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New remains of Pleistocene *Ovibos moschatus* from Germany and its geographic and stratigraphic occurrence in Europe

Ingo Raufuss[1] & Wighart von Koenigswald[2]
Institut für Paläontologie der Universität Bonn, Nussallee 8, D-53115 Bonn, Germany, [1]*e-mail: raufuss@geo.uni-bonn.de;* [2]*e-mail: koenigswald@uni-bonn.de*

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Abstract

All remains of Pleistocene muskoxen from central and western Europe are attributable to a single species, *Ovibos moschatus*. Its occurrence was restricted mainly to the area north of the Pyrenees and Alps, covering lowlands and mountain areas up to 1600 m. In the Middle Pleistocene, *Ovibos* occurred in a cold phase, well before the Elsterian, and again during the Saalian and Weichselian. In the Late Pleistocene, *Ovibos* co-occurred with other faunal elements indicative of severe continental climatic conditions during the early and late Weichselian. During the middle Weichselian, the genus seems to have retreated. A list of European localities that have yielded *Ovibos moschatus*, inclusive of geographical references, is provided.

Introduction

The muskox, *Ovibos moschatus* (Zimmermann 1780) is a significant member of mammalian communities at high northern latitudes. Although the natural occurrence of the extant muskoxen is restricted to Greenland, Canada and Alaska, this species was distributed throughout the Holarctic during cold phases of the Pleistocene. The present distribution in Alaska, Siberia and Norway is due to reintroduction by man.

The first remains of muskoxen in Europe were found at in 1816 Berlin–Kreuzberg (Kowarzik 1912) and in 1840 near Merseburg (Giebel 1846). Since then, numerous additional fossils have been discovered in several European countries, but muskoxen have remained comparatively rare fossils. Several authors have previously listed the European occurrences (Kowarzik 1912, Andree 1933, Soergel 1942, Crégut-Bonnoure 1984). During the last decades, many new specimens have been collected, not only from the continent and the British Isles, but also from the bottom of the North Sea.

The aim of the present contribution is the brief description of fifteen new finds from Germany. Based on the geographical distribution of approx. 200 localities that have yielded *Ovibos moschatus*, the extension across Europe is discussed. Although only few finds have been well dated, it is obvious that *Ovibos moschatus* occurred only during very short phases of the various glaciations.

New material from Germany

Although fossil material was attributed mostly to the recent species, *Ovibos moschatus*, some authors (Ryziewicz 1933, 1954, 1955, Sher 1974, Neas 1991, Tikhonov 1994) attempted a separation of fossil material from Europe as a distinct species: *Ovibos pallantis* Hamilton-Smith 1827. The characters they used were examined in the new and other available material in order to test whether such a separation is warranted (Raufuss 1998).

Bottrop

A well-preserved skull (Figure 1) was collected from the Emscher River near Bottrop (collections of Museum-Bottrop); the strong build and shape of the horn cores indicate this to be an adult male. The

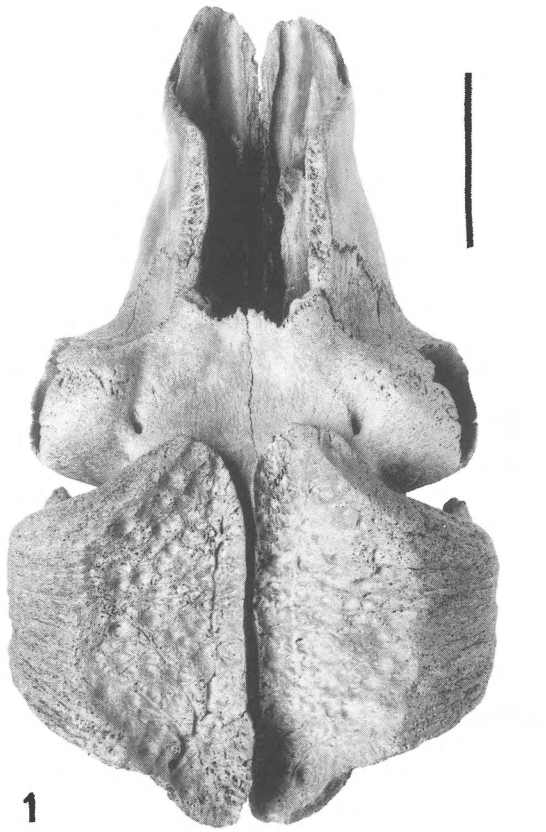

Figure 1. Skull of *Ovibos moschatus* from the Emscher River near Bottrop. Scale bar: 10 cm.

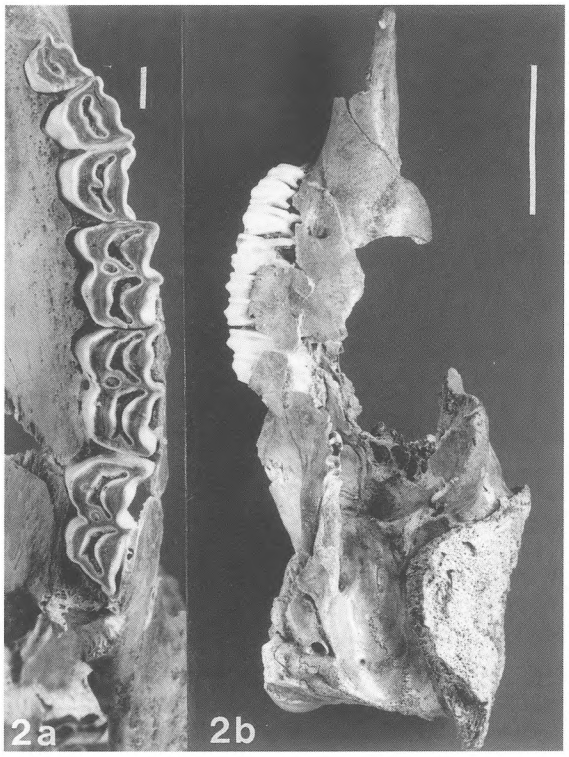

Figure 2. The skull found at Weingarten. a: Dentition of the left maxilla. Scale bar: 1 cm. b: Lateral view. Scale bar: 10 cm.

