Palaeoenvironment at Gravettian Sites in Central Europe with emphasis on Moravia (Czech Republic)

Die Paläoumwelt mitteleuropäischer Gravettien-Fundstellen mit Schwerpunkt auf Mähren (Tschechische Republik)

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Abstract - This paper presents a synthesis of palaeoenvironmental conditions during the Gravettian with an emphasis on Moravia in the Czech Republic, where there is a maximum concentration and density of Gravettian sites (> 50, Oliva 2007) at a highly advanced cultural level. The basis for the synthesis is provided by an analysis of the physical environment, including changes of vegetation cover and animal communities. Alongside global and regional perspectives, the local viewpoint is also presented. Palaeoenvironmental differences between different regions of the eastern part of central Europe are discussed and the importance of faunal migration pathways for the organization of human sites is demonstrated.

Zusammenfassung - *Dieser Beitrag stellt eine Synthese der Paläoumwelt-Bedingungen während des Gravettien mit einem Schwerpunkt auf Mähren in der Tschechischen Republik vor, wo sich eine maximale Konzentration und Dichte der Gravettien-Fundstellen (> 50, Oliva 2007) auf einer sehr anspruchsvollen kulturellen Ebene befindet. Die Basis für die Synthese wird durch eine Analyse der physischen Umwelt, einschließlich der Änderungen der Vegetation- und Tiergemeinschaften zur Verfügung gestellt. Neben einer globalen und regionalen Perspektive wird auch die lokale Ansicht vorgestellt. Unterschiede in der Paläoumwelt zwischen den verschiedenen Regionen des östlichen Teils von Mitteleuropa werden diskutiert und die Bedeutung der Wanderungen der Tiere für die damaligen Menschen wird aufgezeigt.*

Keywords - Central Europe, Gravettian sites, vegetation cover, faunal community, climate, Palaeoenvironment
Mitteleuropa, Gravettien-Fundstellen, Vegetations- und Faunengemeinschaften, Klima, Paläoumwelt

Introduction

The environment and changes to it are the result of an interaction of many factors. From the perspective of faunal communities, the most important of these are plant cover, temperature and, primarily, precipitation. The environment determines the quantity and quality of all factors necessary for the existence of biota and humans. The environment is not constant, but rather changes through time.

The environment may be defined on the basis of several criteria, but we recognize two principal interconnected groups of factors. In the first place, there are physical factors such as landscape topography, the existence of watercourses, the amount of precipitation, processes of accumulation and denudation, and temperature conditions, seen from both regional and local perspectives. Analysis of the physical factors is followed by that of biotic factors, including the vegetation cover (with its dependent faunal communities) or the suitability of a region for particular species (e.g. biodiversity) in the sense of permanent residence (implying reproductive success) opposed to only temporary occupation.

The analysis of an environment requires a multidisciplinary approach because one discipline alone cannot explain highly complex environmental processes. Environmental analysis of different faunal assemblages has indicated very different conditions in both neighbouring and distant regions (Musil & Valoch 2005), demonstrating that only a synthesis of all available data might provide a complete story. The intensity of observed environmental changes may be tolerable for biota and the human population in one region, but not in another. By contrast, we consider the environmental impact of Palaeolithic people on the environment during the Gravettian to be negligible.

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Approaches to environmental analysis

Climatic models

There are numerous possible approaches to environmental analysis, which can be described by several models.

Global Climatic Model (GCM: 1st order changes)

This is the most common approach, which studies the whole of Europe, or at least its northern and central regions, as one entity. This characterisation of the environment is based on the study of marine sediments, changes in ocean water temperature (MIS stages) and also the behaviour of glaciers in Greenland and the Arctic. However, the acquired data are not and (of course) cannot be treated as completely identical for the various regions of Europe.

Regional Climatic Model (RCM: 2nd order changes, scale of 20 - 50 km)

Various physical factors, primarily oceanic impact with reference to longitude, temperature differences regarding latitude, altitude, wind direction, the amount of precipitation etc. form today and in the past have formed different climatic provinces. The boundaries of these provinces were not stable and have changed in the short term. When these changes became intense they caused large scale migrations of fauna and flora.

Local Climatic Model (LCM: 3rd order changes)

The highly differentiated topography of Europe, with mountains, upland zones and lowlands which create local environmental effects, is very conducive to changes of this order, although not only vertical zonation made an impact. Local differences between sites played a very important role, especially during cold periods, with sites being potentially characterized by extremely harsh or, in contrast, very favourable climatic conditions. Sites enjoying the latter conditions, which during cold phases were very unlike the global climatic pattern, functioned as local refuges for species of flora and fauna. They were of course also important for the human population which was supported mostly by hunting. Only at such sites do we find long-term human occupation.

The models introduced above are not necessarily entirely interrelated; the results of their application may not be mutually consistent and these should therefore be interpreted separately (Musil 2002a).

The principal role in long-term human existence and activity was played not only by the macroclimate, but primarily by the mesoclimate with its local environmental changes. These were the decisive factors for long-term survival of the human population because they impacted directly on the living conditions of the fauna and thus on conditions for hunting. Only under a favourable regime can we expect to find a persistent human presence.

Physical (abiotic) environment analysis

We will consider all possible factors which can be used for such an analysis. In theory these can include the temporal evolution of sites, analysis of lacustrine and fluvial sediments or fossil soils, processes of erosion and denudation, periglacial phenomena, the amount of precipitation, thickness of snow cover, the number of days with snow during the year, the direction, velocity and temperature of winds, the soil temperature, minimum and maximum atmospheric temperature extremes and average winter and summer temperatures. Unfortunately, most of these factors are unknown and thus not available for consideration in the region studied.

During glacial periods, Moravia was located between two regions covered by glaciers, the Alpine glacier and the continental glacier of northern Europe. Today we know that the northern European glacier existed during only a limited time period, the whole of northern Europe being without continuous ice cover from 33 - 25 ka BP (c. 35 - 27 ka calBP) until the LGM (Svendsen et al. 2004). The continental ice sheet had reached the northern shore of the Baltic Sea for the first time during MIS 4 and then developed for the second and final time during the LGM, when it extended far to the south into central Poland (Marks 2002) and Germany. During the remaining part of the Last Glacial the continental glacier covered only Scandinavia. During MIS 3, which is important for us, only the highest mountains in Norway were covered by mountain glaciers (van Andel et al. 2003). This situation had a strong impact on the climate at Moravia Gravettian sites.

The climate in Europe has always been influenced by two major gradients, running north-south and east-west respectively. In central Europe the north-south gradient is interrupted by mountain barriers running in a west-east direction, which divide the region climatically into two parts, the north and the south. The significance of these mountain chains is as a climatic barrier.

The palaeoclimate of the eastern part of central Europe was very different from the present day polar climate, which is influenced not only by high latitude, but also by low solar radiation and a lack of days with sunlight (only during 5 – 6 months). In the polar climate there are two types of environments, represented by the climate of the polar tundra and that of polar glaciers. In the case of the former, the warmest month has an average temperature of about 10 °C, with cold winters and short summers characterized by cloudy skies and precipitation. The average annual temperature is -12 °C. Evaporation is limited and the low temperature causes the formation of continuous permafrost and of large swamps during the summer months. The resulting vegetation comprises mosses and lichens, acid grasses, dwarf bushes and, sporadically, dwarf trees. This environment is very different from the conditions found at Gravettian sites in Moravia and the surrounding regions.

Aiello and Wheeler (2003) studied average summer and winter temperatures around Gravettian sites located in Moravia (Kůlna Cave, Milovice I, Dolní Věstonice I, Pavlov I, Předmostí and Petřkovice), Slovakia (Moravany-Lopata), Poland (Krakov-Spadzista) and Austria (Willendorf II). They showed that wind temperatures were relatively constant regardless of site location, with summer values at all sites within the range 7.6 °C to 9.5 °C and winter temperatures from -20.7 °C to -24 °C. These wind temperatures indicate that it was not latitude, but topography and the position of a site which played an important role.

Barron and colleagues (Barron et al. 2003) published results of a computer simulation of environmental conditions for the LGM (27 - 16 ka BP / c. 29 - 18 ka calBP). Their model is based on the principal role of the atmospheric circulation system in the control of glacial climate. During the LGM the position of the pressure minimum over the North Atlantic was similar to today. The zone of maximum pressure reaches from south-western Europe towards the north-west until 53° latitude and is the reason for a strong pressure gradient over the North Atlantic, causing low temperatures in the north of Europe. Another consequence is that central Europe was not influenced by the influx of cold air from the North Atlantic. Average summer temperatures during the LGM ranged from 8 °C to 12 °C and average winter values were between -8 °C and -20 °C. We consider these temperature ranges as valid, in spite of somewhat different temperature estimates due to winds. In central Europe there was a continental climate during MIS 3 with large differences between summer and winter temperatures. This, of course, had an impact on vegetation and fauna. There were significant differences in vegetation cover between valleys containing streams and dry undulating uplands in their neighbourhood. This also implies an important differentiation of vegetation within a relatively small area.

An important factor for animal life is the presence and thickness of snow. Deep snow cover not only limited migration of both animals and humans, but also had an impact on the accessibility of feeding for herbivores. From western Europe towards central Europe, the number of days with snow cover decreased down to between two and three months with the increasing aridity of climate and the structure of animal populations at all Gravettian sites confirms a minimum thickness of snow over the winter months.

Loess sequences furnish an excellent archive for study of regional climatic changes due to excellent recent dating methods and micromorphological analyses. Loess is found from northwestern Europe (northwestern France and Belgium) to central Europe, the Ukraine and Russia. Analyses of gastropods from loess sequences at Gravettian sites confirm a mostly cold and dry climate (loess steppe) or a climate with cold winters and hot summers (warm loess steppe).

Following the relatively warm MIS 3, with its large climatic oscillations, there was a gradual cooling into the LGM with resulting formation of continuous permafrost in Great Britain, northern Belgium, the Netherlands, northern Germany and northern Poland. These regions were very different from the eastern part of central Europe, i.e. southern Poland, Moravia, Austria, Slovakia and Hungary. Although at lower altitudes there was no continuous permafrost in Moravia, even during the LGM, there typically occurred local permafrost episodes of variable magnitude, depending not only on the temperature but also on the type of substrate. We agree with Czudek (1997), who assumes permafrost formation during the LGM but not in the preceding Gravettian. After 20 ka BP (c. 21 ka calBP) the southern margin of the continental ice sheet retreated towards the north and in the period 17 - 15 ka BP (c. 18 - 15 ka calBP) there was only a narrow glaciated strip across the most northern parts of Germany and Poland (Barron et al. 2003).

Formation of permafrost occurs only at an average annual temperature below 0° C. This becomes possible where frozen soil does not thaw completely over two or more years. The criterion for identifying permafrost presence is the occurrence of frost wedge casts (Weinberger 1954). There is a difference between regions with discontinuous and continuous permafrost. Continuous permafrost, which covers about 90 % of a total area, could have been present in Moravia mainly at high altitudes. Both types of permafrost depend not only on temperature and length of summer, but also on the soil lithology and the thickness of snow cover.

Altitudinal factors

Central Europe is divided into two parts by mountain ranges running from west to east. In cold stages the passage and migration of fauna were therefore possible above all in western or eastern Europe, whereas within central Europe movement from north to south was chiefly through Moravia, because only there does there exist a corridor connecting the lowlands of northern Europe and those around the Danube.

The topography of Moravia is also very variable, with an alternation of lowlands, highlands and relatively high mountains over short distances. The flood plain of the Morava River is surrounded in the west by the Českomoravská Highlands, in the northwest by the Oderské Hills and the Nízký and Vysoký Jeseník Mountains (1 400 m a.s.l.) and in the east by the Karpaty and Beskydy Mountains. (1 300 m a.s.l.). This mixed topography presents an exceptional opportunity for the study of environmental changes.

Climate archives in sediments

Soil is a basic abiotic foundation for the vegetation and forms a link between the biotic and abiotic realms. There are numerous articles describing sediments in Moravia.

Gravettian layers in Předmostí, Dolní Věstonice (Smolíková 1991) and Pavlov occur at the base of the upper loess blanket, which directly underlies Holocene sediments. According to Žebera (1962) the Gravettian cultural layers at Předmostí are located in the basal solifluction horizon A and in a basal horizon with typical loess Aa (Fig. 1). Other authors, for example Svoboda, have described two cultural layers with a loess interlayer between them (Svoboda 2001b; 2008 on the basis of Maška´s diary).

The alternation of typical loess with solifluction horizons indicates short-term periods of precipitation during the deposition of the last loess cover, when the loess was not subsequently blown away. This means that Gravettian people at Předmostí did not live in a stable climate and experienced at least two climatic oscillations, firstly an arid climate with the formation of loess and then a more humid period with greater precipitation, solifluction and cooling.

The impact of precipitation on sediments of the Gravettian horizon at Jarošov II, south of Předmostí, is even more pronounced. In strata under the cultural horizon are found concretions of $CaCO_3$, often in the form of carbonate ortstein and crusts on the surface of many bones. This indicates high precipitation following abandonment of the site, which was probably typical for the beginning of the LGM (Musil 2002a).

In the case of southern Moravia, precipitation did not reach the same intensity as that seen at Předmostí. The most recent loess strata at Dolní Věstonice comprise several initial soils (pseudogleys) (Klíma 1994; 1995; Svoboda 2001a). Above the Gravettian strata there follow seven pseudogley horizons and the same number of solifluction horizons. These pseudogley horizons were formed during periods of high precipitation alternating with arid periods characterized by aeolian loess transport. The solifluction horizons of Předmostí and the pseudogley soils of southern Moravia are replaced at contemporary sites in Slovakia by weakly decalcified horizons (for example at Vlčkovice, south-western Slovakia). This means that in the studied area we can distinguish several contemporary sub-regions (RCM - Regional Climatic Models) on the basis of precipitation: the maximum is found in northern and central Moravia, with lower values in the south of Moravia and the minimum in the valleys of Slovakia, which open to the Pannonian Basin. This also means that there was a different climatic regime at the various Gravettian sites.

Loess and pseudogley sequences indicate the cyclic character of the climate. Assuming that depositional rates of loess sequences of about 1 500 years correspond to 1 563 ± 563 year cycles identified in the Greenland ice cap and in marine sediments (Rousseau et al. 2002), this indicates a global validity for arid and humid oscillations of variable intensities during Gravettian. This also applies to sites in other countries, such as the German site of Nussloch, with a loess sequence containing eight pseudogley horizons for the period 31 - 19 ka BP (c. 34 - 22 ka calBP).

The abandonment of the Předmostí site is linked to the beginning of a colder period, i.e. to the onset of the LGM. While climatic changes cannot be the only factor responsible for the decline of Gravettian sites, it is possible that they exacerbated other factors and contributed to the Gravettian decline.

Holocene soil	
Ca	Upper horizon with typical aeolian loess
C	Upper solifluction horizon in loess
Ba	Middle horizon with typical aeolian loess
B	Middle solifluction horizon in loess
Aa	Basal horizon with typical aeolian loess
A	Basal solifluction horizon in loess
Interstadial soil	

Fig. 1. Gravettian cultural layers at Předmostí are located in the basal solifluction horizon A and in the basal horizon with typical loess Aa (Žebera 1962). Other authors described two cultural layers (A and B) separated by loess. The alternation of Gravettian cultural layers indicates in any case short-term climatic variations during sedimentation of the last loess cover layer.

Abb. 1. *Gravettien Schichten in Předmostí befinden sich im basalen Solifluktions-Horizont A und im basalen Horizont mit typischem Löss Aa (Žebera 1962). Andere Autoren beschrieben zwei durch Löss getrennte Gravettien- Schichten (A und B). Der Wechsel der Kulturschichten des Gravettiens zeigt kurzeitige Klimaschwankungen während der Ablagerung der letzten Lössschicht an.*

Environmental changes in central Europe 51 - 15 ka calBP

The pre-Gravettian environment of central Europe

We recognize only two stages of Weichselian continental glacial expansion in Europe, during MIS 4 (70 ka – 60 ka calBP) and MIS 2 / LGM: (26 ka -16 ka calBP) (Fig. 2). Jöris & Weninger (2004) used available data to calculate the timing of oscillations of relatively cold and warm events in central Europe. However, this is a general outline, which may not always agree with local conclusions. Relatively warm climate was recognized at 35 000, 33 000, 31 500, 30 000, 27 500, 26 000 and 21 000. Relatively cold periods existed at 34 000 32 000, 31 000, 29 000-27 500, 25 000-21 500 (all data are in calibrated years BP).

