The Holocene distribution of European bison
– the archaeozoological record

Distribución Holocena del bisonte europeo
- el registro arqueozoológico

KEY WORDS: Europe, Holocene, European bison, distribution, archaeozoological record.
PALABRAS CLAVE: Europa, Holoceno, bisonte europeo, distribución, registro arqueozoológico.

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ABSTRACT
The paper presents a reconstruction of the Holocene distribution of European bison or wisent. It is based on the archaeozoological record of this species. European bison was an early Postglacial immigrant into the European continent. The oldest evidence comes from sites in northern Central Europe and South Scandinavia dating to the Preboreal. In the Mid- and Late Holocene, European bison was widely distributed on the European continent. Its range extended from France in the west to the Ukraine and Russia in the east. Except for an area comprising East Poland, Belarus, Lithuania and Latvia, European bison was a rare species in most regions of its range. In the Middle Ages, there is a shrinkage of the range of wisent in its western part.

RESUMEN
El artículo presenta una reconstrucción de la distribución holocena del bisonte europeo. Está basada en el registro arqueozoológico de esta especie. El bisonte europeo fue un inmigrante al Continente europeo durante el Postglacial inicial. La más antigua evidencia procede de yacimientos del Norte de Europa Central y del Sur de Escandinavia, que datan del Preboreal. Durante el Holoceno medio y tardío el bisonte europeo estaba ampliamente distribuido en el Continente europeo. Su distribución se extendía desde Francia al W hasta Ucrania al E. Salvo para un área que comprende el E de Polonia, Bielorrusia, Lituania y Letonia, el bisonte europeo era una especie rara en la mayor parte de su distribución. En la Edad Media se da una reducción en la extensión del bisonte europeo en su zona W.

LABURPENA

INTRODUCTION
The European bison or wisent is the largest herbivore in Europe. Being at the brink of extinction in the early 20th century, the species survived its complete extermination due to measures of conservation like captive breeding and reintroduction in the succeeding decades (PUCEK 1986, 2004). Today, free-ranging and semi-free herds of bison can be found in various parts of East Europe, i.e. in Poland (Bialowieza National Park), Belarus, Lithuania, Russia, Romania and the Ukraine.

It is generally assumed that the European bison is derived from an unknown form of the long-horned steppe bison (Bison priscus), a species which became extinct by the end of the last glacial (McDONALD 1981; VON KOENIGSWALD 1999; PFEIFFER 1999). The steppe bison was a
characteristic animal of the Mid- and Upper Pleistocene steppes of the Northern Hemisphere. Its range extended from Spain through Central and Eastern Europe into Siberia and across Beringia into North America (Kahlke 1994). In this large area and in the course of so many millennia, the steppe bison evolved into different races that were adapted to various environmental conditions like cold steppes or Interglacial forest-steppes (von Koenigswald 1999). At the end of the Pleistocene, Bison priscus became extinct and was replaced by short-horned bisons. The details of this replacement and the evolution of the Holocene bisons in Eurasia and North America are still unknown.

Following Bohlken (1967), the recent Old and New World forms of the bison are regarded as members of the same species, Bison bison Linné 1758. Other authors, on the base of significantly different morphotypes and extreme disjunctive distribution give the European bison and North American bison the status of a separate species (cf. Wilson & Reeder 1993). Two subspecies are recognised in European bison, i.e. the lowland bison or wisent (Bison b. bonasus) and the extinct highland or Caucasus bison (Bison b. caucasicus).

Concerning the ancient distribution of European bison, attempts of reconstruction have mainly been based on historical written sources so far (e.g. Pucek 2004, Fig. 8.1). Unfortunately, these data are not always unequivocal and reliable for various reasons. For example, medieval authors have mixed up the names of bison and aurochs leading to wrong conclusions (von Lengerken 1953). Beside written sources there exist other data which can be used for a reconstruction of the former range of European bison, i.e. bone finds from archaeological sites and natural deposits. In contrast to written sources which are available only for the last two millennia they cover the whole time span from the period of immigration of this species in the early Postglacial until Modern Times. This article presents the archaeozoological record of bison (wisent) from the Holocene of Europe.

**MATERIAL**

Two species of wild cattle have been identified in Holocene faunal assemblages from Europe: the aurochs, Bos primigenius, and the European bison, Bison bison. In general, the bones of both species are highly fragmented in archaeological sites due to their exploitation as resources for food and raw materials. The morphological discrimination between the two species depends on those rare finds which are well enough preserved for positive identification (Figure 1). Lehmann (1949) and Stammfli (1963) have worked out characters useful for the osteological discrimination of aurochs and European bison. But even with that the distinction between the remains of Bos and Bison requires a lot of experience and is often impossible with fragmented bones.