'Knochenkiese' deposits from which the skull was collected are mainly of Weichselian age, probably early Weichselian (von Koenigswald et al. 1995).

The Bottrop skull combines various characters previously regarded as typical of *O. moschatus* or *O. pallantis*, if Neas (1991) is followed. Most characters apply to *O. moschatus*, but the molar proportions (length of M^1/M^3) are 0.48. Neas (1991) calculated the length of M^1 in relation to M^3 to differentiate *O. pallantis* from *O. moschatus*. The Bottrop skull would be assignable to what Neas called *O. pallantis*; his *O. moschatus* would have higher values, about 0.86. In view of the fact that material of extant *O. moschatus* ranges between 0.5–0.75, such a differentiation appears very questionable (Raufuss 1998).

Weingarten

A gravel pit near Obereschach (Weingarten) has produced a fragmentary, narrow male skull (Figure 2), preserving a major portion of the dentition. The neurocranium is nearly completely preserved, whereas the viscerocranium is partly damaged (collections of Weingarten abbey, near Ravensburg). The stratigraphic age is unclear, but is most probably Weichselian (D. Ellwanger, pers. comm.).

Following Neas's (1991) distinction on molar proportions, the present skull (0.45) would be assignable to *O. pallantis*.

Minden

From several localities in the Minden area, seven skulls and a single vertebra were collected. The preservation of five of the skulls is typical of male specimens, with only the upper part of the braincase covered by the thick bony parts of the horn cores remaining. This part of the skull survived transport in a fluvial environment best. In addition, two fragments of occipital bones were found. Most of the finds came from gravels deposited by the Weser River. The 'Wömpener' gravel pit has produced four finds, but there are no detailed data on their stratigraphic provenance. The Minden Museum houses three skulls (MI 37, MI 61, MI 397), and four specimens are in the col-

lections of the Geological-Palaeontological Institute of Göttingen University.

MI 61 is of special interest as it shows three features in a single specimen that had previously been used for the discrimination of muskox taxa. Following Tikhonov's (1994) scheme, this skull should be attributed to *O. moschatus*, on account of the shape of the lachrymals, but to *O. yukonensis* when the vomera are considered. Features of the basioccipital bone would even fit *O. pallantis*, in Neas's (1991) scheme. These 'features' in fact fall within the range of variation of *Ovibos moschatus* (see Raufuss 1998).

A well-preserved, third cervical vertebra of a male (collections of Bundesanstalt für Geowissenschaften und Rohstoffe, Hannover), from the 'Harre-Meissen' gravel pit near Minden, is slightly more massive than that of a strong, large male from the Holocene of Canada.

Mauer near Heidelberg

A skull fragment of an adult male (M.294) is attributed to the Weichselian loess fauna (von Koenigswald 1992, 1997), rather than to the famous fauna from the Middle Pleistocene. This small neurocranium fragment (collections of the Staatliches Museum für Naturkunde, Karlsruhe) is heavily damaged and the fronto-parietal bones are glued to the occipital bone.

Düsseldorf

In the 'Grüner-See' gravel pit at Haltern (near Ratingen), the skull of an adult male (collections of Löbbecke Museum, Düsseldorf) was found in the lower terraces, of Weichselian age. This fragment shows the typical kind of preservation in fluvial systems.

Wehrden near Höxter

In a skull fragment of an adult male of Saalian age, collected from a gravel pit south of Wehrden (collections of the Geologisch-paläontologisches Institut, Göttingen University), the neurocranium is well preserved. The viscerocranium is missing almost completely.

Bückeburg

This near-complete neurocranium fragment of an adult male, housed in the Bückeburg Museum, most probably belonged to the Ballerstedt collection, most of which is now kept in the collections of the Geological-Palaeontological Institute of Göttingen University. Andree (1933) published a few finds from this collection, but did not mention the present specimen.

Karlsruhe

The gravels of the Rhine River have produced a skull fragment of an adult male (Qp/717), housed in the Staatliches Museum für Naturkunde (Karlsruhe). The exact provenance is unknown. Its age is most probably Weichselian (S. Rietschel, pers. comm.). The neurocranium is nearly completely preserved, whereas the viscerocranium is missing.

Hannover

The 'Eggersmann' gravel pit near Heisede has yielded a skull roof (NLfB Ma 12545) of an adult male with pathological horn bases, as well as a metatarsal (collections of the Bundesanstalt für Geowissenschaften und Rohstoffe, Hannover).

Conclusion regarding the species assignment

Our revision of these skulls and other available material shows that all muskoxen remains from the European Pleistocene represent a single species, indistinguishable from recent *Ovibos moschatus*, although of slightly larger size (Raufuss 1998). There are no consistent features that allow subspecies to be differentiated in material of late Pleistocene age. We regard size difference alone to be an insufficient basis for the distinction of subspecies, since the metric values of all specimens can be approximated to a regression line (Figure 3). The differences used to define *O. pallantis* (Ryziewicz 1933, 1954, 1955, Neas 1991, Tikhonov 1994) as a separate species must be regarded as individual variation.

The only valid subspecies to have been described from Europe to date is *O. m. suessenbornensis* Kahlke 1963, the earliest muskoxen from Süssenborn. This taxon is distinguished on body proportions, such as metapodials that do not fit within the range of variation of late Pleistocene and Holocene muskoxen.