Moravia is the location of the important type site of the Bohunice Interstadial period. A fossil soil with remains of the Bohunician culture was assigned by four dates to between 42 900±1 700 and 36 000±1 100 BP (c. 44 900 - 38 800 calBP). Charcoal

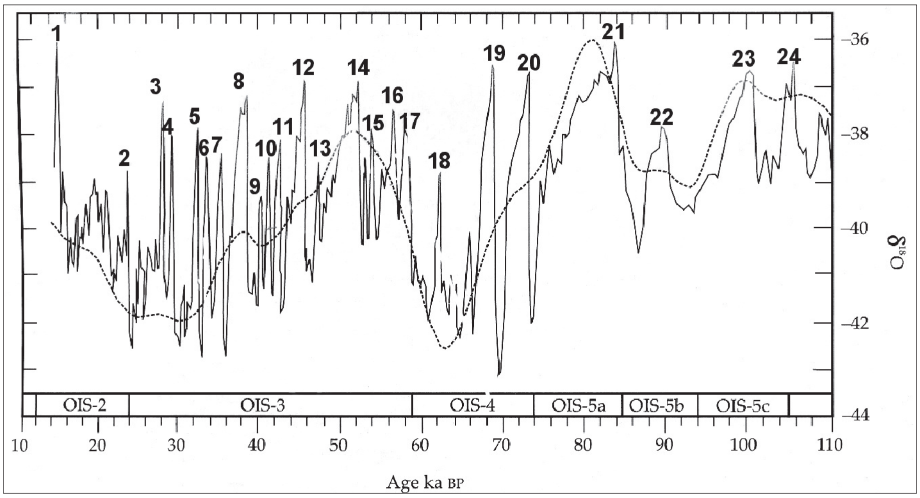

Fig. 2. Climatic oscillations during the Last Glacial (GISP 2 ice core) after van Andel, Davies & Weninger 2003: Fig. 4.1. Interstadial numbers: 1) onset of Holocene, 2) Pavlov, 3-4) Podhradem, 5-6) Denekamp, 8) Hengelo, 9-10) Bohunice, 11-12) Moershoofd, 14-17) Glinde, 18) Oerel, 19-20) Odderade, 21-24) Amersfoort-Brörup.

Abb. 2. *Klimaschwankungen während der letzten Eiszeit (GISP 2 ice core) nach van Andel, Davies & Weninger 2003: Abb. 4.1. Interstadiale Nummern: 1) Beginn des Holozäns, 2) Pavlov, 3-4) Podhradem, 5-6) Denekamp, 8) Hengelo, 9-10) Bohunice, 11-12) Moershoofd, 14-17) Glinde, 18) Oerel, 19-20) Odderade, 21-24) Amersfoort-Brørup.*

was identified as fir, spruce, maple, rowan, elm and hornbeam. Palynological analysis also determined birch, hazel, pine and herbs. The tree species indicate intermediate to high tolerance of arid climate and the possibility of growth of these trees even under highly negative temperature conditions.

Other sites are Stránská skála III (16.403675 E, 49.112545 N) with two dates of 38 500+1 400/-1 200 and 38 200±1 100 BP (c. 40 500 - 40 200 calBP) and Stránská skála IIIa, with a parabrown soil dated to 41 300+3 100/-2 200 (c. 43 300 calBP). The identified tree species comprise pine, fir, alder, spruce, birch, willow, larch and oak, together with different species of herbs. This layer is assigned to the Bohunice Interstadial (Musil 2003) and with few exceptions the species represent mainly intermediate to high tolerance of aridity. All the species did not grow at the same place, but were brought to the locality from different environments.

At the Hungarian site of Érd (18.551928 E, 47.224218 N), dated to the period around 44 ka BP (c. 51 ka calBP) the fauna is dominated by the species *Ursus spelaeus, Coelodonta antiquitatis* and *Equus* sp., while among the tree species identified are pine, stone pine and larch.

The Polish site Piekary II (19.492551 E, 49.593664 N) is dated from 41 460 to 25 840 BP (c. 43-27 ka calBP) and thus covers the entire last stage of the Interpleniglacial. The identified charcoal includes larch (54 %), pine (18 %), yew (2 %), fir (1 %) and oak (2 %), although more detailed stratigraphic classification is not available (Kozłowski 2000). These tree species indicate a high tolerance to arid climate.

The territories of Belorussia, the Ukraine and Russia are relatively well documented (Yelovicheva & Sanko 1999) with regard to changes in vegetation cover (Fig. 3).

From the Last Glacial of north-western Europe there is evidence of arctic brown soils and tundra gley horizons indicative of cold climate from the period 55 ka - 35 ka BP (other dates suggest 49 ka, 39 ka and 32 ka BP) and gley horizons in youngest loess were also documented in Russia. In the period 36 - 33 ka BP there was deposition of loess. In the Netherlands, the period 38 - 37 ka BP (Hengelo Interstadial) is characterized by shrub tundra.

The territories of north-western Europe were climatically different in this period from the territories of central and eastern Europe. In general we can say that western and north-western Europe were much colder and had much higher precipitation than central and especially eastern Europe, which was rather arid. Based on the presented brief outline we can conclude that climate in eastern Europe was generally arid and, in spite of intense climatic changes, more or less covered by sparse coniferous and pine forests of park character with some thermophilous deciduous wood species alternating with open steppe areas.

Some thermophilous trees are already found from the period c. 55 ka BP. This means that over a large area of the eastern part of central Europe and eastern Europe there was an unbroken occurrence of isolated thermophilous deciduous trees at least until the onset of the LGM. It seems that vegetation cover was more or less constant during the period and that there were only oscillations of average temperature and probably also precipitation.

55 ka BP	Interstadial birch and pine forests with some oak, willow, lime, beech and hazel. Relatively high tolerance to drought.
44 ka BP (c. 51 ka calBP)	Interstadial, sparse birch and pine forests alternating with open spaces. This means that there were not closed forests, but rather forests of park character.
37– 35 ka BP (c. 39-36 ka calBP)	Birch and pine. Again, there were not closed forests, but forests of park character.
36– 29 ka BP (c. 38 - 30 ka calBP)	Interstadial, birch and pine with hornbeam, alder, hazel, elm and oak.
32– 24 ka BP (c. 34-26 ka calBP)	Interstadial, formation of soil. The overlying sediment is loess with three tundra gley horizons. There are evident cryogenic structures with frost wedges, probably from the period of accumulation of the overlying loess. Tree species: spruce, birch, dwarf birch, alder, hazel, oak and lime.
28 ka BP (c. 29 ka calBP)	Denekamp Interstadial, birch and pine bush with elms, maples, alders, hazels, willows and dwarf birches.

Fig. 3. Interstadials on the territory of Belorussia, Ukraine and Russia, defined on the basis of plant communities.

Abb. 3. *Interstadiale auf dem Gebiet von Belarus, der Ukraine und Russland auf der Grundlage der Pflanzengesellschaften definiert.*

The Gravettian environment of central Europe

This evidence for environment is based on both the global climatic viewpoint (GCM, RCM) for the whole of central Europe and peripheral territories and also on the environmental analysis of particular sites (LCM). The global climate would not necessarily have matched that of the Gravettian sites in Moravia, but provides an important basis for general comparison between different territories. The time range of the Gravettian in central Europe and Moravia is roughly the same, e.g. between c. 32 and 21 ka BP (c. 36-25 calBP).

The period preceding the occupation of Předmostí falls into the beginning of MIS 3 (Early Cold Phase). Detailed climatic studies of MIS 3 showed several warm events separated by weak cold oscillations (van Andel 2003). The mammal community from southern Poland down to the Pannonian Basin had a typical mammoth fauna. The youngest significant warm period in central Europe was around 33 ka BP (c. 35 ka calBP) and was followed by a significant and rapid change in the fauna, with the next community completely different and marked by a loss of diversity leading to the disappearance of many species.

The valley of the Danube, together with its tributaries Morava and Váh and the surrounding upland region, formed a wide territory between the Alps in the south and the west-east oriented mountain chains in the north. From the climatic viewpoint, it formed a part of the continental zone characterized by warm summers and cold winters. Winter temperatures in the Danube region during the MIS 3 event were between -6.5 and -4 °C, with summer temperatures between 16.5 and 20.5 °C. The LGM saw a fall in both winter temperatures (-12.5 °C to -24 °C) and summer temperatures (12 to 14.5 °C). Summers started later and temperatures increased only in May. Maximum temperatures were then reached in August. The decrease of temperature in autumn was slow and the rapid cooling was only in November with minimum temperatures in January and the end of the cold period in March (Davies et al. 2003). The conclusions above apply not only to the Danube region but are certainly also valid for southern Moravia.

The Pannonian Basin was climatically different. It covers c. 300 000 km^2 and has very heterogeneous geological, climatic, vegetational and soil conditions. Today it comprises four climatic regions. The western part is influenced by oceanic climate, while the southern part and Transdanubia are under Mediterranean influence. The eastern and central parts have a rather continental climate. Climatic changes in the neighbouring mountains are caused by vertical zonality. Conclusions about the environment during the Last Glacial are based on finds of gastropods at sites in loess. Most species have survived until the present day and we know their ecological requirements. Composition structure of gastropod communities depended strongly on the local microclimate, especially on vegetation cover (Sümegi & Krolopp 2002).

A synthesis of 31 sites from the period 32 500 - 28 700 calBP indicates warmer and more humid climate and a relatively high number of short climatic changes of between 1 000 and 7 000 years in duration. Summer climatic conditions were similar to those today, with average July temperatures in the south of 18 - 19 °C and in the north of 16 - 17 °C. In the refugia of the Pannonian Basin there were, besides coniferous forests, also forests with thermophilous deciduous tree species such as hornbeam, oak, hazel, and elm (Willis et al. 2000). In the foothills of the Carpathians Mountains and in the northern part of the Pannonian Basin there was an open landscape of parkland character with pine and larch, while in the southern part pine (probably *Pinus sylvestris*) dominated together with birch. In the period between 32 - 28 ka calBP the Gödöllö-Albertirsa locality documents the formation of soils (Novothny et al. 2002). Based on studies of gastropod communities the climate was similar to that of today. The landscape had a parkland character and the climate was extremely arid. At the end of the period, between 28 - 27 ka calBP,

gastropods	cryophilous	cold-resistant	thermophilous	hygrophilous	woodland	open land
25 – 23 ka calBP	40 – 80 %	20 – 60 %	0 – 2 %	0 – 10 %	0 – 1 %	60 – 98 %
23 – 20 ka calBP	10 – 30 %	20 – 50 %	5 – 10 %	10 – 30 %	5 – 30 %	10 – 85 %
20 – 18 ka calBP	30 – 50 %	30 – 40 %	0 – 1 %	10 – 30 %	0 – 1 %	50 – 94 %

Fig. 4. Changes in the representation of gastropod species in the Pannonian Basin over time.
Abb. 4. *Veränderungen der Schneckenfauna im Pannonischen Becken im Laufe der Zeit.*

finds of gastropods indicate an extremely dry climate without a drop in July temperatures. Only at around 27 ka calBP was there an important change, which resulted in the deposition of loess. Conditions were similar to those of tundra, with significant cooling and the formation of cold continental steppe and forest steppe. In the north, July temperatures decreased to 11 – 12 °C; at some places in the south they dropped to 14 °C. This is the period when the occupation of Moravian Gravettian sites generally ended. However, even during this period some sites with a different and rather mild climate were found in the Pannonian Basin (Sümegi & Krolopp 2002). The representation of specific gastropods species by ecological preference is shown in Figure 4 (calBP, after Sümegi & Krolopp 2000, 2002)

There was a catastrophic change in the gastropod fauna in the period 25 - 23 ka calBP. The number of cryophile species and those indicative of open spaces increased dramatically and all evidence indicates an extremely continental climate and strong cooling. This led to the formation of cold continental steppe or forest steppe, with some sites appearing similar to tundra. July temperatures at this period were around 11 - 12 °C in the northern zone and at some sites in the south c. 14 °C. In general we can say that the vegetation cover was of mosaic character and heterogeneous, with major differences between different regions. Islands of forests survived only in the foothills of the mountains (Sümegi & Krolopp 2002).

Organic sediments from the Polish site of Jutrosin dated to 38 700+3 650/-2 000 BP (c. 40 ka calBP) document gradual cooling of climate at this period, which, according to Kuszell and Winnicki (2002) equates to the Hengelo Interstadial. Organic sediments from the same site indicative of park tundra and dated to 28 500±950 BP (c. 30 ka calBP) correspond to the Denekamp Interstadial (Kuszell and Winnicki 2002).

In eastern Belorussia, close to the frontier with Russia, the Rogachevo event (37 240±720 - 35 300±2 300 BP: c. 39-36 ka calBP) is characterized by birch / pine forest with open spaces, shown by a large proportion (60 - 88 %) of herbs. Broadly the same vegetation cover was also found there during the Shapurovo event (36 400±800 - 29 150±850 BP: c. 38-30 ka calBP), which, according to certain authors, is equivalent to the Hengelo Interstadial. The vegetation here was open birch forest with pines and some hornbeam, alder, hazel, elm and oak. During the Borisov event (equated by the authors with the Denekamp Interstadial) pine / birch forest with rare elm, maple, alder, hazel and dwarf birch is identified for the period around 28 170±750 BP /c. 30 ka calBP (Yelovichova & Sanko 1999).

At the Russian site of Mezin a soil development is recognized from the period somewhat before 24 ka BP (c. 26 ka calBP), with further similar layers overlying it. The loess layer here is sub-divided by three tundra gley horizons with frost wedge formations. The warming of interstadial character (Bryansk Interstadial) was identified in the region between 55° and 65° of northern latitude. Vegetation cover consisted of forest tundra and forest steppe and there is no evidence for any glaciation (van Andel et al. 2003). Based on a written communication from A. Markova (Moscow, 2002), the Bryansk Interstadial was characterized by the tree species spruce, pine, birch, dwarf birch, alder, hazel, oak, lime and elm, in association with the herbs Artemisia and Chenopodiaceae. The composition of vegetation (Opravil 1994) was similar to that known from Dolní Věstonice and Pavlov.

From the data presented above we can conclude that during the period 37 - 24 ka BP (c. 39 - 26 ka calBP) in the lowland steppes of Russia and the Ukraine there existed islands of thin forest composed mostly of birch and pine, with isolated relatively thermophilous deciduous trees (elm, hornbeam, oak and lime). This region (above all the Ukraine and Russia) had vegetation quite different from that of northern Germany and northern Poland, where, at this period, cold and semi-arid conditions dominated and in the period after 28 ka BP (c. 31 ka calBP) there was continuous permafrost. This was also found in England, northern France, northern Belgium and the Netherlands (Renssen & Vandenberghe 2003).

Loess accumulation is documented in this northern region for the period 27 - 25 ka BP / c. 29-27 ka calBP (Guiter et al. 2003), for example in Germany at Koblenz-Metternich (7.331742 E, 50.215769 N) between 24 and 20 ka BP (c. 26 - 22 ka calBP) and at Körner, near to Mühlhausen, around 15 ka BP (c. 17 ka calBP) (Zöller et al. 2004). By contrast, in the foothills of the Alps in Bavaria, where frost processes might be expected in a periglacial climate, there were no signs of the presence of continuous permafrost during the Würm. If there was any permafrost occurrence, it was only local in nature (Ebers 1954). A similar conclusion was arrived at by W. Rosendahl and co-workers for the Swabian Alp on the basis of a studied stalagmite from the Hintere Kohlhalden Cave (Rosendahl et al. 2000). For the period 25 -15 ka BP (c. 27– 15 ka calBP), that is the LGM, they had expected to identify a period of deep permafrost, under which conditions there should not be any growth of stalagmite, but this was not in fact observed. If the dating evidence is correct, then the period of assumed permafrost in the region was shorter or only discontinuous in its occurrence. Similar data were produced in the same region by a stalagmite from the Arbeitslosen Cave.