Aurochs, the most common species of wild cattle in many parts of Europe during the Holocene, is often identified without positive morphological evidence. Its identification is then solely based on the assumption that no other species of cattle is as likely to be present at the particular site. Because of this practice, one can be almost certain that some specimens of European bison are hidden among bone remains more or less tentatively identified as Bos primigenius. Considering the still fairly large subfossil record of European bison, those misidentifications will probably not distort the general picture of the ancient distribution of this species.

The data used here comes from a database with faunal data extracted from archaeozoological site reports from the whole of Europe, considering the period from ca. 15,000 BC to Modern Times (Benecke 1999). At present, the database contains information from about 7500 Late Pleistocene and
Holocene faunal assemblages from 32 European countries. The European part of Russia has not been considered here because of insufficient data with regard to *Bison bison*. European bison has been identified in 169 assemblages. Table 1 presents an overview about the number of records according to countries and periods. There are great differences in the total numbers of records between single periods. This is mainly due to the uneven distribution of the recorded faunal assemblages by chronozones. The Neolithic, Roman Iron Age and Middle Ages have produced much more faunal materials from archaeological sites than other periods.

RESULTS

The oldest evidence of European bison comes from sites in the lowlands of northern Central Europe and South Scandinavia dating to the Early Holocene (Figure 2). In Poland, bones of this species were identified among the animal remains from an Early Mesolithic deposit at Chwalim 1. Three radiocarbon measurements on wood and charcoal from this layer indicate that it was accumulated in the Mid-Preboreal (KOBUSIEWICZ & KABACINSKI 1993). The composition of the fauna and the results of pollen analysis point to a woodland environment (pine and pine-birch forests) in the vicinity of Chwalim 1 in this period.

In Germany, four sites have produced bone remains of European bison belonging to the Early Holocene, i.e. Stellmoor, Hopfenbach, Gladbeck and Neustadt-Glewe. At Stellmoor, bones of European bison have been identified among the faunal remains of the Ahrensburgian settlement phase which is dominated by reindeer and which was dated by pollen analysis and radiocarbon datings on reindeer bones to the very end of the Younger Dryas (FISCHER & TAUER 1986). The presence of woodland species in the bone collection of the Ahrensburgian layer (wisent, wild pig, lynx, red fox) led to the assumption that the assemblage represents a transitional fauna, including both arctic and boreal species. Recently, direct radiocarbon dating was carried out on the bones of the rarer woodland mammals from Stellmoor demonstrating a Postglacial date of those finds (BRATLUND 1999; BENECKE & HEINRICH 2003). The radiocarbon dates on two wisent bones are 10070±50 BP (KIA3331) and 8970±75 BP (Oxa-2873) indicating an Early Preboreal and Late Preboreal/Early Boreal age of those bones.

The remains of European bison from Hopfenbach, Gladbeck and Neustadt-Glewe have been dated on the basis of pollen analysis and archaeological findings to the Early Holocene.

In Denmark, there are a few finds of wisent from peat bog localities which have been dated on the basis of pollen analysis. According to EKSTRÖM et al. (1989, Fig. 3), they can be placed to the Preboreal. Altogether 10 wisent finds are known from South Sweden (LILJEGREN & EKSTRÖM 1996, Table 1). Direct radiocarbon dating was carried out on nine of them. They date from 9500 to 8700 BP, i.e. to the second half of the Preboreal and the Early Boreal period.

There is quite a large number of bones finds of European bison from sites dating to the millennia of the Mid-Holocene (Figure 2, Table 1). They point to a wide distribution of this species during that period. Its range extended from France in the west to Belarus and Ukraine in the east. Bones of European bison have been identified in some faunal assemblages of the Pruth-Dniestr region and at two sites in Northeast Bulgaria (Goljamo Delcevo, Ovcarovo). The species also occurred in areas along the northern Black Sea coast. As data on faunal composition and pollen analysis for the respective sites show, *Bison bison* inhabited various habitats, i.e. dense deciduous forests, open pine and oak forests as well as forest steppes. Remarkably, there is no evidence of European bison in Mid-Holocene faunal assemblages from South Sweden and Denmark.

The bone finds of European bison dating to the Late Holocene are illustrated in Figure 3. They indicate a similar distribution of this species compared to the Mid-Holocene. This is especially true for the Pre-Roman and Roman Iron Age (ca. 1000 BC – ca. 600 AD). The archaeozoological record of the Middle Ages shows that European bison obviously became a very rare species in the western part of its former Central European range in the centuries after 1000 AD and finally got extinct there, while in East Europe its distribution remained more or less unchanged. High frequencies of wisent among the bone finds have been reported from Late Holocene sites in East Poland, Belarus, Lithuania and Latvia. At many sites of this region, wisent bones constitute more than 20% of the remains of wild ungulates (PAAVER 1965; ŠEĽGLOVÁ 1969; Figure 4). In contrast to that, European bison is only represented by single finds in most of the assemblages from Central and Southeast Europe.
Table 1. Number of faunal assemblages with remains of European bison arranged according to countries and periods.

