MIS 3–1 fauna from Krosinko: Implications for the past biogeography, chronology and palaeoenvironments of Poland

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A R T I C L E   I N F O

A B S T R A C T

A faunal assemblage was recently recovered from the Krosinko site in Poland, marking a new site in the War-saw–Berlin ice-marginal valley. Analysis and radiocarbon dating of the remains revealed the presence of two subassemblages: one Late Pleistocene (at least MIS 3–2) and one Holocene (MIS 1), with the former being taxonomically highly diverse. By referring to previous Polish studies, the Pleistocene mammal bone assemblage allowed us to reconstruct the biogeography of its individual components: woolly mammoths, woolly rhinoceri, horses, giant deer, red deer, fallow deer, reindeer, steppe bison, aurochses, bears, and cave lions. The bioge-ography was later combined with radiocarbon chronology using 21 dates from Krosinko. The wide range of radiocarbon dates (48.4–26.4 ka BP) probably reflects different chronological distributions of species resulting from the changing climate and environment as well as the diverse original sources of the bones. The remains, which constituted a single, compact geological horizon, was possibly deposited in a single geological event around 26 ka BP, as inferred from the most recently produced radiocarbon date. Radiocarbon datings of woolly rhinoceros remains have shown the species to have been present around 38 ka BP, a time that it had previously been considered to have been non-existent in Europe (with no evidence having been discovered for the period 40–34 ka BP). This result alters the stratigraphic gap range for the woolly rhinoceros in Europe to 40–38 ka BP. The clear dominance of woolly mammoth and woolly rhinoceros specimens reflects the structure of the *Mam-muthus–Coelodonta* faunal complex. The main representatives of this complex preferred the dry and cold con-ditions that characterized the palaeoenvironmental conditions in Krosinko in MIS 2 and thus in Central Europe, as shown by the integration of the results of the fauna and those of the sediments in which they were deposited. These palaeoenvironmental features are related to the mammoth steppe, which was a long-lived biome in Eurasia and whose diversity influenced the faunal distribution. Thus, the species-by-species review of taxa performed in this paper, against the background of previous results from Poland, illuminates the individual responses of taxa to changing environmental conditions in response to climatic ones. These changes led to the disappearance of the mammoth steppe and near or total extinction of the fauna species inhabiting it.

1. Introduction

The Pleistocene (2.58 Ma–11.7 ka BP) was a time of dynamic change in climate, environment and hominid evolution, and saw the loss of large terrestrial mammals (megafauna) across most of the globe.

The climatic and environmental fluctuations during the Pleistocene are related to the development and disappearance of ice sheets. During the Vistulian Glaciation (MIS 5 d–MIS 2 [Marine Isotope Stage]), there was an alternation between cooler events (Greenland Stadials: GS) and warmer events (Greenland Interstadials: GI) (Rasmussen et al., 2014). About 25 ka ago (MIS 2; The Last Glacial Maximum [LGM]), with a peak at 21 ka ago, the developing ice sheet covered Scandinavia,

north-eastern Europe, the British Isles and north-central Siberia. Poland was covered to as far south as Leszno at that time (Leszno phase; Table 1). A consequence of this was a shift in animal habitat zones from the northern hemisphere far to the south, and a reorganization of mammalian communities and vegetational belts (Lister and Stuart, 2008). During the deglaciation, the process of mammalians appearing in Eurasia underwent a reversal—that is, animals moved farther and farther north with the disappearing ice sheet, which is clearly shown by the distribution of reindeer in Eurasia, including Poland.

Palaeoenvironmental fluctuations have led to the extinction of much of Europe's megafauna in response to changing climate and with the influence in some cases of human impact. For northern Eurasia, detailed

chronologies show a staggered extinction pattern, in which each megafaunal species exhibits unique and complex distributional shifts, culminating in extinction for some species and survival for others (Stuart, 2015). This process of survival into the mid-Holocene, or even to the present day (such as with reindeer and muskoxen) is not entirely clear. The mammalian fossil record also makes it possible to trace how individual species responded to these changes in terms of morphological variations, population size and local adaptations on a time scale of 2.58 Ma. Cases of resettlement and rapid adaptation are well demonstrated by the example of Yakutian horses, which are well adapted to the harsh cold (up to −70 °C) with their thick, dense winter coats. They went extinct in Yakutia at roughly the same time as the woolly mammoth and rhinoceros – around 5000 years ago – but they have again arrived in these parts, probably from Mongolia, within the last 800 years (Librado et al., 2015). Genetic studies of them have shown convergent evolution with native human populations and woolly mammoths, suggesting that only a few evolutionary strategies are compatible with survival in extremely cold environments (Librado et al., 2015).