Over the whole of central Europe, northern France, western Germany, England, northern Belgium and the Netherlands the period 26 to 20 ka BP (c. 28 - 22 ka calBP) is characterized by the accumulation of loess, indicative of an extremely arid climate (Renssen & Vandenberghe 2003). At some sites, for example the Bay of Saint Brieue, the loess contains pseudogley soils formed in short-term cold and humid oscillations similar to those recognized at Moravian localities (Dolní Věstonice or the Gravettian site Jarošov close to Předmostí). These humid oscillations shown by the formation of pseudogleys in the youngest loess are probably typical for whole of western, central and eastern Europe.

It is unclear if this is significant or only coincidence, but at around 25 ka BP (c. 27 ka calBP), when settlement of the site at Předmostí came to an end, a cold event, the so called Heinrich event 3 (H 3) is recorded in marine sediments and in the Greenland Glacier. This Heinrich event starts and ends very abruptly and is characterized as a short period of extremely cold climate with a fall in temperature of up to 3 °C. It is probable that this H3 cooling event is linked to aridity and deposition of loess.

In general we can conclude that European average annual temperatures differed over relatively short distances during the Gravettian. The coldest temperatures were in north-western Europe, where continuous permafrost extended from England to Belgium, the Netherlands, northern Germany and northern Poland. The situation was already different in Bavaria where in the period 25 - 15 ka BP (c. 27 - 15 ka calBP) continuous permafrost was completely missing and discontinuous permafrost, if present at all, occurred only locally.

The behaviour of climate in Russia during this period is surprising and very different from north-western Europe. In the period 37 ka - 24 ka BP there was light pine forest with rare thermophilous deciduous trees. Similar conditions also obtained in the Pannonian Basin. From 32 - 28 ka BP there was a very warm climate with thermophilous deciduous trees. However, around 27 ka BP there was rapid cooling with the resulting formation of continental steppe and forest steppe. This cooling lasted until 23 calBP and is accompanied by decreasing precipitation and even strong aridity, which resulted in the deposition of loess across the whole of Europe. The Gravettian horizons are found at the base of this loess.

From the above, we can conclude that there existed a high differentiation of temperatures across the range of the Gravettian in central Europe. Only after the Gravettian period was there a phase of cooling of variable intensity. The situation was different regarding precipitation, because the whole of Europe initially had a very arid climate, resulting in the deposition of loess. This had a major influence on the vegetation cover and, consequently, on the carrying capacity for the megafaunal species. The arid period was succeeded by phases of greater precipitation, a process repeated several times during the accumulation of the most recent loess.

The post-Gravettian environment of central Europe

The disappearance of Moravian Gravettian sites is linked to the beginning of the second glacial maximum (LGM). The period 27 - 16 ka BP represents the period of maximum Last Glacial cooling, initially with high aridity and followed by a period with increased precipitation and short-term oscillations of strong rains, which were typical across the whole of Europe. Maximum cooling was at around 24 ka BP, when the mountain glaciers of Scandinavia expanded and crossed the Baltic Sea as an ice sheet which reached the lowlands of northern Germany and Poland. The spreading of the continental glacier lasted only a relatively short time, about 9 000 years. Around 15 ka BP (c. 17 ka calBP) the regions south of the Baltic Sea were already again deglaciated (van Andel 2003; Barron et al. 2003).

There is a detailed study from the Pannonian Basin of the period down to 20 ka BP, following the period of occupation of Gravettian sites in Moravia. After a significant period of cooling between 25 - 23 ka calBP, when the climate was similar to that of the tundra, there was decrease in the number of cryophilous species of gastropods and some thermophilous species appeared. This was a period of relatively mild and humid climate with forests. Besides pine, fir, willow and alder there was an expansion of other deciduous trees. From a climatic viewpoint this was an interstadial oscillation (Sümegi & Krolopp 2002). Most important is the presence of smaller "oases" with favourable humidity, temperature conditions and vegetation, which confirm ideas about the existence of refugia in the region of central Europe.

Palynological analysis of the southern Polish Sciejowice site (20.331689 E, 49.283083 N), which is dated to 24 200±600 BP (c. 26 ka calBP), identifies besides herb species the trees *Betula nana, Juniperus* sp. *Salix* f. *glauca* and *Picea abies* (Kozłowski 2000).

In the north of the Ukraine and in central Russia there was sedimentation of loess from 24 000±2 000 - 23 000±1 000 BP (c. 26 - 25 ka calBP) in layers overlying the Bryansk Interstadial. In the period 24 - 12 ka BP there were pines, willows and larches

(Putshkov 1997), which probably occurred as pockets of forest in the steppe. Further to the south and southwest, and close to the Sea of Azov, elm, oak, maple and hazel are documented from the period 24 - 21 ka BP (c. 26 - 23 ka calBP), while from the period 21 -17 ka BP there is evidence of elm, maple, hazel, lime and hornbeam (Markova et al. 1995). The youngest deposition of loess occurred 16 - 10 ka BP.

Following the relatively warm MIS 3, the LGM (25 - 30 ka BP: c. 27 - 22 ka calBP) was characterized by a very cold and arid climate, resulting in the deposition of loess and the formation of continuous permafrost with frost wedges in Britain, northern Belgium, the Netherlands, northern Germany and northern Poland. Tundra gley soils formed during this period. Already by 20 ka BP the southern limit of permafrost moved to the north and by 17 - 15 ka BP only a narrow permafrost band was left in the most northern parts of Poland, Germany, Lithuania and Estonia. In the Netherlands continuous permafrost had disappeared by 20 ka BP (Renssen & Vandenberghe 2003).

In northern France there was accumulation of loess with horizons of pseudo-gley soils formed under very cold climate conditions in the period between 25 - 20 ka BP (c. 27 - 22 ka calBP). These horizons are also known from other parts of Europe, for example from Dolní Věstonice or from the Jarošov site close to Předmostí (Škrdla et al. 2006). Accumulation of loess in Belgium is known from 25 800 - 18 700 BP at Remicourt and 17 100 - 13 200 BP at Rocourt (Musil 2005a).

In general we can say that the LGM represents the coldest period of Last Glacial. North-western Europe was very different from the eastern part of central Europe regarding temperature, with the occurrence of continuous permafrost until 20 - 17 ka BP. A typical feature was the high aridity of climate, leading to the accumulation of loess, which was interrupted by short-term oscillations of precipitation, with differing intensity in different regions. In Moravia the amount of precipitation decreased from north to south. Deposition of loess, interrupted by periods of precipitation, occurred over the whole of western and central Europe at the same time. In the north-west, the climate was rather oceanic, but in the east climate was arid and in the most northerly regions climate was rather similar to polar deserts. This resulted in a large reduction of boreal forest and a spreading of steppes.

A brief characterization of recent and late glacial biomes

When we compare recent biomes (Fig. 5) with the central European biomes identified for the end of the Last Glacial in the flood plains, highlands and mountains of Moravia, none of the former categories provides a match for the latter conditions. Instead, a combination of several biomes would be more

Tundra	Arctic tundra is the most recent biome. This is a landscape with cold climate, permanently frozen soil and an absence of trees, which are replaced by mosses, heather and lichens. In summer there is surface thawing of soil and formation of numerous swamps, wetlands and lakes. There are abundant insects in summer.
Taiga (boreal forest)	This is the largest of the world's biomes, with coniferous forests and deciduous trees. The number of floral and faunal taxa is more limited than in the biome of the deciduous forest. In summer there are many insects.
Steppe (grassland)	This is a biome with low precipitation, which may only sustain growth of grass and small occurrences of bushes and trees.
Deciduous forest	Biome with a mild climate, c. six months of plant growth and deciduous trees. There are distinct seasons and many species of animals.

Fig. 5. Summary of recent biomes of Eurasia.

Abb. 5. *Zusammenfassung der heutigen Biome Eurasiens*

Cool temperate forest	Closed forest, including mixed coniferous – broad-leaved forest.
Southern taiga	Conifers, tall, very dense canopy cover
Mid taiga	Coniferous or broad-leaved forest with a relatively open canopy
Open boreal woodlands	Various open woody vegetation types, coniferous or broad-leaved
Semi-arid temperate woodland or scrub	Various open woody vegetation types, coniferous or broad-leaved in temperate climates
Tundra	Mainly herbaceous or with low shrubs
Steppe-tundra	Non-analogue age vegetation, probably sparse vegetation, herbaceous with a few low shrubs, which resembles both present-day steppe and tundra in certain aspects
Polar and alpine deserts	Very sparsely vegetated with only low herbaceous plants
Forest steppe	Mainly herbaceous, but with stands of trees or bushes in favourable pockets. This corresponds roughly to the environment during the Gravettian
Forest tundra	Mainly herbaceous or low shrubs, with a scattering of trees and bushes

Fig. 6. A detailed division of biomes ("Global Vegetation Classification Scheme") at the end of the Last Glacial (after Adams & Faure 1997).

Abb. 6. *Detailliste der Biome („Global Vegetationsklassifizierungs Schema") am Ende der letzten Eiszeit (nach Adams & Faure 1997).*

Species		Temperature tolerance	Drought tolerance	Substrate tolerance
Fir	*Abies alba*	**-5°**	3	
Juniper	*Juniperus communis*		3	1
Larch	*Larix decidua*	**-10°**	2	
Stone pine	*Picea cembra*	**-10°**	2	
Mountain pine	*Pinus mugo*		5	1
Scots pine	*Pinus sylvestris*	-40°	5	1
Yew	*Taxus baccata*	-4°	4	1
Alder	*Alnus glutinosa*	-15°	1	1
Downy birch	*Betula pubescens*	**-40°**	5	1
Hornbeam	*Carpinus betulus*	**-8°**	3	2
Hazel	*Corylus avellana*	-15°		2
Beech	*Fagus sylvatica*	-3°	2	1
Ash	*Fraxinus excelsior*	**-16°**	2	3
Aspen	*Populus tremula*	**-40°**	4	1
Oak	*Quercus robur*	**-16°**	5	1
Willow	*Salix alba*		1	1
Rowan	*Sorbus aucuparia*		4	1
Lime	*Tilia cordata*	**-18°**	3	3
Elm	*Ulmus glabra*	-15°		3

Fig. 7. Environmental parameters for selected ligneous species (Willis & van Andel 2004). The first column describes temperature tolerance of ligneous species. Boldface values indicate the average January temperatures at which a species may survive; other values indicate the average temperature of the coldest month in the territory of the occurrence of a given species. Numbers in the second column indicate drought tolerance. Number 1 indicates a low tolerance, number 5 indicates high tolerance. The third column indicates the ability of a wood species to grow on nutrient poor substrate. Number 1 indicates a tolerant species, number 2 intermediate tolerance and number 3 lack of tolerance.

Abb. 7. *Umweltansprüche für ausgewählte Holzarten (Willis & van Andel 2004). Die erste Spalte beschreibt Temperaturtoleranz der Holzgewächse. Werte in Fettschrift geben die durchschnittlichen Temperaturen im Januar an, bei welcher die Arten noch überleben, andere Werte geben die durchschnittliche Temperatur des kältesten Monats im Gebiet des Vorkommens einer bestimmten Art an. Zahlen in der zweiten Spalte zeigen die Toleranz gegenüber Trockenheit. Von 1, niedrige Toleranz, nach 5, hohe Toleranz. Die dritte Spalte zeigt die Fähigkeit einer Holzart an, auf nährstoffarmem Substrat zu wachsen. Von 1, hohe Toleranz, nach 3, geringe Toleranz.*

appropriate. We can exclude completely recent biome 1. Of the other biomes, a combination of biomes 2 and 3 would probably be most appropriate, although taking into account the limited occurrence of deciduous trees and the large diversity of mammals, there were also some features of biome 4. This combination means that such a type of biome no longer exists at the present day.

Palynological data from the Furamoos locality, to the north of the Alps in southwestern Germany (9.533492 E; 47.595021 N), indicated that there was not a complete disappearance of trees in the foothills of the Alps, when colder periods were not long and intense. When complete deforestation occurred, there was relatively fast reforestation, on a time frame of hundreds of years, at the beginning of a warmer period (Miller et al. 2003).

A detailed division of biomes at the end of Last Glacial is given by J. M. Adams & H. Faure (1997) (Fig. 6). In our opinion, this division cannot be applied to our study area because it does not take into account the differences in height and changes linked to local topography typical for the vicinity of Moravian Gravettian sites, which result in rapid changes of vegetation over short distances (LCM - Local Climatic Model). The best match for the region can be probably found in the forest steppe.

Vegetation cover

In the continental steppe of eastern Europe and southern Siberia there is a domination of grasses, which require a minimum precipitation of 300 mm per year. This region is very different from the tundra, taiga and polar desert. Evergreen taiga and montane forest are typical for northern Europe and Siberia, while mild temperate deciduous forest is typical for central Europe.

Huntley and Allen (2003) tried to reconstruct the biome for Europe during the LGM and concluded that there were lower temperatures, but more intense solar radiation than in the north of Europe today. This fact, plus the longer period of growth, definitely had an impact on vegetation. For these reasons alone, even without taking into account the lower concentration of atmospheric CO_2 relative to the Holocene, it is not possible to consider the Pleistocene central European biome, with its vegetation and faunal communities, as analogous to recent northern Siberia. All studies indicate the continuous presence of coniferous trees and sporadic occurrence of thermophilous deciduous trees in the eastern part of central Europe and eastern Europe, at least for the period 35 - 20 ka BP (c. 36 - 21 ka calBP).

The LGM climatic scenario for in central Europe admits the possibility of plant cover similar to taiga from 40 - 20 ka calBP. The dominant vegetation was coniferous forest. Environmental temperatures for the particular species of tree (Fig. 7) were taken from Willis & van Andel (2004).

We summarize the characteristic requirements of tree species identified at Gravettian sites in Figure 8.

Huntley and Allen (2003) proposed a detailed division of environmental types on the basis of the vegetation cover and placed specific taxa into different classes of plant associations. We reproduce the plant species classifications in Figure 9.

The vegetation associations based on palynological analyses from warm and cold events of Last Glacial were very different from those known today. The most important fact is that Last Glacial temperature changes did not merely result in a simple geographical shift of vegetation zones.

Current studies emphasize the role of local climatic deviations and postulate relatively numerous refuges in some parts of central Europe. If we compare these

Fir	*Abies alba*	Humid sites, sensitive to winter cold, retreats when humidity decreases, forests at foothills and mountains.
Larch	*Larix deciduas*	Extends to the polar limits of forest and there also are isolated occurrences in tundra. Mountain and sub-alpine forests.
Spruce	*Picea excelsa*	Boreal forest zone, large ecological range, stands long cold periods (5 - 7 months with average minimum temperature below 0°C), mildly warm summers with average July temperatures 12 - 17°C, average year temperatures 5 - 6°C, resistant against deep frosts, precipitation 450 - 650 mm/year. Isolated trees may occur in dwarf forms much above the limit of forest.
Hazel	*Corylus avellana*	Light deciduous forests as shrub and as a significant component of thermophilous shrubs, occurs from lowlands up to mountains. It cannot stand low temperatures and permafrost.
Beech	*Fagus sylvatica*	Occurs in wide ecological range, humid summers and mild winters. It is sensitive to late frost. It grows exceptionally up to 1 500 m.
Willow	*Salix herbacea*	Low wood species growing in polar region today.
Oak	*Quercus* sp.	Thermophilous wood species, it occurs up to 650 m.
Lime	*Tilia* sp.	Thermophilous wood species
Wych Elm	*Ulmus glabra*	Grows at altitudes up to 1 000 m. It grows in shady ravines and stony forests, exceptionally in floodplain forests, on humid soils with high content of humus and nutrients, with basic and slightly acid reaction, at shady sites with higher air humidity.
Fluttering Elm	*Ulmus laevis*	Thermophilous wood species. It does not stand extremely low temperatures and the presence of permafrost.
Scots pine	*Pinus sylvestris*	Grows at altitudes up to 1 200 m. It stands fluctuations of temperature and humidity and high humidity and temperature.
Stone Pine	*Pinus cembra*	Forms mixed forests with spruce, at high altitude with larch and dwarf pine.
Hornbeam	*Carpinus betulus*	Occurs from lowlands to the foot of mountains, mixed deciduous forests.
Blackthorn	*Prunus* sp.	Do not require high temperature and humidity.
Birch	*Betula* sp.	Do not require high temperature and humidity.

Fig. 8. Characterization of tree species found at Gravettian sites (Musil 1997; van Andel 2003).