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Figure 2: Bone finds of European bison dating to the Early Holocene (triangles) and Mid-Holocene (circles).
Figure 3: Bone finds of European bison dating to the Pre-Roman / Roman Iron Age (triangles) and the Middle Ages (circles).

Figure 4: Frequencies of European bison among the bone finds of wild ungulates on Mid- and Late Holocene sites (NISP > 100). Symbols: open circles <5%, hatched circles 5–20%, black circles >20%.
DISCUSSION AND CONCLUSIONS

According to the archaeozoological record, *Bison bison* was an early Postglacial immigrant into the European continent. There is firm evidence of this species in the lowlands of northern Central Europe already in the Early Preboreal. At that time, there was still a broad land bridge connecting Continental Europe and South Sweden which allowed the immigration of the wisent into the latter area. But European bison seems to have had only a rather brief occurrence in South Scandinavia, being confined to the open birch-pine period of the Preboreal (AARIS-SØRENSEN 1992, Fig. 3; LILJEGREN & EKSTRÖM 1996). There is no evidence of this species in Sweden and Denmark in the succeeding Boreal and Atlantic. Probably, the local extinction of wisent in South Scandinavia was mainly caused by the transformation of that area into a group of peninsulas and islands as a result of the *Littorina* transgression. The distribution of European bison in other parts of Europa during the Early Holocene is still unknown due to the lack of bone finds from this period.

In the Mid- and Late Holocene, European bison was widely distributed on the European continent with main areas of distribution in its central, eastern and southeastern parts. The species is missing in the western areas of the continent, on the Iberian and the Apennine peninsula as well as on the southern Balkan peninsula. In Northeast Europe, the 60° degree of latitude seems to have marked the northernmost border of the range. To the east of the Ukraine, European bison probably inhabited most of the territories of the boreal and temperate zones up to the Urals. There is also evidence of this species from sites in the forest steppe of Western Siberia (KOSINTCEV 1999).

The archaeozoological data point to differences in the abundance of European bison within its Mid- and Late Holocene range (Figure 4). In most parts of Central and Southeast Europe, wisent was a rare species. For example, in areas like Mecklenburg-Vorpommern and Brandenburg the ratio between wisent and aurochs, calculated on the basis of the number of identified specimens, is 1:9 and 1:6 respectively (BENECKE 2000, 2001). In contrast to that, European bison was a quite frequent species among the wild ungulates in parts of East Europe, mainly in those regions where it survived until the 19th century.

Wisents are mostly browsers, but can graze where grasses are available. As primary consumers they browse on a wide range of deciduous trees, shrubs and heathers, and on coniferous trees and shrubs in the winter (PUCEK 1986). Dense deciduous or mixed forests interspersed with marshland, peat bogs and meadows are regarded as favoured habitats of European bison. According to HEPTNER et al. (1966), a thick snow cover exceeding a depth of 50 cm is a limiting factor for the occurrence of this species. As the bone finds show, European bison must have found favourable living conditions in an area of East Europe nowadays comprising East Poland, Belarus, Lithuania and Latvia throughout the millennia of the Mid- and Late Holocene. Only in this part of the European continent, wisent was more competitive than aurochs.

The archaeozoological evidence from the Middle Ages points to a shrinkage of the range of *Bison bison* in its western part. The main reason for the extinction of this most impressive animal in parts of Central Europe may have been the large-scale clearing of primeval forests at that time which led to a fragmentation of the range. This would have resulted in decreasing numbers and an increasing isolation of sub-populations making the species more vulnerable to overhunting.

The Early to Late Holocene bone finds of European bison exhibit great morphological similarities with recent skeletons of the lowland bison (*Bison b. bonasus*). Taxonomically, they should belong to this subspecies. Recently, mt-DNA studies on subfossil wisent bones have confirmed this view (BOLLONINO personal communication).

In contrast to the wisent, the limits of the ancient range of highland or Caucasus bison (*Bison b. caucasicus*) are still unknown. A few bone finds from various Holocene sites in Armenia and Azerbeijan have been assigned to this subspecies (MIZLUMJAN 1988). Most probably, the few wisent remains known so far from the Middle East can be referred to the Caucasus bison as well (ÜERPMANN 1987). Further archaeozoological research in those areas is necessary for a reliable reconstruction of the ancient distribution of this subspecies of *Bison*. 
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