Geographical distribution of *Ovibos* in Europe

The map (Figure 4) and list of localities which have yielded muskoxen remains (Appendix 1) comprises most countries in central and western Europe. A closer

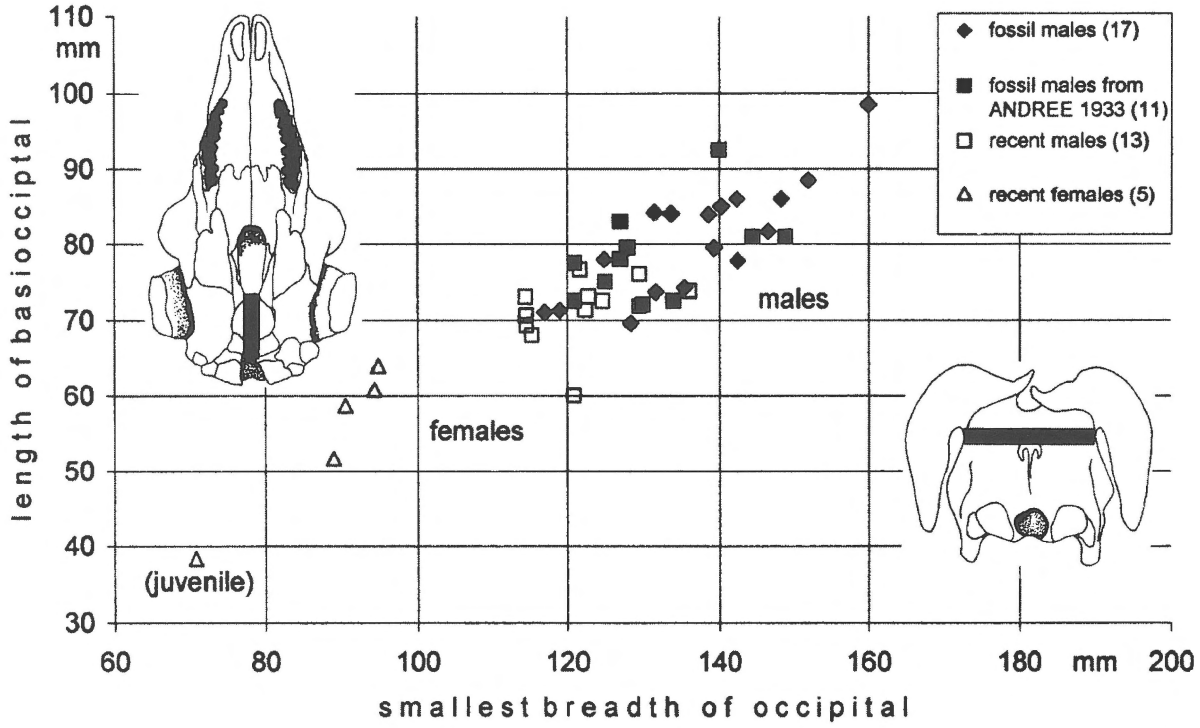

Figure 3. Size difference in skull measurements of *Ovibos moschatus*. The Pleistocene muskoxen from Europe exceed Holocene individuals from the Arctic. Note that all dots are near one regression line although males and females, adults and young adults are included. This diagram shows the size difference well; many other correlations would show a similar picture.

look reveals, however, that *Ovibos* occurred only north of the Pyrenees and Alps. There are no records from the entire Iberian or Apennine peninsulas. In contrast, *Mammuthus primigenius* and *Coelodonta antiquitatis* are known from Andalusia. The northern limit of muskox distribution corresponds to the variable margin of the ice shield in Great Britain and Scandinavia. Since parts of the North Sea fell dry during cold phases, *Ovibos* remains are to be found there as well. The Scandinavian finds may represent immigration following the retreat of the ice shield.

The muskox localities are distributed rather unevenly. The majority of the 191 localities are in Germany. This may, in part, be an artefact since the literature was screened more completely for Germany than for other countries. Particularly in countries further to the east, one would expect more localities to yield *Ovibos*. Although data are incomplete, the number of finds decreases towards the Atlantic Ocean, which may be due to the fact that *Ovibos* was restricted to continental climates with little snow fall, corresponding to today's situation.

The geographic range of extant *Ovibos moschatus* comprises areas of open tundra with permafrost. During the last decades, it has become clear that the arctic tundra cannot be used as an analogue to the 'mammoth steppe' of the glacial Holarctic region. That hosted a diverse fauna of large herbivores (Guthrie 1990, von Koenigswald 1994). The large size of European Weichselian muskoxen suggests favourable ecological conditions with optimal feeding (Raufuss 1998). It is obvious that *Ovibos* localities are all situated within the area of fossil permafrost but the stratigraphic record indicates that only specific phases during the Weichselian were suitable for *Ovibos*.

The area inhabited by *Ovibos* comprises the large plains extending from France to Poland and the low mountain ranges to the south. Although there are relatively few finds in the lowlands, this does not necessarily indicate that this area was less densely inhabited. Only in fluvial strata can the Pleistocene faunas be found; in the low mountain area, caves and archaeological sites are additional fossil sources. We assume the entire low mountain range to have been populated by muskoxen. The localities of highest altitude that