Abb. 8. *Aufstellung der Baumarten, welche in Gravettien Siedlungen gefunden wurden (Musil 1997; van Andel 2003).*

Taiga with deciduous trees / mountain forest	*Picea, Pinus, Haploxylon, Betula, Larix, Juniperus, Diploxylon, Alnus, Populus, Salix, Rubus chamaemorus.*
Taiga with coniferous trees / mountain forest	*Picea, Pinus, Haploxylon, Betula, Larix, Abies, Juniperus communis, Diploxylon, Alnus, Populus, Salix, Rubus chamaemorus.*
Mixed forest in cold climate	*Rubus chamaemorus, Picea, Betula, Larix, Taxus, Abies, Juniperus, Pinus, Diploxylon, Alnus, Populus, Salix, Carpinus betulus, Corylus, Fagus, Frangula, Tilia, Ulmus, Cedrus, Taxus.*
Coniferous forest in mild climate	*Picea, Betula, Larix, Abies, Juniperus, Pinus, Diploxylon, Lonicera, Sambucus, Sorbus, Viburnum, Alnus, Populus, Salix, Carpinus betulus, Corylus, Fagus, Frangula, Tilia, Ulmus.*
Deciduous forest in mild climate / forested landscape in mild climate	*Pinus, Haploxylon, Betula, Larix, Abies, Juniperus, Diploxylon, Sorbus, Viburnum, Carpinus betulus, Corylus, Fagus, Frangula, Tilia, Ulmus, Cedrus, Taxus, Acer, Euonymus, Fraxinus excelsior, Quercus robur, Viscum, Fraxinus ornus, Alnus, Populus, Salix, Castanea, Celtis, Juglans, Platanus, Pterocarya, Vitis, Zelkova, Buxus, Hedera, Ilex, Rhamnaceae.*
Mixed forest in cold climate	*Picea, Pinus, Haploxylon, Betula, Larix, Abies, Juniperus, Diploxylon, Sorbus, Viburnum, Alnus, Populus, Salix, Acer, Euonymus, Fraxinus excelsior, Quercus robur, Viscum, Carpinus betulus, Corylus, Fagus, Frangula, Tilia, Ulmus, Cedrus, Taxus.*
Mixed forest in warm climate	*Juniperus, Pinus, Diploxylon, Sorbus, Viburnum, Alnus, Populus, Salix, Acer, Euonymus, Fraxinus excelsior, Quercus robur, Quercus ilex, Buxus, Hedera, Ilex, Viscum, Carpinus betulus, Corylus, Fagus, Frangula, Tilia, Ulmus, Fraxinus ornus, Castanea, Celtis, Juglans, Platanus, Pterocarya, Vitis, Zelkova, Rhamnaceae.*
Forested landscape / shrubs in moderately warm climate	*Gramineae, Olea, Pistacea, Quercus ilex, Juniperus, Pinus, Diploxylon.*
Meadows in mild climate	Gramineae, *Calligonum*-type, *Hippophae, Oxyria*-type, Polygonaceae, *Polygonum persicaria, Polygonum bistorta, Rumex, Aconitum, Ajuga, Allium,* Campanulaceae, *Centaurea, Compositae, Filipendula, Galium*-type, *Geranium, Geum, Helianthemum,* Liliaceae, *Linum, Matricaria, Plantago, Potentilla,* Ranunculaceae, Resedaceae, Rosaceae, Rubiaceae, *Urtica, Valeriana, Veronica, Ephedra, Artemisia,* Chenopodiaceae.
Steppe tundra, steppe in warm climate	*Artemisia,* Chenopodiaceae, Gramineae, *Armeria,* Boraginaceae, Cruciferae, Crassulaceae, *Echium*-type, *Euphorbia, Hypericum,* Labiatae, Leguminosae, *Mentha*-type, Malvaceae, *Papaver,* Scrophulariaceae, Solanaceae, Thymelaeceae, *Aconitum, Ajuga, Allium,* Campanulaceae, *Centaurea,* Compositae, *Filipendula, Galium*-type, *Geranium, Geum, Helianthemum,* Liliaceae, *Linum, Matricaria, Plantago, Potentilla,* Ranunculaceae, Resedaceae, Rosaceae, Rubiaceae, *Urtica, Valeriana, Veronica, Ephedra, Artemisia,* Chenopodiaceae.
Desert with shrubs and steppe	*Aconitum, Ajuga, Allium,* Campanulaceae, *Centaurea,* Compositae, *Filipendula, Galium*-type, *Geranium, Geum, Helianthemum,* Liliaceae, *Linum, Matricaria, Plantago, Potentilla,* Ranunculaceae, Resedaceae, Rosaceae, Rubiaceae, *Urtica, Valeriana, Veronica, Ephedra, Artemisia,* Chenopodiaceae.
Desert in warm climate	*Aconitum, Ajuga, Allium,* Campanulaceae, *Centaurea,* Compositae, *Filipendula, Galium*-type, *Geranium, Geum, Helianthemum,* Liliaceae, *Linum, Matricaria, Plantago, Potentilla,* Ranunculaceae, Resedaceae, Rosaceae, Rubiaceae, *Urtica, Valeriana, Veronica, Ephedra fragilis, Artemisia,* Chenopodiaceae.
Tundra with dwarf shrubs	Gramineae, *Betula nana, Dryas octopetala,* Gentianaceae, *Salix.*

Fig. 9. Detailed environmental division on the basis of the vegetation cover (Huntley & Allen 2003). This is only a selection of taxa.

Abb. 9. *Ökologische Verteilung der Biome auf der Grundlage der Vegetationsgemeinschaften (Huntley & Allen 2003). Dies ist nur eine Auswahl von Taxa.*

certainly incomplete plant communities with earlier models, we must clearly admit greater local differences (typical LCM). Even in the coldest stadial of the Würm, according to Lang (1994), dispersed and isolated islands of widely differing tree species existed in Europe. These warmer pockets were probably in river valleys and sub-mountainous regions (LCM) and contained not only coniferous forests, which are fully documented on the basis of macro-remains, but also many different species of deciduous trees (Lang 1994).

Willis and van Andel (2004) also presented such viewpoint. They collected data from 40 sites in central and eastern Europe and their analyses are based only on remains of charcoal. They showed that during the period 32 - 16 ka calBP (e.g. in the severe glacial climate of the LGM) some regions did not correspond to the steppe biome, but rather resembled thin forests of a parkland character. Besides coniferous trees, there was also a limited occurrence of thermophilous deciduous trees much farther to the north and east than had been previously expected. Taxa of thermophilous trees survived in small pockets under favourable conditions and they were always present during all stadial / interstadial cycles. It was concluded that the significant limiting factor for the presence of trees was the degree of aridity (Willis & van Andel 2004).

As a model case in point for such conditions we may mention the site of Sevsk (Bryansk region, Russia), which is dated to 13 950 ± 70 BP and 13 689 ± 60 BP (c. 15 ka calBP: "Bølling"). Together with a large amount (3 800) of mammoth bones there were also found bones of other animals: *Equus latipes, Bos* sp. and *Coelodonta antiquitatis*. Palynological analysis indicated the presence of not only grasses, but also shrubs (53 %) and trees (*Pinus sylvestris* and *Pinus sibirica* 94 %), with a limited occurrence of *Betula pubescens, Betula nana*, *Larix* sp., *Abies* sp., *Alnus* sp. and even *Quercus* sp. and *Fraxinus* sp. This means that species of the recent taiga and present day subarctic species were found together with thermophilous species. Analysis of the microfauna indicated arid cold steppe and a landscape with a mosaic pattern of vegetation (Maschenko et al. 2006).

Limiting factors of tree growth are, above all, temperature, the amount of precipitation, type of soil, presence of permafrost, length of growth period and the concentration of atmospheric CO_2. When we consider the impact of these factors and the tolerance of recent plants in central and northern Europe to them, we can conclude that all the taxa from the Gravettian mentioned above could exist under the climatic conditions recorded between 38 - 27 ka calBP, and even under the still colder conditions of the LGM (27 - 18 ka calBP) (Willis & van Andel 2004).

A genetic study of *Quercus* sp., *Fagus* sp. and *Abies* sp. showed genetic differentiation within these taxa caused by their isolation in refuges during cold periods. (Willis & van Andel 2004).

There are many palynological analyses and charcoal analyses from the Gravettian sites in Moravia (Klíma 1963; Damblon 1997), the results of which are very important because they show the immediate vegetation cover of particular sites. Around the Gravettian sites at Dolní Věstonice and Pavlov there are forests in the proximity of the river, which rise up to the surrounding hillsides, where they are dominated by coniferous trees with sparse thermophilous deciduous species (*Abies alba, Larix decidua, Picea excelsa, Pinus sylvestris, Pinus cembra, Pinus mugo, Juniperus communis, Taxus baccata*, cf. *Ulmus* sp., *Salix* sp., *Fagus sylvatica* and *Betula* sp.: Klíma 1963; Musil 2003). Tree rings indicate less favourable conditions for growth compared to the present day, but the diameter of some trees reached 40 cm. In this case, the factors limiting growth were cold climate and low precipitation, however, detailed dendrochronological analyses do not exist.

Peat at Bulhary, located c. 6 km from Pavlov, is of roughly same age as the Dolní Věstonice and Pavlov sites (25 675+2 750/-2 045 BP ~ 27 675 calBP). There are rich finds of both aquatic and wetland plants (more than 50 species) and of the following tree species: *Pinus sylvestris, Pinus* cf. *mugo, Pinus cembra, Picea* (*abies*?), *Larix europaea, Juniperus communis, Betula* sp., *Ulmus* sp., *Acer* sp., *Corylus* sp., *Quercus* sp., *Tilia* sp., *Salix* sp. and *Alnus* sp. (Rybníčková & Rybníček 1991).

Very detailed data are available for the Gravettian period vegetation cover from the Dzeravá skála Cave in western Slovakia (Hajnalová & Hajnalová 2005). The authors present an overview of tree species found at sites in Slovakia from the period 50 ka - 20 ka BP (Fig. 10). The reconstruction of local climate and vegetation changes is made here on the basis of

38 – 34 ka BP	c. 38 – 36 ka calBP	Pine (*Pinus*), fir (*Abies*), dwarf birch (*Betula nana*), alder (*Alnus*), poplar (*Populus*), beech (*Fagus*), hazel (*Corylus*), maple (*Acer*), oak (*Quercus*)
31 ka BP	c. 33 ka calBP	Pine (*Pinus*), spruce (*Picea*), fir (*Abies*), beech (*Fagus*)
31 ka BP	c. 33 ka calBP	Dwarf birch (*Betula nana*), willow (*Salix*), alder (*Alnus*), pine (*Pinus*), larch (*Larix*), spruce (*Picea*), hazel (*Corylus*), oak (*Quercus*): This period is interpreted as a "climatic" optimum
24 – 22 ka BP	c. 26 – 24 ka calBP	Pine (*Pinus*), fir (*Abies*), oak (*Quercus*), maple (*Acer*), beech (*Fagus*)

Fig. 10. Gravettian vegetation cover around the Dzeravá Skála Cave in western Slovakia (Hajnalová & Hajnalová 2005).

Abb. 10. *Flora des Gravettien in der Umgebung der Dzeravá Skála-Höhle in der westlichen Slowakei (Hajnalová & Hajnalová 2005).*

charcoal analyses and these indicate the existence of a warmer climatic oscillation at this time and show the presence of gallery forests around watercourses with willows, alder and ash, with stands of maple, hazel and beech at the base of surrounding slopes.

The reconstructed Gravettian biome does not correspond to any biome at the present day. It was specific to this period and cannot be found anywhere today. It can basically be interpreted as a mixture of several present biomes. In the sparse coniferous forest of a parkland character there were also always found isolated thermophilous deciduous trees.

The faunal community and environmental requirements of mammals

Each ecosystem tends to achieve an optimum number of species and individuals. The composition of communities changes constantly, dependent upon the climatic conditions. Adaptive capacity, e.g. a theoretical or real capacity of adaptation to environmental changes, differs between species. Favourable changes result in an increasing population and non-favourable changes vice versa. All organisms living in the same biotope are interconnected by many mutual relationships. Oscillations in temperature and precipitation lead to changes in the composition of communities, but also in the numbers of different species.

At the level of a particular mammal species we observe several biogeographical impacts during the Last Glacial:

1. Changes in the geographical and altitudinal occurrence of species, which occur at a scale of up to hundreds of kilometres.
2. Climatic changes of high intensity caused the migration of vegetation and animals. Because hunting constituted the principal economic resource of the Gravettian population, animal migrations were probably in a close relationship to the migration of human populations.
3. Large and relatively rapid changes of whole faunal community occurred at roughly 33 000 BP and then again at the Pleistocene / Holocene boundary. The composition of the new, replacement communities was always very different from that of the previous ones.
4. The populations of some species decreased so dramatically that this could lead to their extinction.

Our characterization of the archaeologically recovered species is based on recent data and it is necessary to keep in mind that it may not correspond exactly to the way of life of the different species in the Pleistocene. Species typical today for boreal forest were found then together with species typical for deciduous forest and steppe. Modern faunal communities were formed only few thousands years ago and there is no modern analogy for the Pleistocene communities. The comparison of biota from the Last Glacial with recent biota demands caution, especially when we compare the glacial environment of central Europe with the recent climatic conditions of northern Siberia.

Fig. 11 presents a brief ecological characterization of Last Glacial mammal species (Musil 1985; 2003; Stewart et al. 2003). In publications, there is generally a presentation of the diversity of species and of the MNI (minimum number of individuals) for particular species and conclusions are generally based only on these data. The feeding requirements of particular animals during the year are not generally discussed or explained. The larger herbivores grow the more energy they require and their food needed to be more variable and richer, not only in summer, but especially in winter. The analyses of Gravettian cultural layers represent average conditions over a period of several thousands years. On the basis of Greenland glacier studies we know that the duration of climatic oscillations was relatively brief, meaning that our evaluation averages several climatic oscillations and does not correspond to a distinct climatic event.

Alongside mammals, gastropods also provide an important component of ecological analyses and provide good information about Quaternary environment and climate. The composition of their communities, in contrast to the communities of mammals, strongly depends on the microclimatic conditions of the local environment (LCM).

There was a high diversity of animal species at the Gravettian sites in Moravia. The recovered specimens are generally interpreted as forming a single entity, although there is an important division into two groups. One group lived and reproduced permanently in the region while the second group only entered the region during certain periods. The former group is more important for environmental analyses.

The Gravettian environment in Moravia and adjacent regions

Moravia has the greatest concentration of the largest Gravettian sites in central Europe. It was a central region of this culture, especially in the period 33 - 25 ka BP, probably as a consequence of its favourable geographic position.

Analysis of the topography of Moravia reveals a very complex situation. If we omit the surrounding high mountains, which are of no interest in the present context, the north-south orientation of the topography resulted in the intersection of several climatic influences. In the north there was a cold and humid climate, which is especially typical for northern Moravia and southern Poland. In southern Moravia there was a rather warmer and more arid climate, extending into the region from the Pannonian Basin.

