual ecological mammal groups.

Biomes	5. the Alps	6. the southern part of the FRG	7. Central Germany
End of W_3	in the same ratio tundra, steppe, taiga and central European forest cold climate	steppe and taiga dominating, central European forest receding climate very cold	tundra and steppe prevailing, little taiga and central European forest. cold climate.
$W_{2/3}$—W_3	steppe prevailing, others balanced mildly cold climate		
W_2		abundant steppe elements, others balanced cold climate	
$W_{1/2}$	forest and taiga elements prevailing, taiga subordinate. warm climate		central European forest, taiga, tundra, steppe. cold climate.
W_1	animals of all environments. *Sus* and *Felis silvestris* finishing.	steppe and tundra elements, central European forest. mildly cold climate	
Early Würm		steppe and tundra elements prevailing very cold climate	

Tab. 2 (continued)

8. Northern part of FRG, Jutland	9. Belgium	10. Czechoslovakia
steppe dominant, others balanced. cold climate.		steppe dominant others in the same ratio. cold climate.
	steppe prevailing, much tundra and central European forest mildly cold climate.	steppe, tundra, taiga prevailing. very cold climate.
	roughly balanced, abundant central European forest, steppe + tundra, steppe + forest. mildly cold climate.	steppe and tundra dominating, others in the background. extremely cold climate.
		tundra, steppe, taiga prevailing. mildly cold climate.
		steppe and tundra elements. very cold climate.
		taiga, tundra, steppe. very cold climate.

11. Poland	12. Hungary	13. Rumania
tundra dominating, other elements little represented.	tundra dominating, others little represented, central European forest missing.	
cold climate.	climate extremely cold.	
everything balanced.	central European forest, steppe, others suppressed.	steppe.
mildly cold climate.	warm climate.	cold climate.
	central European forest and taiga dominate, steppe very frequent.	
	warm climate.	
tundra and steppe dominant, elements of central European forest missing altogether.	tundra, steppe, taiga, weak central European forest.	steppe, taiga dominant, weak central European forest.
very cold climate.	mildly cold climate.	warm climate.
steppe and tundra elements dominate.		
very cold climate.		warm climate.
taiga, tundra, steppe.	taiga, central European forest, steppe.	
mildly cold climate.	mildly warm climate.	

Tab. 2 (continued)

14. the Danube delta	15. the Dniester	16. south of Kiev
steppe and tundra dominate, central European forest suppressed. extremely cold climate.		
steppe dominant, others weakly represented. very cold climate.	steppe dominant, less tundra and taiga. extremely cold climate.	steppe dominant, tundra and taiga abundant. extremely cold climate.
steppe dominant, tundra and taiga abundant. very cold climate.		
	clean-cut steppe. cold climate.	
steppe elements prevailing. very cold climate.		

18. between the Don and the Volga	20. Southern part of the South Urals	21. Upper stretch of the Pechora
	all elements. cold climate.	
steppe dominant, other elements abundant. cold climate.	steppe dominant, other elements less, but also central European forest. mildly cold climate.	steppe and tundra dominant, other elements less.
open steppe.		

Table 1: Percentual Representation of the Individual Ecological Groups of Animals in the Individual Regions during the Last Glacial

	Regions	Late Glacial W_3				Substage $W_{2/3}$ W_3				Substage W_2				Substage $W_{1/2}$				Substage W_1				Early Würm			
		●	○	▲	■	●	○	▲	■	●	○	▲	■	●	○	▲	■	●	○	▲	■	●	○	▲	■
1	northern part of Iberian Peninsula	42	27	19	11,5					41	25	22	12,5					45	30	20	5	38	31	23	8
2	the Pyrenees	31	23	27	19					28,5	21	32	18												
3	France	25	25	32,5	17,5	26	27	33	11	36	25	28	11	44	25	25	6	44	23,5	23,5	9				
4	Italy, Yugoslavia	28	30,5	30,5	11	27	34	25	14	21	31	31	17	37	26	26	11	48	26	22,5	3	33	33	25	8
5	the Alps	32,5	21	25,5	21	21	26	37	16					27	27	30	16	30	27	23	13				
6	southern FRG	17	21	38	24					16	21	42	21					26	18	34	21	15	23	38	23
7	central Germany	17	17	32	34									23	23	33	20								
8	northern part of FRG, Jutland	22,5	22,5	32	22,5																				
9	Belgium					23,5	18	35	23,5	25	20	30	25												
10	CSSR	24	22	32	22	19	24	32	24	9	13	53	42	26	26	33	14	19	19	37,5	25	20	27	33	20
11	Poland	25	18	36	21	25	20	30	25					13	22	35	30	16	16	40	28	25	25	28	22
12	Hungary	0	20	30	50	33	17	33	17	27	27	33	13	24	21	36	18					31	23	31	14
13	Rumania					0	0	80	20					28	24	36	12								
14	the Danube delta	0	14	57	28,5	8	25	50	17	7	21	50	21									20	25	35	20
15	the Dniester					12	24	39	24					19	25	37,5	19								
16	region south of Kiev					10,5	21	47	21																
17	the Crimea	24	28	40	8	17	25	50	8					22	22	39	17	18	18	54,5	9				
18	region between the Don and the Volga					27	18	36	18																
19	the Caucasus	43	27	23	7	48	35	13	4									43	22	26	9				
20	southern part of the South Urals	22	11	44	22	16	25	41	19																
21	northern part of the Pechora River					18,5	18,5	31	26																

—— very warm climate

– – – warm climate

..... cold climate

–.–.– mildly cold climate

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