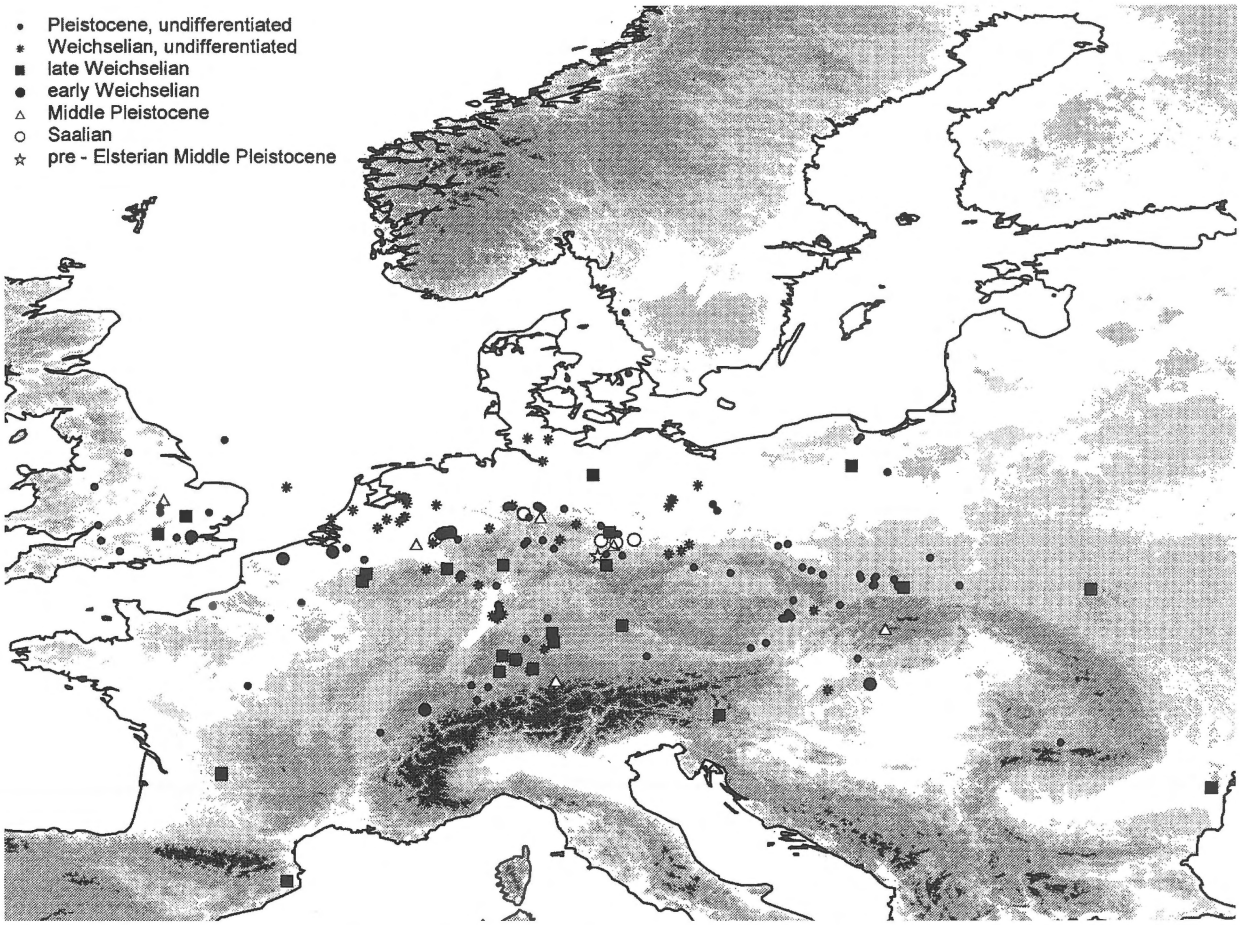

Figure 4. European localities that have yielded *Ovibos moschatus*.

have yielded *Ovibos* are Schnurenloch (Switzerland, 1250 m; see Rathgeber 1994) and Potocka cave (Slovenia, 1650 m; see Rakovec 1938). Data on higher European elevations are lacking, since remains of Pleistocene faunas are very rare in the high mountain regions, with only the cave bear, *Ursus spelaeus*, as a notable exception (found at nearly 3000 m above sea level in the Conturines cave; see Rabeder 1991).

In Canada, *O. m. moschatus* and *O. m. wardi* inhabit the flat plains as well as low mountain ranges of continent and islands alike. The highest occurrence observed is at about 2500 m (Tener 1965).

Stratigraphic occurrence

The earliest record of *Ovibos moschatus*, of early Middle Pleistocene age, is from Süssenborn near Weimar (Kahlke 1963, 1965); the site is characterised by *Mimomys savini* amongst rodent faunas. Kahlke (1965) assumed the co-occurrence of *Ovibos* and *Rangifer* to be related to climatic deterioration during the earliest Elsterian. This interpretation must be reconsidered, since the change from *Mimomys* to *Arvicola* faunas has now been shown to predate the Elsterian (von Koenigswald & Heinrich 1998), suggesting the occurrence of *Ovibos* to predate the Elsterian by at least one climatic oscillation.

Additional localities of Middle Pleistocene age, such as Barnwell (eastern England; see Reynolds 1934), Neersen (western Germany; see Von Lehmann 1968), Alfeld and Wehrden (northern Germany; see Soergel 1942), Obergünzburg (Bavaria; see Andree 1933, Graul et al. 1951), Lipova cave (Slovakia; see Vorös 1987), have produced remains of *Ovibos*. Unfortunately, the precise stratigraphic position of these finds is unknown.

There are no finds of *Ovibos* that can be firmly related to the Elsterian. Between the Elsterian and

Saalian, several climatic oscillations must have occurred but *Ovibos* does not re-occur before the Körbisdorf terrace deposits in Thuringia, which are considered to be of early Saalian age (Toepfer 1963). Other supposedly Saalian localities with *Ovibos* are Mühlheim/Ruhr (Edinger 1931, Andree 1933, Soergel 1942), two localities at Hameln (Andree 1933), Schweizerling near Wettin (Andree 1933) and Möckern near Leipzig (Kowarzik 1912, M. Böhme, pers. comm.). The area covered by Middle Pleistocene localities with *Ovibos* lies within that occupied during the Late Pleistocene. The limited data apparently indicate that *Ovibos* did not expand its range as far southwest as in later times.

The majority of European Pleistocene muskoxen are assigned to a Weichselian age. Whether *Ovibos* was present throughout the entire Weichselian or only during phases of specific ecology, remains to be determined. There are a few, yet significant records from older Weichselian strata, e.g., at Dendermonde (Belgium; see Gautier 1976), Schnurenloch (Rathgeber 1994) and Bockstein-Schmiede (Lehmann 1954). The stratigraphic age at the last-named locality has been confirmed by archaeological finds (Wetzel & Bosinsky 1969).

Ovibos moschatus is missing from faunas attributed to the Aurignacien or Gravettien in central Europe, although rich finds are available from carefully excavated archaeological sites, such as Vogelherd cave (Lehmann 1954), Mauern (von Koenigswald et al. 1974), Brillenhöhle (Boessneck & Van den Driesch 1973) and Geißenklösterle (Hahn et al. 1976). More than sixty other faunas covered by our EUQUAM database from that time period did not comprise *Ovibos*, although faunal lists were fairly complete. The only muskox records from this interval are from Beckford (Worcestershire), dated at 27,650 BP (Stuart 1982), and from Potocka cave, dated between 27,000 and 35,750 BP (D. Nagel, pers. comm.). This indicates a geographical differentiation of Europe even within glacial periods, due to ecological conditions. During the Middle Weichselian, *Ovibos* most probably reduced its range to patchy refugia in marginal areas and high mountain ranges.