Reindeer (*Rangifer tarandus*)	Ecologically plastic species tolerant of low temperature. These are social animals living in large herds and completely adapted for life in boreal coniferous forests (taiga) and tundra, especially in places where they alternate with open space. They avoid large closed and deciduous forests and are well adapted for life in mountains (up to 2,500 m). Their nutrition is based on lichens, mosses, mushrooms, plants and leaves of shrubs. At the beginning of summer they migrate to different regions to avoid large numbers of insects, returning in August. Some populations live more or less sedentarily, other migrate over distances of 500 km during a year. Daily movements can be up to 55 km. Hearing and vision are not well developed.
Elk (*Alces alces*)	Is typical for boreal forests, forest steppes and the peripheral zone of steppes. Optimum environment is sparse boreal forest alternating with open steppe landscape. It is adapted for life with high thickness of snow in winter. It is a solitary animal living in swampy landscapes with small lakes and in mild or rather colder climate. It eats any vegetation, in summer it prefers aquatic plants. Its migration radius is up to 600 km.
Giant deer (*Megaloceros giganteus*)	Lives in forest steppe and steppe and prefers mild climate.
Roe deer (*Capreolus capreolus*)	Lives in both oceanic and continental climate. Its lifestyle is solitary, preferring open landscape with sparse coniferous, deciduous or mixed forests, in some cases with small forest islets. Today it also occurs in open landscape. In winter it forms herds, small in forest biotope and larger in open landscapes. The northern limit of its occurrence is determined by climate and by the thickness of snow cover in winter (maximum 50 cm).
Aurochs (*Bos primigenius*)	Prefers landscape with sparse forests and forest steppe, wetlands and water courses. In mountains it lives up to the alpine zone. Maximum tolerated thickness of snow cover in winter is 50 cm. It is very tolerant to temperature.
Bison (*Bison priscus*)	Is perfectly adapted to landscapes such as forest steppe and steppes with cold climate; exceptionally it lives in forests. It tolerates a large range of temperatures from arctic conditions to a very warm climate. It probably lived in herds. In winter cows and young animals formed large herds. Former theories about life in continuous forests have been rejected.
Musk ox (*Ovibos moschatus*)	Is highly adapted to cold climate. In summer it lives in groups of about five animals, in winter forming herds of up to 60 animals. In summer it lives close to bodies of water and tend to stay in the same territory. The animals are well adapted to life on tundra above the limit of forest, but also to northern boreal forest and periglacial steppe. In summer they migrate up to 200 km, but in winter only up to 70 km.
Saiga antelope (*Saiga tatarica*)	Cold and dry climate, steppe.
Mammoth (*Mammuthus primigenius*)	The body of the animal was well adapted to the life in cold arid steppe climate, but also for mild climate. It avoided continuous forests and preferred open landscape of tundra character or arctic steppe. It also avoided hilly landscapes with major altitude changes. Only females with offspring lived in herds.
Woolly rhinoceros (*Coleodonta antiquitatis*)	Animal with similar requirements to the mammoth.
Horse (*Equus* sp.)	Typical species of the steppe, also part of the forest steppe, exceptionally living in semi-deserts. It does not depend on temperature and can live in both very cold and warm regions of the steppe.
Collared lemming (*Dicrostonyx torquatus*)	Is tolerant to low temperature. In summer it lives in dry and rocky regions of the tundra and northern coniferous boreal forest. In winter it migrates to more southern meadows where snow cover is thicker.
Norway lemming (*Lemmus lemmus*)	Is tolerant to low temperature. It lives mostly on arctic tundra and the steppe, in higher mountains and grassy highlands, in small birch and pine forests and in the proximity of bodies of water. Typical climate: in winter temperatures from -30 °C to 0 °C, in summer from 0 °C to 18 °C; precipitation in winter 0.05 mm/day, in summer 0.5 - 3 mm/day, e.g. prefers arid climate. With the spring thaws it migrates to sites where snow still occurs or to lower altitudes where it lives during summer. In autumn it migrates back to the original territories. Its optimum conditions are represented by short winters without sudden thaws and frosts and long summers. In such periods its numbers increase dramatically. Has a four year population cycle, when increase of population results in increased mortality.
Arctic hare (*Lepus timidus*)	Ecologically plastic species. It lives especially in polar and mountainous regions, mostly in boreal forest, but also in forest steppe and tundra. Recent isolated populations are also known from the mountains of northern Scotland. In winter it migrates to more protected areas.
European hare (*Lepus europaeus*)	Adapted for open landscape with mild climate.
Beaver (*Castor fiber*)	Its living territory is linked to forested areas with the proximity of lakes and water courses. Its food includes a rich variety of plants, but it does not eat alder and oak.
Mole (*Talpa* sp.)	There are five species, which require relatively mild climate. Climate in their territory: in winter from -20 to 12 °C, in summer from 8 to 25 °C, precipitation in winter of 0.5-5 mm/day, in summer 0.5-5 mm/day.
Wolf (*Canis lupus*)	Ecologically plastic species with large tolerance to environment and large geographical variability. Its living environment is very variable – temperate forest, boreal forest with dominant birch, mountains, tundra, steppe and even semi-deserts. It avoids larger closed forest. In mountains it may live up to 4 000 m and in tundra lives in the valleys of water courses. It hunts in packs of 5 to 9 individuals. In a territory with many reindeer there are larger groups of wolves. Each pack has its own territory, which defends against other packs. The wolf pack has a sedentary period in spring and summer and a migrational period in autumn and winter. In winter, wolves migrate large distances, especially in situations when migratory animals like reindeer are their principal prey. The daily migration distance is up to 200 km. If there are only few reindeer, hares, marmots, mice and other small fauna species are also hunted.
Cave bear (*Ursus spelaeus*)	Species with a large ecological tolerance and with extremely high individual and geographical variability.
Brown bear (*Ursus arctos*)	Species with great ecological plasticity. Typical inhabitant of large coniferous and deciduous forests, periodically also occurs in tundra. It has high individual and geographical variability. Migration is negligible.
Red fox (*Vulpes vulpes*)	Species with great ecological plasticity. It prefers open and semi-open landscape, but lives in all types of landscapes – tundra, boreal forest, gallery forest around water courses, continuous forests, semi-deserts and even deserts, and mountains up to 4 000 m. Optimum conditions are represented by mixed forests alternating with open spaces and valleys of water courses.
Arctic fox (*Alopex lagopus*)	It has a high tolerance to low temperature. These animals live much farther to north (in spring and summer) than other Canidae, mostly in tundra and boreal forest, penetrating the latter along water courses. In autumn they move to more favourable territories. They migrate up to 2 000 km during a year. There principal prey is lemmings, birds and their eggs, and hares; they also scavenge carcasses. Climate: in winter from -30 to 0 °C, in summer from -8 to 18 °C; precipitation in winter 0.5 - 3 mm/day, in summer 0 - 3 m/day. Small geographical variability.
Badger (*Meles meles*)	Animal with high adaptability. Optimum landscape comprises small forests alternating with meadows; it occurs only at the margins of In large forests. In steppes it lives in the proximity of water. In some cases it lives also in semi-deserts. It looks for food mostly in open landscape. It has a large geographical variability.

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Wolverine (*Gulo gulo*)	Species with great ecological plasticity. Circumpolar occurrence and high adaptability in different environments. High tolerance to low temperature and thick snow cover (50 – 70 cm).Typical for coniferous boreal forests and also penetrates hundreds of km onto the tundra. Southern limit of occurrence is the forest steppe, but can be found in the steppe. Also mountains and open landscape with mild climate and temperate forest. Possible daily migration up to 45 km. Its presence is linked to reindeer; when they disappear, so does wolverine. It has a small geographical variability.
Hyaena (*Crocuta spelaea*)	Species with large tolerance to climate and environment.
Leopard (*Panthera pardus*)	Euryoecious species. Of all felines it is the most adapted to variable environments from deserts to forests with deciduous forest as an optimum. It may live up to high mountains altitudes (3 500 m). In winter the animal tolerates only a thin snow cover.
Lion (*Panthera spelaea*)	Had a large territory of occurrence from western Europe to eastern Asia, it also lived in high mountains and mostly in regions with cold forest steppe.

Fig. 11. Synthesis of ecological characteristics of selected Last Glacial mammal species.

Abb. 11. *Synthese der ökologischen Charakteristika ausgewählter, letztglazialer Säugetierarten.*

Central Moravia experienced alternations of the various strong climatic impacts from both the previous regions. With regard to wind direction, we know from all available studies that it was towards the west during the periods of accumulation of loess. It is necessary to include a local perspective in this synoptic climatic viewpoint. All evidence shows that the climate of the entire territory of Moravia was variable during this period.

Moravia not only formed the connection between north and south, but also provided a climatic transition between the always warmer and more arid Pannonian Basin and Danube regions to the south and the colder and more humid lowlands of northern Europe. There were thus three climatic units, comprising southern Moravia and northern Austria (Sub-province A), another unit made up of northern Moravia and neighbouring Silesia and southern Poland (Sub-province B), with central Moravia representing an intermediate unit (Sub-province C) between these.

Sub-province A (northern Austria - southern Moravia)

A model for the Gravettian vegetation cover of Sub-province A is provided by the region of Dolní Věstonice and Pavlov. At this period there was rich vegetation in the alluvial plain, which comprised many species of herbs and tree species, represented not only by coniferous species, but also by occasional thermophilous deciduous trees like oak, beech, elm etc. Considering the fact that this was towards the end of the Last Glacial (before the onset of LGM), it is hard to believe that the deciduous species had migrated to this region during this period. They would have needed to move here much earlier, probably in the Last Interglacial or during the earliest Würm Interstadials (when climate was still similar to the Last Interglacial), and would have survived there since then. This means that this region of southern Moravia and northern Austria must be considered as a long-term refuge for thermophilous species.

About 6 km from Dolní Věstonice, at the village of Bulhary (16.441359 E, 48.482325 N), peat underlying the loess layers is dated to 25 675+2 750/-2 045 BP (c. 27 675 ka calBP), which is the same age as the cultural layers in Dolní Věstonice and Pavlov. From the layer were recovered 16 aquatic and wetland taxa, 40 taxa of herbs and also the tree species pine, dwarf pine, stone pine, fir, larch, juniper, birch, elm, maple, hazel, oak, lime, willow and alder (Rybníčková & Rybníček 1991).

This site probably represents the southern limit of the taiga zone, which is difficult to define (Larsen 1980), showing a transition through isolated deciduous trees to a landscape of park land character (represented by *Ulmus, Fraxinus* and *Acer* in North America, and by *Quercus, Tilia* and *Fraxinus* in Europe and Asia) and then to steppe, conditional upon regional climate and altitudinal zonality. In North America it has been found that coniferous, mixed and deciduous all forests existed in relatively close proximity to the glacier front. Isolated thermophilous tree species are found in central and eastern European coniferous forests from at least 55 ka BP.

Sub-province B (northern Moravia and southern Poland)

A very different environment was present in the north of Moravia (Sub-province B). In layers overlying the Gravettian horizon at the site of Petřkovice, which is however much younger than above mentioned sites (23 370±160 BP - 20 790±270 BP; c. 25 370 - 22 790 calBP) there was a brown or ochre loessic soil with signs of solifluction at its base. The whole layer is penetrated by cracks due to soil shrinkage which are filled by whitish material (Jöris & Weninger 2004). The entire region is marked by the occurrence of a mainly loessic soil formed by decalcification of the original loess due to high precipitation. The latter also had a major impact on the preservation of osteological material, of which only the densest fragments have survived, e.g. tooth enamel of *Mammuthus primigenius*.

Sub-province B extends northwards from northern Moravia to parts of southern Poland. Here sites are located at 500 - 600 m a.s.l. and can be characterized following J. Kozłowski (2000):

At the Jaslo-Bryly site in the Carpathians Mountains (21.260577 E, 49.462602 N) the upper part of the sedimentary deposit is dated to 35 500±1500 BP (c. 39 ka calBP) and 34 300±1 000 BP

(c. 36 ka calBP), with a TL determination of 37 000±5 000 BP. There is evidence for a gradual change of vegetation type towards a more open landscape with groups of trees comprising *Larix* sp., *Betula* sp. and *Pinus cembra*.

Also in the Carpathians Mountains, the Dobra site close to Krakow (18.244578 E, 49.401916 N) is dated to 32 550±450 BP (c. 34 ka calBP). Here, palynological analysis found herb taxa but also the tree species *Pinus cembra, Picea* sp., *Alnus* sp., *Betula* f. *alba, Betula* cf. *nana, Salix* sp. and *Populus* sp.

At the Kryspinow site (19.480644 E, 50.022670 N), dated to 32 400±110 BP (c. 36 ka calBP) there were found besides herbs the tree species: *Betula nana, Juniperus* sp., *Salix* f. *glauca*, *Ephedra* sp., *Pinus cembra, Betula* f. *alba, Populus* sp. and *Larix* sp.

The main cultural layer (6) at Krakow-Spadzista is dated to between 20 600±1 050 BP and 24 000±300 BP by seven results, most of them from 23 - 24 ka BP. The recovered fauna comprises *Mammuthus primigenius* (NISP 5 845 / MNI 86), *Coelodonta antiquitatis* (1), *Ursus* sp. (2), *Canis lupus* (NISP 4 / MNI 1), *Lepus timidus, Alopex lagopus* (NISP 3 / MNI 2) and *Rangifer tarandus* (NISP 4 / MNI 1) (Kozłowski & Sobczyk 1987; Wojtal 2007), while the identified tree taxa are pine, fir and larch.

Wojtal (2007) assumes a moist and harsh climate for this region and Kozłowski and Sobczyk (1987) state that warmer, interpleniglacial events were not very much in evidence on the territory of southern Poland. They believe that there were nevertheless some differences in vegetation cover and that pockets of forest can be expected at sheltered sites. At this period there existed besides *Gulo gulo* and *Sicista betulina* other important species, such as *Lepus timidus, Alopex lagopus*, lemmings and the typical steppe species *Ochotona* sp.

Sub-province C (central Moravia)

South of Předmostí, many Gravettian sites are present in the alluvial plain of the Morava River and on its slopes and the surrounding hills. One of these sites, Jarošov II-Podvršťa (17.300013 E, 49.052336 N), is dated to the period 26 950±200 - 25 020±600 BP (c. 29 450 - 27 020 ka calBP). The Gravettian (terminal Pavlovian) cultural horizon here was influenced by solifluction, probably after desertion of the site. The upper part of the cultural layer was in loess, but the lower part was in the underlying soil horizon and bones are covered with precipitated $CaCO_3$. In the loess there are numerous tundra ice polygons and vertical cracks formed by gravitational displacement (Škrdla 2005).

Other Gravettian sites in the region are Boršice, Spytihněv and Chrástka. The latter site (17.210116 E, 49.034146 N) is dated 26 950 - 25 020 BP (c. 29 - 27 ka calBP) and 29 066 - 26 469 BP (c. 30-28 ka calBP) (Jöris & Weninger 2004). At these sites there also are signs of solifluction and vertical cracks similar to those at Jarošov.

This region had environmental conditions different from those in Sub-province A. The loess bed was susceptible to the development of solifluction and all evidence indicates more abundant precipitation here than was present in Sub-province A. The data suggest that this happened after abandonment of the Gravettian sites or during their decline. In the layers overlying the cultural horizon there are numerous concretions of $CaCO_3$, often forming a crust, while many fragments of bones linked to human activities were also covered by $CaCO_3$ crusts up to 2 cm thick. Many bones showed signs of secondary transport by solifluction (Nývltová-Fišáková 2005) and the high precipitation probably indicates the onset of the LGM (Musil 2005b). Erosion processes frequently occurred in the form of solifluction and vertical cracks linked with slope failure. The summits and ridges of hills in this region are without loess, which was either eroded or never deposited there. The beginning of the LGM was thus marked by a major change of climate, which influenced strongly the environment.

Neighbouring regions

New environmental data are also available from western Slovakia, at the Dzerava skala site (Kaminská et al. 2005). Here, Layer 5 was composed of a loessic soil similar to Layer 4, and both layers may in fact be identical. The dating of Layer 4 (24 760±130 BP, c. 27 ka calBP) marks the final period of occupation at the Předmostí site. Pieces of charcoal from this layer are identified as both coniferous and thermophilous deciduous trees, which according to the authors characterize an open to semi-open landscape. The tree species *Ulmus* sp., *Fraxinus* sp., *Rubus* sp., *Acer* sp., *Quercus* sp. and *Fagus sylvatica* indicate mixed deciduous forest and a relatively favourable climate (Hajnalová & Hajnalová 2005). In the mammalian microfauna (Horáček 2005) steppe elements were rare and some species indicated a forested landscape. In the case of gastropods, the decrease in number of cryophilous species is compensated by increase in species with tolerance of high temperature. The biotic communities indicate a warmer climatic period with an open landscape and dispersed pockets of forest vegetation.

H. Vaněková (2006) described a loess profile at Kaplná site in the western Slovakian Trnava Highlands (17.272157 E, 48.173245 N). In horizon C of the Gravettian layer 7, dated to 31 350±350 BP (c. 33 ka calBP), there are charcoal remains of pine, oak, beech and birch. The author interprets the environment here as scrubby pine taiga with an average July temperature of 18.5 °C.

One of the most important (late Gravettian) sites in Slovakia is Moravany-Lopata II, dated from 27 632±1 135 to 24 630±635 BP (c. 29 - 26 ka calBP). Unlike at the Moravian sites the dominant hunted animal was reindeer (*Rangifer tarandus*) with a NISP of 14 446 and MNI of 42. Other hunted animals were *Ursus arctos* (11 / 6), *Ursus* cf. *arctos, Canis lupus* (14 / 1), *Vulpes vulpes* (18 / 6), cf. *Gulo gulo* (7 / 1), *Mammuthus primigenius* (12 / 4), *Lepus* sp. (11 / 3) and *Equus* sp. (1/1) (Lípecki & Wojtal 1998; Kozłowski 1998). Arctic fox and woolly rhinoceros are here completely absent.