In Poland, most palaeontological sites of Pleistocene age are scattered across the south of the country, as shown by studies of fauna (Hrynowiecka et al., 2018; Kowalski, 1959; Nadachowski et al., 2011; Pawłowska et al., in press; Pawłowska, 2015; Woroncowa-Marcinowska et al., 2017). This part of Poland is thus much better recognized, with abundant evidence of Pleistocene fauna in the form of findings of remains and radiocarbon datings that show how their distributions changed. Many fewer palaeontological sites are known in central Poland to date, as shown by studies carried out in the 1960s and 1980s (Kowalski, 1959; Rutkowski, 1967; Stankowski and Tobolski, 1982; Stankowski, 1988). This has to do with the cycles of ice sheet development during successive glaciations (Cromerian–Elsterian Complex, Saalian and Weichselian). However, detailed queries and field studies of recent years (Pawłowska, unpublished data) show that there may be more of these sites, especially of those dating to the Late Pleistocene. An analysis and review of this material is currently being undertaken to assess whether the detailed analysis of fossils from these sites can expand the biostratigraphy of this region. The results of this will be the subject of a separate publication. The present work will focus on one

location, the open-air site Krosinko (52°13′05.9″N 16°49′16.5″E), which yielded over 270 animal remains (Fig. 1).The location of Krosinko in western Poland makes it important to our understanding of the palaeoenvironment of Central Europe. During the deglaciation at the LGM, conditions in Central Europe were potentially conducive to cold-hardy animals and to animals well adapted to the prevailing harsh environmental conditions. Apart from its geographic location in front of, though not close to the ice sheet, the uniqueness of Krosinko is further emphasized by the recognized geological context in which the remains occur. Unfortunately, the stratigraphy is unknown at most Polish sites with megafauna (usually woolly mammoth) (Kubiak, 2001). This geological context provides an opportunity to integrate faunal records with the biological, chemical and physical nature of the environment at Krosinko in the Pleistocene at the time of accumulation of the fine-grained and coarse-grained sedimentary series in which they were found (Pawłowska et al., in press). However, the main objective of this work is to reconstruct the faunistic structure of the assemblage recovered from Krosinko, a unique site in Central Europe, and to establish the radiocarbon chronology of the fauna by radiocarbon dating the mammalian remains. Further, placing the results in the context of previous records of megafauna from Poland provides an overview of Pleistocene and Holocene mammals in terms of biogeography and chronology, and points to directions for further research.

2. Site and geological background

Krosinko is a gravel pit in Poland, located approximately 10 km south-west of Poznań within the Warsaw–Berlin ice marginal valley (Fig. 2); this, together with Warta River entrenched valley (Fig. 2), is the dominant geomorphological feature surrounding the site. Warta River entrenched valley is a narrow valley section that was formed after the deglaciation of this area. The site was discovered in 2003 by the author. In the following years, studies of faunal remains, sediments, flints (*sensu stricto*) and botanical materials have been conducted.

Considering the glaciation history of Polish territory, the geological profile at Krosinko and surrounding area records successive glaciations from the Elsterian (MIS 12) through the Saalian Glaciation (MIS 8–6) to

Table 1
Chronologic chart of the Pleistocene and Holocene succession at Poland, with references to Western Europe.

MIS	Dates (ka)	Western Europe		Poland		Epoch
MIS 1	11.7–present	Holocene		Holocene		Holocene
MIS 2	29–11.7	Late Weichselian Glaciation, including LGM		Vistulian Glaciation (MIS 2)	Late Glacial Interstadial (LGI) Gardno Phase (14.5) Pomeranian Phase (16) Poznań Phase (18.5) Leszno Phase (21)	Late Pleistocene
MIS 3	57–29	Middle Weichselian Glaciation	Denekamp Huneborg Hengelo Hasselo Moershoofd Glinde Ebersdorf Oerel	Grudziądz Interstadial		
MIS 5d–4	123–57	Early Weichselian Glaciation		Vistulian Glaciation (MIS 5d–4)		
MIS 5e	130–123	Eemian Interglacial		Eemian Interglacial (MIS 5e)		
MIS 8–6/MIS 10–6	300–130/ 347–128	Saalian Glaciation		Warthanian Glaciations (MIS 6) Odranian Glaciations (MIS 6) Lublinian Interglacial (MIS 7) Krznanian Glaciations (MIS 8) Zbojnian Interglacial (MIS 9) Liwiecian Glaciations (MIS 10)		Middle Pleistocene
MIS 11/9	424–374/ 337–300	Holsteinian Interglacial		Mazovian Interglacial (MIS 11)		
MIS 12	478–424	Elsterian		Sanian 2 (MIS 12)		
MIS 19–13	790–478	Cromerian Complex		Ferdynandovian (MIS 15–13) Sanian 1 (MIS 16) Kozi Grzbiet (MIS 21–17) Nidanian (MIS 22)		