No detailed faunal data are available for central Europe during the maximum Weichselian glaciation at about 22,000 BP. Following this maximum is a phase with a continental climate, in which *Ovibos moschatus* is well represented again. The continental influence is documented by the majority of *Dicrostonyx gulielmi* in the small mammal faunas and the immigration of *Saiga tatarica* from the steppes of southern Russia (von Koenigswald & Heinrich 1996). This period is represented by localities such as Olten Hammer (Switzerland; see Stehlin 1916, Soergel 1942) and Clifford Hill (Great Britain, dated at 18,200 BP; see Stuart 1982). Some archaeological sites attributed to the Magdalenian provide a detailed insight into the mammalian faunas. Many of these (Dietfurt: Brunnacker et al. 1981; Kesslerloch, Thayngen: Ammann et al. 1988, Gorge d'Enfer, Laugerie Haute: Crégut-Bonnoure 1984) contain remains of *Ovibos moschatus*, suggesting that Magdalenian humans hunted them. The great number of muskox remains lacking precise stratigraphic information may date from this period. The muskoxen from Denmark and Sweden (Kowarzik 1912) may be even younger, since this area could have been inhabited only after the glaciers had retreated. Because of the general rarity of *Ovibos*, the decline and demise of the genus in Europe and Asia cannot be traced in detail.

A distributional acme of *Ovibos moschatus* during the early and late Weichselian is parallelled by other taxa restricted to continental environments, such as *Equus hydruntinus*, *Allactaga*, *Lagurus*, and *Saiga* (von Koenigswald & Heinrich 1996).

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Appendix 1: List of European localities with Pleistocene *Ovibos moschatus*

In this list, the countries are arranged from north to south, as are the localities.

Sweden

Nol (Bohuslän: E 12°10, N 57°39), Pleistocene (Kowarzik 1912)

Denmark

Bannebjerg (Sjælland: E 12°15, N 55°58), Pleistocene (Soergel 1942)

Great Britain

Doggerbank (E 1°07′, N 54°07′), Pleistocene (Reynolds 1934)
Stourton (near Leeds: W 1°32′, N 53° 46′), Pleistocene (Reynolds 1934)
Pontnewydd (north of Newport: E 2°27′, N 52° 49′), Pleistocene (Crégut-Bonnoure 1984)
Barnwell (near Corby: E 0°34′, N 52° 28′), Middle Pleistocene (Crégut-Bonnoure 1984)
Earl's Barton (south of Wellingborough near Northampton: E 0°41′, N 52°16′), Pleistocene (Crégut-Bonnoure 1984)
Cossgrove (near Wolverton: E 0°41′, N 52°07′), Pleistocene (Crégut-Bonnoure 1984)
Clifford Hill (Northamptonshire: E 0°41′, N 52°07′), Pleistocene (Stuart 1982)
Beckford (Worcestershire: E 0°02′, N 52°01′), late Late Pleistocene (Stuart 1982)
Frampton-on-Severn (Gloucestershire: W 2°21′, N 51°46′), Pleistocene (Reynolds 1934)
Maidenhead/Thames (W 0°44′, N 51°31′), late Late Pleistocene (Stuart 1982)
Erith (north of Crayford, Kent: E 0°11′, N 51°30′), Pleistocene (Crégut-Bonnoure 1984)
Plumstead (E 0°07′, N 51°28′), Pleistocene (Reynolds 1934)
Crayford (Kent: E 0°11′, N 51°27′), early Late Pleistocene (Stuart 1982)
Green (near Bromley, Kent: W 0°22′, N 51°25′), Pleistocene (Reynolds 1934)
Freshford (near Bath: W 2°17′, N 51°19′), Pleistocene (Crégut-Bonnoure 1984)
Ightham (Kent: E 0°9′, N 51°19′), Pleistocene (Reynolds 1934)
Fisherton (W 1°46′, N 51°03′), Pleistocene (Stuart 1982)

The Netherlands

Giesbeek (E 6°03′, N 52°), Late Pleistocene (Mol & Zijlstra 1994)
Havikerwaard (near Giesbeek: E 6°05′, N 52°), Late Pleistocene (Mol & Zijlstra 1994)
Bruine Bank (North Sea: E 2°50′, N 52°49′), Late Pleistocene (Mol & Zijlstra 1994)
Kampen (E 5°55′, N 52°34′), Late Pleistocene (Crégut-Bonnoure 1984)
Rechter Diep (near Kampereiland: E 5°55′, N 52°33′), Late Pleistocene (Kerkhoff & Mol 1991)
Berkumer Brug (E 6°06′, N 52°31′), Late Pleistocene (Kerkhof & Mol 1991)
Zwolle (E 6°05′, N 52°31′), Late Pleistocene (Crégut-Bonnoure 1984)
IJssel (between Olst and Wijhe: E 6°08′, N 52°22′), Late Pleistocene (Kerkhof & Mol 1991)
Rossum (E 6°56′, N 52°19′), Late Pleistocene (Kerkhoff & Mol 1991)
Braassemer Meer (E 4°39′, N 52°12′), Late Pleistocene (Kerkhoff & Mol 1991)
Maasvlakte (E 4°03′, N 51°57′), Late Pleistocene (Mol & Zijlstra 1994)
Grebbeberg (E 5°34′, N 51°56′), Late Pleistocene (Kerkhoff & Mol 1991)
Bemmel (near Nijmegen: E 5°55′, N 51°52′), Late Pleistocene (Kerkhoff & Mol 1991)
Den Bosch (E 5°19′, N 51°42′), Late Pleistocene (Crégut-Bonnoure 1984)
Ellewoutsdijk (E 3°50′, N 51°22′), Late Pleistocene (Kerkhoff & Mol 1991)
Wadden, Late Pleistocene (Mol & Zijlstra 1994)