The Trenčianske Bohuslavice site is located at the Váh River, a few kilometres from the town of Nové Město nad Váhom. Radiocarbon dates here cluster around 25 500 - 22 500 BP. The identified mammal species are *Rangifer tarandus*, *Equus germanicus*, *Mammuthus primigenius*, *Alopex lagopus*, *Bos* sp. / *Bison* sp., *Ursus arctos*, *Canis lupus*, *Castor fiber*, *Coelodonta antiquitatis* and *Cervus elaphus*. Based on the number of recovered bones and teeth, reindeer is the dominant taxon, followed by horse and woolly mammoth. The other mammal species are rare (Vlačiky, written report 2008).

In the Danube region the most important site is Willendorf I, II (Layers 5-9, dated from 23 180±120 to 30 500±900 BP / c. 25 to 32 ka calBP). The vegetation identified here comprised *Pinus cembra, Pinus* sp., *Picea* sp. / *Larix* sp, *Betula* sp. and *Salix* sp.

Discussion

From the above data we can conclude that the environment of Gravettian sites in the eastern part of central Europe (from southern Poland to northern Austria) was quite variable. It differed not only in average temperatures, but also in precipitation. It also differed both in the composition of vegetation cover and in that of the animal species present, with a major difference in the faunal community in comparison to that from sites in western Slovakia. The latter region formed a distinct sub-province from the viewpoint of both vegetation cover and also the large fauna.

The beginning of the LGM led to general and significant cooling and increased aridity, which was then replaced by renewed greater precipitation. The intensity of this was variable across the whole region. However, the variability of environmental conditions was not of such magnitude as to cause the decline of Gravettian sites, as shown by sites in northern Moravia and Poland. Proof of the rapid changes in the faunal community is provided by the Grubgraben site in northern Austria, which dates to 22 ka - 20 ka calBP and thus follows the time period occupied by Gravettian sites. However, the composition of the Grubgraben fauna is completely different from that at Gravettian sites (Musil 2002b).

Differences were observed not only in average temperatures, but also in the amount of precipitation. A first period with high precipitation occurred only during the final stage of the existence of Gravettian sites. The greatest amount of precipitation was in Sub-province B and for this reason most of loess was there transformed into loessic soil. Above this horizon is a soil developed as a gley podsol. The leaching of loess by rain was sometimes so intense that there was formation of carbonate ortstein. In Sub-province C, carbonate coatings found on bones and sometimes carbonate ortstein show a regime of precipitation similar to Sub-province B. By contrast, Sub-province A had a rather arid climate.

Sub-province B (northern Moravia and part of southern Poland) was thus very different from central Moravia (Sub-province C) and, above all, from southern Moravia (Sub-province A), especially in its vegetation cover, in which isolated thermophilous trees did not occur, and in its more humid and colder climate (Musil 2003). There were also some differences regarding the faunal communities; exceptionally, at Moravian sites there were already some species present which are more typical for later periods. These had penetrated here from the warmer Danube region but are missing at Polish sites.

Environmental change at specific Gravettian sites

There follows a brief summary of the environment in the various regions of central Europe occupied by Gravettian settlement. The presented data (Fig. 12, Fig. 13) do not cover the complete period of the existence of Gravettian sites.

Moravia

The site of **Dolní Věstonice I** is characterized by six warm temperature oscillations. The oldest one (in MIS 3) was the most intense and settlement here finished with the coldest oscillation at the onset of the LGM. **Dolní Věstonice II** had four warm temperature oscillations and the end of settlement at the site also falls in the coldest LGM oscillation. Occupation at **Dolní Věstonice III** dates to the beginning of the Upper Pleniglacial cold period.

The oldest date from **Pavlov I** is from the soil of the Pavlov Interstadial, below the cultural layer. Two warm oscillations are identified here at the very end of MIS 3. The **Petřkovice** site similarly includes two warm oscillations with the end of site occupation coinciding with the coldest LGM stadial oscillation. Occupation at the site of **Milovice I** also came to an end with the coldest LGM oscillation, while that at the site of **Jarošov II** was in close proximity to the onset of Upper Pleniglacial cooling.

It can be concluded that the beginning of Gravettian site occupation in Moravia corresponds to the end of the Pavlov Interstadial (Musil 2001) and that sites continued to be occupied until the beginning of the Upper Pleniglacial cold period (OIS 2) but were generally deserted by the period of maximum cooling marked by the LGM stadial.

Austria

There are relatively many Austrian sites with long time spans of Gravettian occupation. The most important site and also the one with the longest time span is Willendorf. The Willendorf II site preserves five warm oscillations and Gravettian occupation finished here at the beginning of the period of maximum cooling leading to the LGM. The time span of occupation at the site of Krems-Wachtberg covers most of MIS 3. It

Pavlov Highland	Dolní Věstonice I (48.531746 N / 16.383554 E), Dolní Věstonice II (peak, western hillside), Dolní Věstonice II (northern hillside above brickyard), Dolní Věstonice II (brickyard), Dolní Věstonice III (Rajny)
	Pavlov I (eastern hillside of Děvičky Hill, 48.522812 N / 16.401601 E), Pavlov II (Malé Záhumenky), Pavlov V (northern hillside of Děvičky Hill)
	Milovice I (48.510848 N / 16.415314 E), Milovice II (eastern hillside), Milovice III (Brněnský Hill)
	Bulhary I (brickyard, 48.82325 N / 16.441359 E)
	Klentnice (48.501474 N / 16.372873 E)
	Pouzdřany (48.560683 N / 16.373076 E)
South-west Moravia	Hodonice (brickyard, 48.510384 N / 17.073739 E)
	Krhovice (48.485254 N / 16.102618 E)
	Hrušovany nad Jevišovkou (48.495019 N / 16.240528 E)
	Šatov (48.471956 N / 16.010376 E)
	Znojmo (48.512087 N / 16.025579 E)
	Jaroslavice (48.452647 N / 16.135830 E)
Drnholec Highland	Jiřice (brickyard)
West Moravia	Kožichovice (49.120020 N / 15.551812 E)
Brno Basin and surrounding region	Brno II (49.112041 N / 16.364045 E), Brno-Maloměřice
	Blučina III (49.031804 N / 16.384722 E)
	Bratčice III (49.035430 N / 16.312246 E)
	Prštice (49.065406 N / 16.281476 E)
	Měnín (49.035191 N / 16.393098 E)
	Židlochovice (49.014941 N / 16.365118 E)
	Telnice (49.055702 N / 16.424743 E)
	Horákov IV (49.173505 N / 16.290803 E)
	Tvarožná V (49.113030 N / 16.462020 E)
	Moravské Knínice III (49.173705 N / 16.290803 E)
	Oslavany (49.063280 N / 16.201697 E)
Moravian Karst	Sloup (Kůlna Cave, 49.235609 N / 16.415679 E)
	Ochoz IV (Kříž Cave, (49.143863 N / 16.443499 E)
	Suchdol (Pod Hradem Cave, 49.221339 N / 16.430674 E)
Central Moravia	Radslavice (Zelená Hora, 49.192622 N / 17.000661 E)
	Nezamyslice (Končiny, (49.193199 N / 17.102557 E)
	Droždín VI (Zadní Doleček, 49.365763 N / 17.195984 E)
	Blatec (brickyard, 49.303391 N / 17.131462 E)
	Mladeč III (Plavatisko, 49.422067 N / 17.011243 E)
	Předmostí I (Chlum Hill, 49.280210 N / 17.261305 E), Předmostí II (Hradisko), Předmostí III (southeast hillside of Chlum Hill)
	Přerov (49.272258 N / 17.272258 E)
East Moravia	Napajedla I (Šardica, 49.035594 N / 17.312229 E), Napajedla II (eastern hillside of Maková Hill), Napajedla III (brickyard), Napajedla V (Jastřabí), Napajedla VI (Dubová Hill), Napajedla VII (Kotáry)
	Spytihněv I (Němeča, 49.082645 N / 17.295372 E), Spytihněv II (Podvinohradí), Spytihněv III (Duchorce)
	Boršice I (Chrástka, 48.494052 N / 17.212042 E), Boršice II
	Ostrožská Nová Ves (Padělky, 49.001653 N / 17.260366 E)
	Mařatice (brickyard, 49.034955 N / 17.291359 E)
	Jarošov I (Kopaniny, 49.052314 N / 17.300002 E), Jarošov II (Podvršťa)
	Březolupy (Čertoryje, 49.071647 N / 17.344601 E)
	Pohořelice (Čtvrtky, 49.104334 N / 17.320810 E)
Kyjov Highland	Kyjov-Boršov (49.013922 N / 17.074184 E)
Fryšták Furrow	Lechotice (49.161240 N / 17.352023 E)
Bílé Karpaty Mts.	Bylnice (49.044381 N / 18.005399 E)
Northern Moravia and Moravian Silesia	Petřkovice (Landek Hill, 49.515455 N / 18.154798 E), Petřkovice II, Petřkovice III
	Hošťálkovice I (Dubeček, 49.505149 N / 18.125060 E), Hošťálkovice II (Hladový Hill)
	Opava I (brickyard, 49.561301 N / 17.535380 E), Opava II (sandpit)

Fig. 12. List of major Moravian Gravettian sites (with latitude / longitude) and locations of Gravettian finds (basis Oliva 2007).

Abb. 12. *Liste der wichtigsten mährischen Gravettien Fundstellen mit der geographischen Breite / Länge (Grundlage nach Oliva 2007).*

starts during a very warm oscillation and six such oscillations were recorded here altogether, the maximum number for all Gravettian sites, with occupation ending shortly after the beginning of the LGM. The sites of Langenlois and Aggsbach have only a very short time span of occupation with one recorded warm oscillation. The Gravettian occupation of sites in Austria mainly ended at the beginning of the LGM, just as observed for the sites in Moravia.

Slovakia

Occupation of the site of **Nitra-Cerman** falls into the period of LGM cooling before the maximum stadial oscillation, while that at **Moravany-Lopata II** occupies the period shortly before and during the maximum LGM cooling. Gravettian occupation at **Trenčianské Bohuslavice** begins in the Denekamp Interstadial and ends with the coldest LGM stadial event. The Moravany site is interesting because

	Site	Longitude (E)	Latitude (N)	Range of dating results (calBP)	Number of samples	Number of warm oscillations	Duration (years)
Moravia	Předmostí	17.270	49.272	34 802±476 - 29 926±572	3	4	-
	Dolní Věstonice I	16.384	48.532	37 351±1 189 - 23 604±300	13	6	14 000
	Dolní Věstonice II	16.384	48.532	33 525±799 - 25 086	28	4	c. 8 000
	Dolní Věstonice II triple grave	16.384	48.532	29 993±593	1	-	-
	Dolní Věstonice III	16.384	48.532	27 633±988	1	-	-
	Pavlov I	16.402	48.523	30 233±790 - 28 272±767	13	2	c. 2 000
	Milovice I	17.213	49.132	32 932±927 - 25 223±104	4	3	c. 4 000
	Petřkovice	18.153	49.522	29 926±572 - 24 113±842	2	2	c. 6 000
	Jarošov II	17.300	49.052	~27 200 - ~25 110	-	-	-
Austria	Willendorf II			36 131±3 008 - 25 436±231	24	5	c. 11 000
	Krems-Wachtberg			39 404±2 308 - 27 485±1 046			c. 12 000
	Langenlois			30 568±1 326 - 28 826±1 363	1		c. 2 500
	Aggsbach			30 485±890 - 29 756±531	1		c. 2 000
Slovakia	Nemšová			32 332±1 354	1		
	Nitra-Cerman			26 039±1 354	1		
	Moravany			21 378±474	1		
	Moravany-Lopata II			27 632±1 135 - 24 630±635	2		
	Trenčianské Bohuslavice			~20 280 - ~29 310	10		
Hungary	Balla Cave			37 202±1 047 - 23 344±236	5		c. 14 000
	Bodrogkeresztur			25 530±221	1		
	Puspokhatvan			32 677±3 517	1		
Poland	Krakow-Spadzista Layer 6			20 600±1 050 - 24 000±300			c. 4 000
	Obłazova Cave			36 956±1 310 - 21 449±326	4		c. 15 000
Germany	Geissenklösterle			35 600±2 500 - 26 564±333	3		c. 5 000
	Bockstein-Törle			36 541±1 605 - 23 733±330	5		c. 13 000
	Obere Klause			28 827±1 218	1		
	Mauern II			33 145±631 - 28 005±822	2		c. 5 000
	Hohler Fels			32 916±563 - 29 822±563	2		c. 3 000

Fig. 13. List of Central European Gravettian sites (for Moravia with longitude / latitude) showing the number of recorded warm oscillations and estimated total duration of settlement.

Abb. 13. *Liste der mitteleuropäischen Gravettien Fundstellen, welche im Text angeführt wurden (für Mähren mit geographischer Länge / Breite), mit Anzahl der Warmoszillationen und geschätzter Gesamtdauer der Siedlung.*

occupation here is dated to after the maximum cooling oscillation. The site **Nemšová** was occupied during a warm oscillation. The dating of Slovakian Gravettian sites is somewhat different compared to that of the Moravian sites. In contrast to Moravia the Slovakian Gravettian is dominated by sites dated to the period of maximum cooling or even after this.

Hungary

Five warm oscillations are recognized in the **Balla** cave, the end of site occupation here lies in the period of maximum LGM cooling. Similarly, the Gravettian cultural layer from the **Bodrogkeresztur** cave dates to the period of maximum cooling. By contrast, occupation at the site of **Puspokhatvan** was only during a warm oscillation in MIS 3. Occupation at all sites was ended by the period of maximum LGM cooling.

Poland

Occupation in the Gravettian cultural layer at **Krakow-Spadzista** started in the MIS 2 warm event and continues into the maximum cooling of the LGM. The **Obłazova** cave site shows altogether a total of four warm oscillations. Gravettian occupation here continued in spite of the maximum LGM cooling and only ended some time after this. Gravettian site occupation in Poland started relatively early and lasted not only until the period of maximum cooling, as at most sites located to the south, but persisted even longer. This means that the decisive factors for the occupation or desertion of Gravettian sites were not average temperatures but some other factors.

Germany

At the **Geissenklösterle** cave three warm oscillations are recorded and Gravettian desertion of the site falls at the beginning of the LGM cold period. Gravettian occupation at **Bockstein-Törle** covers five warm oscillations and survived the coldest period of the LGM before ending when the average temperature was already increasing again. The Gravettian layer from the **Obere Klause** cave dates to the very end of the period of MIS 3 warm oscillations. The **Mauern II** site documents two warm oscillations and Gravettian occupation of the site ended at the onset of LGM cold period. At **Hohler Fels** cave, only two warm oscillations are documented and the end of site occupation already occurred before the beginning of the LGM cold period. Important is the fact that Gravettian occupation of the sites ended before or during the onset of the LGM cold period.

Mammal assemblages at individual Moravian and Slovakian sites

According to the frequencies of the animal species at Gravettian sites we can divide them into several groups (Musil 1958, 1997, 2003, 2005c).

1. Woolly mammoth predominant (most abundant group).
2. Wolf, fox and hare (second most abundant group).
3. Reindeer and bear.
4. Occasional representation of all the following species: wolverine, horse, woolly rhinoceros, giant deer, elk, beaver, hyena, lion, leopard, roe deer, caprids, ovibovines.

The first and second groups of animals are common in the majority of cultural layers of Gravettian sites, they differ only in numbers.

Předmostí

From the outline of species at Předmostí (typical LCM) it is evident that Gravettian hunters exploited all available animals. The quantities of bones and abundance of different animal species are given in Figure 14.

In spite of the fact that the data are from only part of the cultural layers at Předmostí, we believe that they represent the relative numbers of animals available for hunting in the surrounding area. However, in any case they do not represent the total number of hunted animals, since they are not derived from systematic investigation of the whole site, but only limited areas and most finds were destroyed during exploitation of loess for local brickworks. More detailed examination of the quantity of particular species at Předmostí reveals several important aspects:

1. There are high numbers of woolly mammoth but low numbers of woolly rhinoceros. Woolly rhinoceros had the same ecological requirements as woolly mammoth and they generally occurred together. This observation was also made at other Gravettian sites in Moravia and probably has a general validity. This probably means that the number of woolly rhinoceros in the region decreased much earlier than that of woolly mammoth.
2. Large numbers of wolves and foxes occur compared to the other animals. Based on other Gravettian sites we know that these animals mostly provided fur and only exceptionally served as food. The preservation of the bones is quite different from that of the other animals. Bones are not broken open and parts of skeletons are recovered in anatomical order. The animal carcase was therefore discarded in its entirety after skinning (Musil 1994, 1997).
3. There are only relatively low numbers of reindeer and horse. These are animals living in large herds, probably inhabiting hilly areas covered by grassy vegetation in the proximity of Předmostí. This phenomenon is also encountered elsewhere. **Trenčianské Bohuslavice** in Slovakia is an exception, but this site is a little younger. Only later, in the cultures of the Epigravettian and Magdalenian, was there hunting of these species in large numbers.
4. There is strikingly low number of carnivore species.

		NISP	%	MNI	%
Mammoth	*Mammuthus primigenius*	unknown		> 1000	
Wolf	*Canis lupus*	4143	*43.2*	103	*7.4*
Arctic fox	*Alopex lagopus*	2250	*23.7*	96	*6.5*
European hare	*Lepus europaeus*	52	*0.4*	8	*0.6*
Arctic hare	*Lepus timidus*	860	*9*	79	*5.6*
Reindeer	*Rangifer tarandus*	890	*9.3*	36	*2.6*
Wolverine	*Gulo gulo*	581	*6.1*	12	*0.9*
Horse	*Equus germanicus*	194	*2*	5	*0.4*
Brown bear	*Ursus arctos*	233	*2.4*	8	*0.6*
European brown bear	*Ursus arctos arctos*	82	*0.9*	2	*0.1*
Woolly rhinoceros	*Coelodonta antiquitatis*	5	*0.1*	1	*0.1*
Giant deer	*Megaloceros giganteus*	13	*0.1*	1	*0.1*
Elk	*Alces alces*	13	*0.1*	2	*0.1*
Beaver	*Castor fiber*	4	*<0.1*	2	*0.1*
Hyaena	*Crocuta spelaea*	4	*<0.1*	1	*0.1*
Lion	*Panthera spelaea*	1	*<0.1*	1	*0.1*
Leopard	*Panthera pardus*	1	*<0.1*	1	*0.1*
Bison	*Bison priscus*	25	*0.3*	2	*0.1*
Aurochs	*Bos primigenius*	9	*0.1*	1	*0.1*
Badger	*Meles meles*	23	*0.2*	2	*0.1*
Roe deer	*Capreolus capreolus*	2	*<0.1*	1	*0.1*
Ibex	*Capra ibex*	2	*<0.1*	1	*0.1*
Musk ox	*Ovibos moschatus*	4	*<0.1*	1	*0.1*
Norway lemming	*Lemmus lemmus*	12	*0.1*	3	*0.2*
Collared lemming	*Dicrostonyx torquatus*	16	*0.2*	4	*0.3*
Mole	*Talpa europaea*	25	*0.3*	2	*0.1*

Fig. 14. Species diversity among the mammals at Předmostí (Late Gravettian / Pavlovian), shown by numbers of identified specimens (NISP) of recovered bones and established minimum numbers of individuals (MNI) together with their percentage contributions to the assemblages. For percentage of NISP, Mammoth not taken into account; for percentage of MNI, Mammoth taken as 1000.

Abb.149. *Artenvielfalt unter den Säugetieren bei Předmostí (Spätes Gravettien / Pavlovien), dargestellt durch die Zahl der identifizierten Reste (NISP) und durch die Mindestindividuenzahl (MNI) zusammen mit ihren prozentualen Anteilen. Für prozentualen Anteil an NISP, Mammut nicht berücksichtigt; für prozentualen Anteil an MNI, Mammut mit 1000 angesetzt.*

Based on the long period of existence of this site we would expect more such animals.

5. All other animal species lived in the surrounding landscape in low numbers.

6. Species which had different ecological requirements from most of the faunal community were found only occasionally.

South of Předmostí, along the Morava River, there is a high number of Gravettian sites with similar climatic conditions to Předmostí.

Jarošov-Podvršťa

At this site (17.300013 E, 49.052336 N) (26 950 ± 200 to 25 020 ± 600 BP: 29 450 to 27 020 calBP) the composition of the suite of hunted animals was similar to that at Předmostí, but the degree of preservation and quantity were different. The highest number of remains belonged to *Alopex lagopus*, the second most common hunted species was Lepus sp. and other species represented were *Lynx lynx*, *Canis lupus*, *Vulpes vulpes*, *Gulo gulo*, *Mammuthus primigenius*, *Equus* sp. and *Rangifer tarandus*. Small animal species predominated (Musil 2003, 2005b).

Along the Dyie river (southern Moravia)

Dolní Věstonice

This is a typical LCM Fauna: *Lepus timidus* (dominant), *Castor fiber, Lynx lynx* (rare), *Panthera leo* (rare), *Canis lupus* (dominant), *Vulpes vulpes* (rare), *Alopex lagopus* (dominant), *Gulo gulo* (rare), *Ursus arctos* (rare), *Mammuthus primigenius*, *Coelodonta antiquitatis* (rare), *Equus germanicus, Rangifer tarandus* and *Bos* sp or *Bison* sp. (rare) (Musil 1959; 2003).

Pavlov

The site has a typical LCM Fauna. The avifauna comprises *Corvus corax, Lyrurus tetrix, Alectoris* sp., *Lagopus* sp., Phasianinae gen. *et sp*. indet. and *Cygnus* sp.. Mammals are diverse. A well presented group (10 - 18% of the total amount) includes *Canis lupus, Vulpes vulpes, Alopex lagopus* and *Rangifer tarandus.* A group with medium representation (4 - 8 % of the total amount) contains *Gulo gulo, Mammuthus primigenius* and *Equus germanicus.* Only sporadically represented (0.2 - 0.7 %) are *Citellus* sp., *Cricetus cricetus, Felis silvestris, Panthera leo, Lynx lynx, Ursus arctos arctos, Cervus elaphus* and *Bos* sp. or *Bison* sp. (Musil 1994; 2003).

Milovice

At Milovice (17.212674 E, 49.131639 N) values are given as NISP and percentage of the assemblage folowing Seitl in Musil (1994): *Mammuthus primigenius* (6 748 / 25%), *Equus germanicus* (145 / 1.9%), *Canis lupus* (37 / 0.5%) and *Panthera leo* (7 / 0.1%). Four radiocarbon dates place the site between 25 220+/-280 and 21 200+/-1.100 BP, the latter result on woolly mammoth bone.

Western Slovakia

Dzeravá skála

This is a Gravettian site in western Slovakia, which was subjected to comprehensive analysis (Horáček 2005; Ďurišova 2005; Alexandrovicz 2005) and provides a detailed picture of species (vertebrates and gastropods) associated with the Gravettian. According to Alexandrovicz (2005), none of the identified species of gastropods corresponds to those of the recent polar climate of tundra and forest tundra. He considers the course of the Carpathians Mountains as forming a climatic barrier against the penetration of cold air to south.

In the mammal microfauna, cold-loving species dominate in all samples (Horáček 2005). This also applies to Layers 1 and 2, which are of Holocene age. This suggests that the gastropod communities and probably also communities of mammalian microfauna were strongly influenced by the cold climate of the deep karstic valley here and therefore cannot be used for the interpretation of the climate of the larger surrounding area.

While Layer 3 (25 050 + 540/-510 BP, c. 27 ka calBP) probably also includes younger (intrusive Holocene) finds, most of them belong to the beginning of the LGM, before the maximum period of cooling. The larger mammal fauna comprises *Lepus* sp., *Ursus spelaeus*, *Rangifer tarandus, Alopex lagopus* and *Vulpes vulpes*. According to Hajnalová and Hajnalová (2005) the fauna represents species typical for an open cold steppe, but charcoal finds indicate rather mixed deciduous forest. According to Alexandrovicz (2005) the identified gastropods had high ecological tolerance, i.e. some species preferred cold climate and other species warm climate. Micro-mammal species typical for steppe were missing and some species indicated a forested landscape (Horáček 2005).

Layer 4 (24 800±130 BP, c. 27 ka calBP) is overlain by big limestone blocks and is middle Gravettian on the basis of archaeological finds. The communities of gastropods in Layers 4 and 5 were similar, with a reduced number of cryophilic species and increased number of species with high temperature tolerance. The number of cold adapted species of the small mammal fauna also decreased. The interpretation is of an open landscape with dispersed forest vegetation and isolated spots of forest. The following large mammals were present: *Rangifer tarandus, Vulpes vulpes, Alopex lagopus, Ursus spelaeus* (many), *Lepus* sp., *Equus* sp., *Lynx lynx, Rupicapra rupicapra, Gulo gulo* and *Meles meles*.

Layer 5 is a loessic deposit similar to Layer 4 and it is possible that both layers were identical. It is dated to 24 760±130 BP (c. 27 ka calBP). There were only few finds of faunal remains: *Ursus spelaeus, Lepus* sp., *Rangifer tarandus* and rarely horse. These represent an open or semi-open landscape.

Principal migration and transport routes

Moravia takes up an exceptional position in central Europe. All mountains in the surrounding region run from west to east and form a barrier to north-south migrations during cold periods. Only the territory of Moravia itself and its wide lowlands connect the southern Danube with the northern Polish lowlands through the Moravian Gate. These circumstances were of major importance for the migrations of large mammals, which were both seasonal in nature and caused by larger climatic oscillations. All Gravettian sites are located in the valleys of principal Moravian rivers: the Dyje, Svratka, Morava, Bečva and Odra.

Předmostí was the most important site with regard to movements of fauna, being located in a distinct strategic position (Fig. 15, No. 2) where two major south-north-running migration routes coming from the Danube region converged, to continue through the Moravian Gate as a single route to the broad lowlands of northern Europe. The length of the migration route connecting the Danube region and the Polish lowlands is about 200-250 km.

Migration paths for animals also served as transport paths for human groups and for the import of raw materials for the production of artefacts. The collections of Absolon and Klíma from the Dolní Věstonice site contain c. 84% flint (Oliva 2007). According to J. Svoboda (1999, 2000, 2001b, 2001c), between 60 % and 90 % of the raw materials from Gravettian sites in southern Moravia are derived from Silesia. Analysis of lithic raw materials from Pavlov I indicates that the distance to their source is up to 150 km.

Regarding animal migrations, it is necessary to distinguish between seasonal migrations, which were repeated every year, and other migrations caused by climatic changes. Seasonal migrations were caused primarily by different availability of food during the course of a year, by competition in a given region, by the beginning of the reproduction period and by the onset of unfavourable living conditions (e.g. insects). Migration routes generally remained the same and even the crossing of rivers and mountains took place at unchanged locations. Nevertheless, this did not imply the complete seasonal disappearance of a species from its territory and a certain number of animals stayed there permanently (Musil 1994, 1997).

Another category of migration, which is important

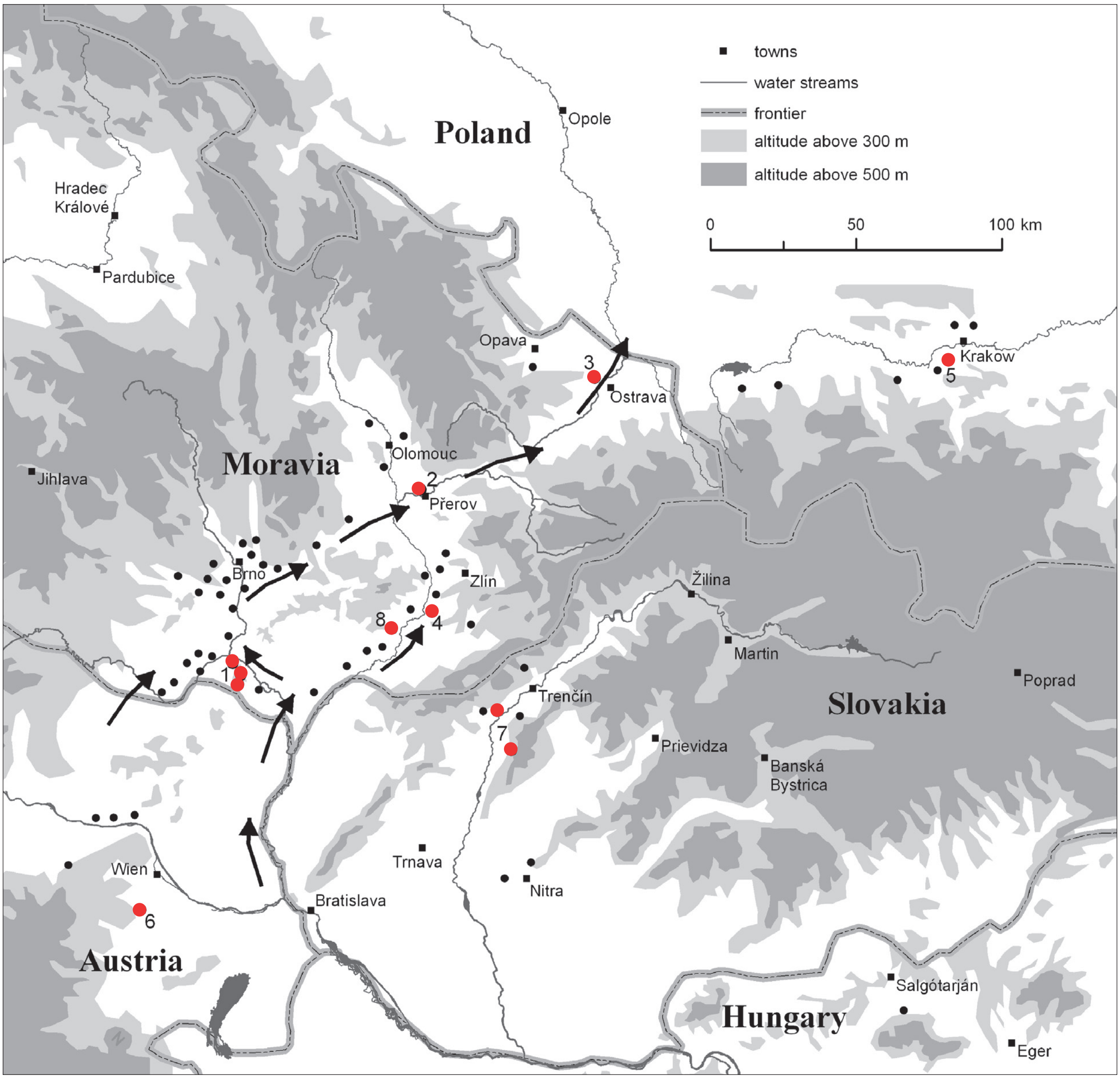

Fig.15. Location of Gravettian sites in Moravia and neighbouring regions showing main migration routes of animals and ancient humans (arrows). White: flood plains; pale grey: uplands (300 - 500m a.s.l.); dark grey: mountains (above 500 m). Red dots show major Gravettian sites: 1 - Dolní Věstonice, Pavlov and Milovice; 2 – Předmostí; 3 – Petřkovice; 4 – Jarošov; 5 - Krakow-Spadzista; 6 – Willendorf; 7 - Trenčianské Bohuslavice and Moravany; 8 - Boršice. Black dots show further locations of Gravettian finds in the territory of Moravia and in neighbouring areas. All Moravian sites were located in the valleys of principal rivers. The Předmostí site lies at the confluence of two major animal migration routes. Such migration routes also served human groups and for the import of raw materials for the production of artefacts. We can differentiate between three categories of Gravettian localities. The first ones are the largest and most spacious sites such as Dolní Věstonice-Pavlov, Předmostí and Krakow-Spadzista Street. They are the central sites in this region. The second level is represented by lesser sites such as Milovice, Jarošov, Petřkovice, Moravany etc., but the greatest number of Gravettian localities belongs to the third level, that of occasional and short-term localities.