Belgium

Rupelmonde (E 4°28′, N 51°07′), Pleistocene (Van Lerberghe & Gautier 1980)
Dendermonde (E 4°06′, N 51°01′), early Late Pleistocene (Van Lerberghe & Gautier 1980)
Poperinge (E 2°44′, N 50°51′), early Late Pleistocene (Van Lerberghe & Gautier 1980)
Tienen (E 4°57′, N 50°49′), Pleistocene (Soergel 1942)
Trou de Goyet 3 (E 5°01′, N 50°26′), late Late Pleistocene (Van Lerberghe & Gautier 1980)
Trou de Chaleux (E 4°55′, N 50°22′), late Late Pleistocene (Van Lerberghe & Gautier 1980)
Furfooz (= Trou de Reuviau: E 4°55′, N 50°13′), late Late Pleistocene (Van Lerberghe & Gautier 1980)

Germany

Note: the following abbreviations for the so-called 'Bundesländer' are used: BW = Baden Württemberg; BY = Bayern; BE = Berlin; BB = Brandenburg;

HH = Hamburg; HE = Hessen; MV = Mecklenburg-Vorpommern; NI = Niedersachsen; NW = Nordrhein-Westfalen; RP = Rheinland Pfalz; SN = Sachsen; ST = Sachsen-Anhalt; SH = Schleswig-Holstein; TH = Thüringen.

Nord/Ostsee (channel at km 38,07, SH: E 9° 28′, N 54°11′), Late Pleistocene (Gripp 1964)

Russee (near Kiel, SH: E 10°03′, N 54°09′), Late Pleistocene (Soergel 1942)

Langenfelde (near Altona HH: E 9°54′, N 53°33′), Late Pleistocene (Gripp 1964)

Dömitz (MV: E 11°26′, N 53°09′), late Late Pleistocene (Soergel 1942)

Hohensaaten/Oderberg (BB: E 14°09′, N 52°53′), Late Pleistocene (Soergel 1942)

Kemnade (near Eschershausen, NI: E 13°24′, N 52°29′), Late Pleistocene (unpubl.)

Kreuzberg (Berlin: E 13°24′, N 52°29′), Late Pleistocene (Soergel 1942)

Rixdorf (Berlin: E 13°26′, N 52°28′), Late Pleistocene (Soergel 1942)

Frankfurt/Oder (BB: E 14°33′, N 52,21′), Pleistocene (Soergel 1942)

Warber (north of Bückeburg, NW: E 9°03′, N 52°19′), Late Pleistocene (Soergel 1942)

Niederlehme (near Königswusterhausen, BB: E 13°20′, N 52°18′), Late Pleistocene (Soergel 1942)

Nottorn (east of Minden, NW: E 9°01′, N 52°18′), Pleistocene (Soergel 1942)

Minden (several localities, NW: E 8°54′, N 52°18′), Pleistocene (Raufuss 1998)

Arnum (near Hannover, NI: E 9°44′, N 52°18′), Pleistocene (unpubl.)

Harkenbleck (near Hannover, NI: E 9°47′, N 52°17′), Pleistocene (unpubl.)

Neesen (south of Minden, NW: E 8°53′, N 52°16′), Pleistocene (Soergel 1942)

Bückeburg (NW: E 9°03′, N 52°16′), Pleistocene (Raufuss 1998)

Heisede (NI: E 9°48′, N 52°16′), Pleistocene (Raufuss 1998)

Innerste (near Hannover, NI: E 9°51′, N 52°15′), Pleistocene (Raufuss 1998)

Sarstedt (NI: E 9°51′, N 52°14′), Pleistocene (unpubl.)

Thiede (near Braunschweig, NI: E 10°29′, N 52°13′), Pleistocene (Soergel 1942)

Ahrbergen (NI: E 9°53′, N 52°13′), Pleistocene (Raufuss 1998)

Fürstenberg/Oder (BB: E 14°40′, N 52°10′), Pleistocene (Soergel 1942)

Basberg (Hameln, NI: E 9°22′, N 52°06′), Saalian (Soergel 1942); overlapped in the map by no. 68

Sintelberg (near Hameln, NI: E 9°23′, N 52°05′), Saalian (Soergel 1942)

Bodenwerder (NI: E 9°31′, N 51°59′), Pleistocene (unpubl.)

Alfeld (north of Northeim, NI: E 9°49′, N 51°59′), Middle Pleistocene (Soergel 1942)

Rübelandhöhlen/Harz (NI: E 10°48′, N 51°48′), Late Pleistocene (Schütt 1969)

Aschersleben (TH: E 11°28′, N 51°45′), Pleistocene (Soergel 1942)

Niedereddinghausen (near Lippstadt, NW: E 8°25′, N 51°41′), Late Pleistocene (Siegfried 1982)

Treis/Lumda (near Gießen, HE: E 8°48′, N 51°40′), middle Late Pleistocene (Soergel 1942)

Siersleben (near Mansfeld, ST: E 11°44′, N 51°35′), late Late Pleistocene (Soergel 1942)

Herne (NW: E 7°19′, N 51°34′), early Late Pleistocene (Soergel 1942)

Rhein-Herne-Kanal (near Krange, NW: E 7°09′, N 51°33′), early Later Pleistocene (Soergel 1942)

Wanne/Westfalen (NW: E 7°10′, N 51°33′), early Late Pleistocene (Soergel 1942)

Trotha (near Halle, ST: E 11°57′, N 51°32′), Pleistocene (Soergel 1942)

Zeche Wilhelmine-Victoria II/III (near Gelsenkirchen, NW: E 7°06′, N 51°32′), Pleistocene (Soergel 1942)

Gelsenkirchen (NW: E 7°04′, N 51°32′), early Late Pleistocene (Soergel 1942)

Emscher River (near Bottrop, NW: E 6°58′, N 51°31′), Pleistocene (Raufuss 1998)

Mühlheim/Ruhr (NW: E 6°54′, N 51°24′), Saalian (Edinger 1931)

Möckern (near Leipzig, SN: E 12°24′, N 51°23′), Saalian (Kowarzik 1912)

Sondershausen im Schersental (TH: E 10°22′, N 51°22′), Late Pleistocene (Soergel 1942)

Balver Höhle/Hönnetal (NW: E 7°32′, N 51°22′), Pleistocene (Soergel 1942)

Schweizerling (near Wettin, ST: E 11°29′, N 51°21′), Saalian (Soergel 1942)

Arenshausen (TH: E 9°54′, N 51°21′), Pleistocene (Soergel 1942)

Kassel (HE: E 9°28′, N 51°19′), Pleistocene (Jacobshagen 1956)

Körbisdorf (near Merseburg, TH: E 11°54′, N 51°18′), Saalian (unpubl.)

Haltern (near Ratingen, NW: E 6°50′, N 51°17′), Late Pleistocene (Raufuss 1998)

Riesa (SN: E 13°54′, N 51°15′), Late Pleistocene (Soergel 1942)
Neersen (near Viersen, NW: E 6°22′, N 51°15′), Middle Pleistocene (Lehmann 1968)
Breda (near Merseburg, ST: E 11°49′, N 51°14′), Middle Pleistocene (Soergel 1942)
Wehrden/Weser (NI: E 9°23′, N 51°13′), Pleistocene (Raufuss 1998)
Heldra (Kreis Eschwege, HE: E 10°12′, N 51°07′), Pleistocene (Jacobshagen 1956)
Cotta (near Dresden, SN: E 13°41′, N 51°04′), Late Pleistocene (Soergel 1942)
Prohlis (near Dresden, SN: E 13°33′, N 50°59′), Late Pleistocene (Soergel 1942)
Hohe Saale (between Kunitz and Wenigenjena, ST: E 11°38′, N 50°58′), Pleistocene (Soergel 1942)
Süssenborn (near Weimar, TH: E 11°24′, N 50°57′), early Middle Pleistocene (Kahlke 1963)
Zschippach (near Gera, TH: E 12°04′, N 50°55′), Pleistocene (Soergel 1942)
Ilsenhöhle (near Ranis, TH: E 11°39′, N 50°40′), late Late Pleistocene (Soergel 1942)
Unkelstein (near Remagen/Rhein, RP: E 7°14′, N 50°34′), late Late Pleistocene (Von Koenigswald 1994)
Kartstein/Eifel (NW: E 6°39′, N 50°33′), Late Pleistocene (Soergel 1942)
Brexbachtal (RP: E 7°37′, N 50°25′), Pleistocene (unpubl.)
Vallendar (near Koblenz, RP: E 7°38′, N 50°23′), Late Pleistocene (Soergel 1942)
Moselweiß (near Koblenz, RP: E 7°34′, N 50°2′), Late Pleistocene (Soergel 1942)
Wildscheuer (near Steeden/Lahn, HE: E 8°06′, N 50°08′), Late Pleistocene (Kowarzik 1912)
Frankfurt–Höchst/Main (HE: E 8°36′, N 50°06′), Pleistocene (Soergel 1942)
Laudenbach (near Weinheim/Bergstraße, BW: E 8°39′, N 49°35′), Pleistocene (Rathgeber 1994)
Schlangenbühl (near Weinheim, BW: E 8°40′, N 49°33′), Late Pleistocene (Rathgeber 1994)
Pleikartsförsterhof (BW: E 8°40′, N 49°24′), Late Pleistocene (Rathgeber 1994)
Mauer (near Heidelberg, BW: E 8°47′, N 49°19′), Late Pleistocene (Raufuss 1998)
Rheinhausen (near Hockenheim, BW: E 8°29′, N 49°16′), Late Pleistocene (Rathgeber 1994)
Langenbrücken (BW: E 8°04′, N 49°13′), Pleistocene (Rathgeber 1994)
Langenbrücken (near Bruchsaal, BW: E 8°38′, N 49°12′), Late Pleistocene (Rathgeber 1994)
Mistlau (BW: E 10°01′, N 49°12′), Pleistocene (Rathgeber 1994)
St. Jakob (near Konstanz, BW: E 8°47′, N 48°11′), late Late Pleistocene (Rathgeber 1994)
Regensburg (BY: E 12°04′, N 49°01′), late Late Pleistocene (Steinmetz & Eckes 1937)
Bocksteinschmiede (Lonetal near Langenau, BW: E 10°09′, N 48°48′), middle Late Pleistocene (Rathgeber 1994)
Kirchheim unter Teck (BW: E 9°26′, N 48°38′), Pleistocene (Rathgeber 1994)
Vogelherd (Lonetal near Ulm, BW: E 10°11′, N 48°34′), late Late Pleistocene (Rathgeber 1994)
Hohlefels (Achtal near Ulm, BW: E 9°56′, N 48°22′), Late Pleistocene (Nehring 1880)
Burgkirchen/Alz (BY: E 12°44′, N 48°10′), Pleistocene (Heissig, 1980)
Burghöhle Dietfurt (near Sigmaringen, BW: E 9°08′, N 48°05′), late Late Pleistocene (Rathgeber 1994)
Langenbrunn/Donau (BW: E 9°09′, N 48°04′), early Late Pleistocene (Rathgeber 1994)
Baindt (near Ravensburg, BW: E 9°38′, N 47°49′), middle Late Pleistocene (Rathgeber 1994)
Obereschach (BW: E 9°32′, N 47°46′), Late Pleistocene (Raufuss 1998)
Obergünzburg (BY: E 10°15′, N 47°30′), Middle Pleistocene (Soergel 1942) 1942)
Rheinvalley (near Karlsruhe, BW), Pleistocene (Raufuss 1998)

Poland

Skowarcz (E 18°40′, N 54°12′), Pleistocene (Kowalski 1959)
Schönwarling (E 18°34′, N 54°06′), Pleistocene (Kowalski 1959)
Przechowo (E 18°25′, N 53°24′), late Late Pleistocene (Kowalski 1959)
Brodnica (E 19°24′, N 53°14′), Pleistocene (Kowalski 1959)
Pogalewo Wielkie (E 16°37′, N 51°15′), Pleistocene (Kowalski 1959)
Brzeg Dolny (E 16°39′, N 51°15′), Pleistocene (Kowalski 1959)
Legnica (E 16°22′, N 51°12′), Pleistocene (Soergel 1942)
Raj Cave (near Kielice: E 20°34′, N 50°53′), Pleistocene (Kowalski 1959)
Ziebice (E 17°03′, N 50°36′), Pleistocene (Kowalski 1959)