***Abb. 15.** Lagen der Gravettien Fundstellen in Mähren und Nachbarregionen mit Angabe der wichtigsten Wanderwege von Tieren und damaligen Menschen (Pfeile). Weiß: Flussniederungen, hellgrau: Mittelland (300-500 m ü.d.M.); dunkelgrau: Berge (über 500 m). Rote Punkte zeigen die wichtigsten Gravettien Siedlungen : 1 – Dolní Věstonice, Pavlov und Milovice; 2 - Předmostí; 3 - Petřkovice; 4 - Jarošov; 5 - Krakow-Spadzista; 6 - Willendorf; 7 - Trenčianské Bohuslavice und Moravany; 8 - Boršice. Schwarze Punkte zeigen weitere Gravettien Fundstellen im Gebiet von Mähren und in benachbarten Gebieten. Alle mährische Siedlungen sind in den Tälern der wichtigsten Flüsse gelegen. Die Siedlung Předmostí liegt am Zusammenfluss der beiden großen Tier-Migrationsrouten. Diese Migrationsrouten dienten auch den menschlichen Gruppen für die Einfuhr von Rohstoffen zur Herstellung von Artefakten. Es können drei Kategorien von Gravettien Fundstellen unterscheiden werden. Die ersten sind die größten und geräumigsten Siedlungen wie Dolní Věstonice-Pavlov, Předmostí und Krakau-Spadzista Gasse. Sie sind die zentralen Siedlungen in diesem Gebiet. Die zweite Kategorie sind kleinere Siedlungen wie Milovice, Jarošov, Petřkovice, Moravany, etc., die größte Anzahl von Gravettien Lokalitäten gehört aber zur dritten Katergorie, welche gelegentliche und kurzfristige Aufenthalte darstellt.*

in the context of changing faunal composition, was caused by climatic changes. This was especially important for stenoec organisms. Latitudinal migrations were caused primarily by temperature changes. Longitudinal migrations generally responded to the amount of precipitation, with increasing aridity of climate causing the expansion of the eastern European steppes to western Europe and, consequently, the immigration of eastern European and Asian species to the region. By contrast, increased humidity did not extend so fast to eastern central and eastern Europe, at least not over long periods of time. This means that the species adapted to arid climate and, during the Last Glacial, to cold climate had a greater potential for westward migration than did warm and humid climate species for eastward migration.

The Gravettian environment at Předmostí and in the surrounding region

I start this chapter by emphasizing the statement of Ložek (2002), that there is no recent analogy for the conditions in the Pleniglacial. The development of soils and composition of the vegetation and fauna are very different from those under recent conditions in sub-polar regions, with which the environment of central European glacial periods is frequently compared. For example, the fossil gastropod fauna includes sub-arctic and arcto-alpic species, but also several steppe species found today in warm and dry zones of the temperate region, which indicate that conditions were much more favourable than those in far north today. For this reason the use of terms like “loess steppe” and especially “tundra” in the description of the glacial environment describe ecosystems which are in fact only superficially similar to the recent steppe of Eurasia or the sub-polar tundra.

As a model example for Gravettian sites in Moravia we choose the Předmostí site. Its analysis is based on both a regional and especially a local perspective, because together they characterize well the environment and its mesoclimate in the past. From the point of view of altitude it is possible to distinguish three distinctly different environments in the proximity of Předmostí. These are flood plains of variable size in the river valleys, highlands with an altitude of 300 - 500 m flanking the river valleys and the higher mountains.

In close proximity to the Předmostí site are the fluvial plain of the Bečva Rive valley, which is about 5 km wide and flanked by lowland and hilly relief, and the broad (about 10 km) fluvial plain of the Morava River. To the southeast of the Předmostí site is a large area of mostly flat uplands, with altitude of about 300 m a.s.l., while to the north is the ancient upland of the southern tip of the Oderské Hills. There also is a similar topographical situation at the other side of the fluvial plain of the Morava River.

Hunting of animals was thus focused on animals occurring in low hilly uplands of steppe character and also on those which gathered in the gallery forests in valleys over the winter. This means that we have to consider two different locations for of animal hunting separated in time, which would have increased the potential economic basis and influenced the size of human population. It is hardly possible to find a site for the hunting of animals with such a favourable and unique position as at Předmostí.

Temperatures based on modelling show that there was a much larger difference between winter temperatures at the Předmostí period and today, than is the case for summer temperatures. In winter temperatures were between -17.8 and -23.4 °C, in summer between 13.7 and 19.2 °C (Aiello & Wheeler 2003). Average wind temperatures in the region around Předmostí were low in both winter and summer.

Finds of charcoal from fir, hazel, oak and hornbeam were recovered from the upper Gravettian (Pavlovian) cultural layer at Předmostí (Musil 2001). Even from this small sample we can assume that tree species around water courses were similar to those from southern Moravia, where in river valleys there are sparse occurrences of thermophilous deciduous trees (*Quercus* sp., *Carpinus* sp., *Fagus sylvatica, Alnus* sp., *Betula* sp., *Tilia* sp., *Corylus* sp., *Acer* sp., *Salix* sp., *Populus* sp. and *Ulmus* sp.). However, the composition of plant communities here was different from that of the Gravettian sites of southern Poland, where thermophilous deciduous trees did not grow.

The great diversity of the faunal community is directly linked to the diversity of vegetation and indicates that the surrounding landscape was not monotonous from the viewpoint of vegetation cover. We must distinguish between the surrounding highlands and the wide river valleys. The high diversity of species does not correspond to the diversity of species in the recent taiga, where the number of taxa is much lower, and probably rather corresponds to that of recent temperate forest, although this analogy is not appropriate with regard to the faunal communities represented.

The faunal communities of southern Poland and Moravia differ in the species present. Animals represented at Předmostí include species living in both forests and in an open landscape. For some of them optimum conditions were found in wetlands and close to bodies of water, while for others it was arid steppe (Musil 2008). This confirms the presumption that two different biotic provinces existed in the Předmostí region. The composition of species observed shows that galleries of coniferous forests with isolated deciduous trees could occur around water courses and abandoned river branches in both cold and mild climates. The flood plains were connected to highlands with grassy steppe, with shrubs present at optimum sites and with isolated occurrences of trees. This assumed pattern is not consistent with the relatively small number of horses, which are typical for an open steppe landscape, and of reindeer. Both species would have lived in the highlands around Předmostí in large herds and their hunting was not difficult.

The extensive hunting of woolly mammoths at Předmostí has no parallel at other Gravettian sites in Moravia. These were animals living on the steppe, but they were also linked to water bodies and lakes since woolly mammoths required daily large amounts of water, which was difficult to find in the winter period. This region is marked by the occurrence of travertines formed by the discharge of warm springs and it is possible that these sources of warm water attracted large herds of woolly mammoths in winter, meaning that these sites were favourable for their hunting (Haynes 2006). Such specialization in mammoth hunting could thus be explained by these features specific to the region.

From the viewpoint of present biotopes, hunting activities at Předmostí can be divided as follows:

1. Hunting in the highlands, but not in the winter months.
2. Hunting in gallery forests around water courses, mostly in the winter months.
3. A specific feature of the Předmostí site is the hunting of woolly mammoths around warm springs, especially in the winter months.

Occupation of the Předmostí site came to an end at the beginning of a period of major climatic changes. All data indicate that in the period after 26 ka BP (c. 28 ka calBP) there was not only cooling, but also increasing aridity of climate, resulting in the beginning of the deposition of loess. Increasing aridity linked to cooling is found everywhere in central Europe at this period, but there are differences with regard to temperatures between the south and north of central Europe. In spite of this, cooling is precisely recorded, even in the Pannonian Basin. From 28 - 27 ka calBP there is an extremely dry climate, from 27 - 25 ka calBP follows strong cooling and the appearance of tundra and from 25 - 23 ka calBP cryophilous species of gastropods dominate. When such climatic deterioration occurred in the Pannonian Basin, we have to assume that it was even more intense in Moravia.

The deterioration of climate at the beginning of Last Glacial Maximum (LGM) and the increasing aridity necessarily resulted in changes in the vegetation cover, especially in the surrounding highlands, and in the shrinking of previously continuous gallery forests in the catchments of water courses. The subsequent rise in short-term precipitation multiplied the impact of these changes. All these factors necessarily caused a large reduction in the availability of plant food and, thus, in the number of herbivores. Another consequence could be the human population migrations, which may have been one of factors leading to the decline of the Předmostí site.

New data have changed our view of the environment in the period under consideration. Already earlier, on the basis of ecological analyses of the Pavlov and Dolní Věstonice fauna, we were able to propose the existence around water courses of coniferous forest of boreal type (taiga) with isolated thermophilous deciduous trees (Musil 1959, 1999).

The vegetation changed from the river valleys towards the highlands, initially probably into a landscape of park character, then to steppe with sparse trees and shrubs. What did the landscape around Předmostí look like? In the valley alluvium around both banks of the Bečva and Morava Rivers were coniferous forests with sparse deciduous thermophilous trees and marshland in the abandoned river arms. This more or less swampy environment was caused by the presence of water courses and not by high precipitation. In the highlands surrounding the river alluvium there were arid steppes, probably with small forests at optimum locations. The highest mountains were almost worthless for animals and, thus, for human hunting. At intermediate altitudes the highlands had only seasonal importance during the humid period, i.e. in the spring and to a lesser extent in summer, when the grass was dry. From the viewpoint of human hunting only the river valleys were important all year around, but especially in winter when they attracted animal herds down from higher altitudes.

The economic foundation of the lifestyle of the Gravettian people at Předmostí was provided primarily by woolly mammoths, together with a number of other animals of medium size (hare, fox and wolf). This indicates a relatively narrow subsistence base, which could only be successful when large numbers of animals were hunted. The deterioration of climate linked to increasing aridity caused essential changes of vegetation cover, lack of food for herbivores and a reduction of the number of animals. Once there was a significant change in the number of available animals, this had an impact on the economic base and the livelihood of the Gravettian people. The reduction in number of animals was possibly one of the factors responsible for the abandonment of the Předmostí site.

Summary

From the information summarized above we can conclude that Gravettian sites were occupied especially at the end of the MIS 3 period, which was characterized by intense short-term temperature oscillations and that most sites were deserted at the onset of cooling (MIS 2) leading up to the maximum cold of the LGM stadial, some of them being abandoned even earlier. Only a tiny number of sites survived the period of cooling. The time span of the occupation of Gravettian sites is the same in territories located to the north and to the south. This means that decisive factor for human residence was not only temperature, but must also have included some other features.

Moravia contains the most important concentration of large and complex Gravettian sites in central Europe. Their size, the large numbers of hunted animals and the diverse archaeological inventories show that the region was a cultural centre of the Gravettian, especially between 33 ka - 25 ka calBP, caused principally by the favourable location of the territory Svoboda et al. 2000).

Moravia provided the only natural central European passage (Moravian Gate) between the Danube region and the lowlands of northern Europe. All Gravettian sites in Moravia are linked to the valleys of the principal Moravian rivers, the Dyje, Svratka, Morava, Bečva and Odra. For central Europe, Moravia not only formed the connection between north and south, but also represented a region enjoying a certain climatic transition between the always warmer and more arid Pannonian Basin and the Danube region to the south and the colder and more humid lowlands of northern Europe. From the perspective of north-south migrations, the site of Předmostí played a key role. It was located at a strategic site of the confluence of two migration routes, which were very important for the transfer of both flora and fauna and, consequently, for the movements of humans of the period. The importance of the site was strengthened by the occurrence here of warm springs.

At Předmostí, hunting was focused on the animals living in the lower surrounding highlands, but also on those which gathered in winter in the gallery forests along river valleys. In winter, the warm water springs were important for woolly mammoths. When we also consider the important location of Předmostí on the north-south migration route, not many other Gravettian sites could match it in importance. All these factors increased the potential of the economic basis and thus influenced the size of human population. Few sites had such a significant and unique strategic location for animal hunting as Předmostí.

All these factors were very decisive for long-term residence of Gravettian peoples and extended occupation probably only occurred at sites like Předmostí. Climatic analysis of Gravettian sites has showed that the longitude and latitude of a site did not play as important a role as topography and site location. The regions of north-western Europe were climatically different from central and eastern Europe, with the aridity of climate increasing from western towards central Europe and the number of days with snow decreasing dramatically to between two and three months. The composition of the large mammal fauna at all Gravettian sites confirms this unambiguously.

If we compare recent biomes with those in the alluvial valleys of the River Morava from the end of the Last Glacial, no exact analogy exists at the present day and an approximation would need to consider a combination of several recent biomes. Of these, it is necessary to exclude tundra completely from the alluvial valleys. Regarding other biomes the largest part of these would match conditions of recent taiga and steppe landscapes and, when the sparse occurrence of thermophilous deciduous trees and the great diversity of mammals are taken into account, there would also be a limited analogy with the deciduous forest biome.

The Last Glacial biome was thus completely different from recent ones, probably resembling the southern limit of the taiga with a transition through a sparse presence of deciduous trees to a landscape of parkland character and then to steppe, the details being dependent upon the regional climate and altitudinal zonality. All available information points to a continuous presence of isolated thermophilous deciduous trees in the coniferous forests located around water courses, not only during the Gravettian period itself, but also during the whole preceding period of the Last Glacial.

The diversity of animals present at Moravian Gravettian sites was large. The commonest species was the woolly mammoth, whereas numbers of woolly rhinoceros were negligible. Compared to other mammal species, there were disproportionate numbers of wolves, hares and foxes, while the rather limited numbers of hunted reindeer and horse are surprising, since these are herd animals which definitely lived in the proximity of the Gravettian sites. Species typical for recent boreal forest were found together with species typical for deciduous forests and steppe. Modern mammal communities were formed only a few thousands years ago and the Pleistocene communities have no modern analogy. Analysis of the fossil mammals shows that even the migration radius of particular species changed.

In contrast to the other finds, the analyses of gastropods indicate a cold and dry climate (loess steppe) at the Gravettian sites, with cold winters and warm summers (warm loess steppe). This difference can be explained only by the different migration radius of the particular groups of animals, for example between gastropods, birds and large mammals. Unlike in the case of mammals, the composition of gastropod communities was highly dependent on microclimatic conditions of the local environment.

After the relatively warm period of MIS 3, with relatively large climatic oscillations, there was strong cooling leading to the LGM, which resulted in the formation of continuous permafrost in Britain, northern Belgium, the Netherlands, northern Germany and northern Poland. These regions were very different from those of central Europe, e.g. from southern Poland, Moravia, Austria, Slovakia and Hungary.

The Gravettian people at Předmostí did not live in a constant climate and during the period of occupation experienced several climatic oscillations, at least two of which were intense, with initially arid climate accompanied by the accumulation of loess followed by period with greater short-term precipitation, solifluction and further cooling. The phase of highest precipitation, which must have been intense in central and northern Moravia, occurred at the very end of the Gravettian occupation of Moravia; the abandonment of the Předmostí site falls at the onset of a colder period with intense precipitation and so, basically, to the beginning of the LGM. It cannot be ruled out that these unfavourable conditions (initially increased aridity, then intense precipitation) could be one of the reasons leading to the disappearance of Gravettian sites in the region.

The environment at central European Gravettian sites reveals differences not only in average temperatures, but also in precipitation. There were also differences in vegetation cover and in the composition of the animal species hunted. The territory of Slovakia and the Pannonian Basin formed a distinct subprovince with regard to both their vegetation cover and the animal community.

The beginning of the LGM brought not only strong cooling, but also increased aridity, which was then followed by a period of high precipitation. Although these events occurred everywhere, their intensity differed between regions, suggesting that the variability of environment did not in itself limit the presence of Gravettian sitesWithin the chronological framework we can conclude that the beginning of Gravettian occupation fell at the end of the Pavlov Interstadial (Musil 2001), coinciding with the beginning of loess accumulation, and that the duration of occupation was in total about 14 000 years. Site occupations ended in the period of maximum LGM cooling, not only in the case of the Moravian sites, but also at other sites in central Europe and this can be regarded as one of the great human and cultural catastrophes. In spite of the decline of most Gravettian sites at this period, some of them survived for a limited period of time. If their disappearance was caused by the changes in the environment, there should then have been terminal Gravettian sites in climatically more favourable regions like Slovakia and Hungary. Younger sites indeed existed there, but we also find contemporary sites in southern Poland and even in Germany. This means that we must be cautious in the evaluation of the impact of climatic factors because they represent only one among many factors and are in no way the decisive ones. The problem is that all the available analyses of finds represent an average from cultural layers deposited over many thousands of years. Since the amplitude of the climatic oscillations during the Gravettian was relatively small, the presented interpretation is based upon a grouping of a large number of oscillations and does not equate to singular climatic events. In fact, we do not know what caused the disappearance of the Gravettian sites, but in any case, changes of climate were not the single or indeed decisive factor.

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