Kamnig (near Münsterberg: E 17°18′, N 50°31′), Pleistocene (Soergel 1942)
Milowice (E 17°37′, N 50°24′), Pleistocene (Kowalski 1959)
Pyskowice (E 18°38′, N 50°24′), Pleistocene (Kowalski 1959)
Grodziec k. Sosnowwca (E 19°04′, N 50°21′), Pleistocene (Kowalski 1959)
Dzierzno (E 18°40′, N 50°18′), Pleistocene (Kowalski 1959)
Saturn (E 19°01′, N 50°18′), Pleistocene (Kowalski 1959)
Beblo (E 19°34′, N 50°17′), Pleistocene (Kowalski 1959)
Ojców (E 19°34′, N 50°17′), Pleistocene (Kowalski 1959)
Wierzchowie (E 19°34′, N 50°17′), Pleistocene (Kowalski 1959)
Tunnel near Orlowitz (near Rybnik: E 19°03′, N 50°07′), Pleistocene (Soergel 1942)
Latoszyn (E 21°22′, N 50°07′), Pleistocene (Kowalski 1959)
Czernitzer Tunnel (E 18°58′, N 50°06′), Pleistocene (Soergel 1942)
Czulów (E 19°40′, N 50°05′), Pleistocene (Kowalski 1959)
Murek Cave (Mnikow: E 19°51′, N 50°03′), late Late Pleistocene (Kowalski 1959)

Czech Republic

Ústi (near Teplice: E 14°01′, N 50°36′), Pleistocene (Soergel 1942)
Prachover Felsen (near Jicin, Bohemia: E 15°01′, N 50°27′), Pleistocene (Soergel 1942)
Dachshöhle (E 16°48′, N 49°42′), Pleistocene (Soergel 1942)
Sipka Cave (near Petrcovice: E 18°04′, N 49°34′), Pleistocene (Soergel 1942)
Predmosti (near Brno: E 17°22′, N 49°26′), Late Pleistocene (Soergel 1942)
Schoschuwka cave (Blansko: E 16°39′, N 49°22′), Pleistocene (Soergel 1942)
Stiefelshöhle (near Brno: E 16°37′, N 49°19′), Pleistocene (Soergel 1942)
Malmeritz (near Brno: E 16°28′, N 49°18′), Pleistocene (Soergel 1942)
Lateiner Berg (near Brno: E 16°36′, N 49°18′), Pleistocene (Soergel 1942)
Sveduv stul (near Brno: E 16°43′, N 49°17′), Pleistocene (Soergel 1942)
Pekarna Cave (Backofenhöhle, near Brno: E 16°45′, N 49°14′), Pleistocene (Soergel 1942)
Zebegény (E 18°34′, N 48°06′), Pleistocene (Kretzoi 1942)

Slovakia

Lipva Cave (near Hronic: E 19°20′, N 48°55′), Middle Pleistocene (Vorös 1987)

Ukraine

E 32°, N 52°, late Late Pleistocene (Markova et al. 1995)
E 25°, N 50°, late Late Pleistocene (Markova et al. 1995)

Romania

Pörgolhegy cave (Bakony mountains: E 17°30′, N 47°15′), Late Pleistocene (Musil 1980)
La Adam (Dobrudscha: E 28°18′, N 44°32′), middle Late Pleistocene (Malez 1972)

Hungary

Érd-Parkváros (E 18°54′, N 47°14′), early Late Pleistocene (Jánossy 1986)
Szeben (E 24°09′, N 45°48′), Pleistocene (Soergel 1942)

Slovenia

Potocka cave (E 14°43′, N 46°33′), middle Late Pleistocene (Rakovec 1938)

Austria

Raschaala (near Hollabrunn: E 16°18′, N 48°31′), Pleistocene (Thenius, pers. comm.)
Hundssteig (near Krems: E 15°36′, N 48°28′), Pleistocene (Soergel 1942)

Switzerland

Keßlerloch (near Thayngen: E 8°42′, N 47°45′), late Late Pleistocene (Soergel 1942)
Thayngen (E 8°66′, N 47°45′), Pleistocene (Soergel 1942)
Schaffhausen/Ebnatquartier (E 8°37′, N 47°42′), Pleistocene (Soergel 1942)
Olten-Hammer (E 7°54′, N 47°22′), Pleistocene (Soergel 1942)

Bremgarten (Kanton Aarau: E 8°22′, N 47°20′), Pleistocene (Soergel 1942)
Dreiswil (Wrobental: E 8°03′, N 46°58′), Pleistocene (Soergel 1942)
Schnurenloch (Simmental: E 6°36′, N 45°42′), early Late Pleistocene (Rathgeber 1994)
Eriz, Late Pleistocene (Rathgeber 1994)

France

Viry-Noureuil (near Channy: E 3,13′, N 49°38′), Pleistocene (Soergel 1942)
Graville Sainte Honorine (E 0,46′, N 49°33′), Pleistocene (Crégut-Bonnoure 1984)
Precy (near Creil, Oise: E 2,22′, N 49°18′), Pleistocene (Soergel 1942)
Roc en Pail (near Challonnes sur Loire: E 1,45′, N 47°21′), Pleistocene (Crégut-Bonnoure 1984)
La Colombière sur Ain (E 5,22′, N 46°05′), Pleistocene (Crégut-Bonnoure 1984)
Laugerie Hautes Ouest (near Eyzies: E 1,0′, N 44°57′), late Late Pleistocene (Crégut-Bonnoure 1984)
Eyzies, Dordogne (Abri du Poisson, Gorges d'Enfer: E 1°02′, N 44°56′), late Late Pleistocene (Soergel 1942)
La Madeleine (E 1,1′, N 44°55′), late Late Pleistocene (Piveteau 1969)

Spain

L'Arbreda (E 2°49′, N 44°01′), late Late Pleistocene (Estevez-Escalera 1978)

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