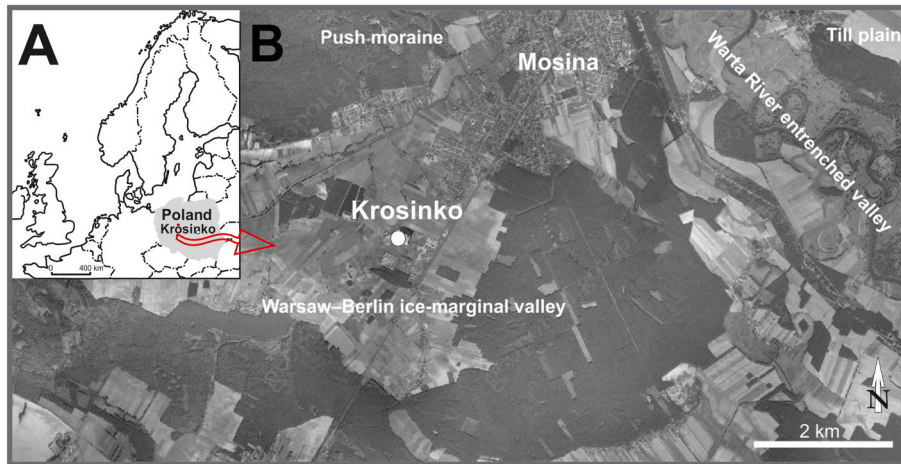**Fig. 1.** Gravel pit in Krosinko; view from the south-east.

Fig. 2. A – Location of the study site in Europe. B – Orthomap showing location of Krosinko and main geomorphological forms.

the Weichselian, separated by interglacial deposits (Holsteinian and Eemian Interglacial). During the Saalian Glaciation, glacial tills were deposited in the study area; large-scale glaciotectonic deformations in the foreland of the advancing ice sheet led to the formation of a push moraine landform (Figs. 2 and 3). Sediments of the Weichselian Glaciation, in the form of till, fluvioglacial sands and gravels, are associated with the advance and retreat of the ice sheet during the Last Glacial Maximum (LGM; MIS 2) (Pawłowska et al., in press, Fig. 3). Finally, during the deglaciation phase, a latitudinal broad marginal valley (the Warsaw–Berlin ice marginal streamway) was formed; it is here that the Krosinko site is located (Fig. 3).

The integration of sedimentological analysis, including quartz grains analysis and quartz surface microtexture analysis revealed a change in the river regime (MIS 5e and MIS 2) under changing palaeoclimate conditions (Pawłowska et al., in press). During the Eemian interglacial (MIS 5e), a meandering river existed in Krosinko whose sediments (silt, unit A) form basal part of the geological profile (Fig. 4). These sediments, together with overlying deposits of fine-grained sand (lower unit B), record a low-energy river (Pawłowska et al., in press). This is consistent with the generally warm climate of that time. The change in river regime in MIS 2 (around 19 ka BP; Poznań Phase) is marked in the sedimentary succession by the occurrence of a gravel-sand series (the upper part of unit B and unit C). This high-energy braided river left not only sediments but also wood fragments, cones and animal remains. The sediments of this unit were affected by chemical weathering (etching, crusting), mechanical weathering (crushing, abrasion), and frost weathering, as evidenced by the microtextural features of the grains (Pawłowska et al., in press). In the geological profile, the Pleistocene sediments are terminated by a sand series (unit D) that accumulated between 18 ka and 11.7 ka BP (MIS 2; LGI), and which is associated with a decrease in fluvial energy (Pawłowska et al., in press).

Overlying the Pleistocene sediments are peats of Holocene age (MIS

1), which occur in the northern and western parts of the studied site.

3. Material and methods

The material for the study consisted of animal remains found in the gravel pit at Krosinko. In total, the collection includes 271 bones, teeth, horncores and antlers.

The faunal material is stored as a private collection. Access to the specimens is available by request to the author. Each fragment received a general identification number (GID) composed of the site abbreviation (KR), unit number (111, 112, 116 for Pleistocene context or 211 for Holocene context), the letter code for finds (F), and a unique ID number for each item.

3.1. Field study

Due to the high groundwater table (1.8 m a.s.l.), a reservoir reconnaissance by divers was used to locate the remains in the stratigraphic and lithological profile. Because of the high degree of siltation of the water (due to the presence of silty–sandy sediments) it was impossible to determine their precise occurrence in the sedimentary succession. A series of geological drillings (BH1–8) was therefore carried out, which allowed precise determination of their depth of occurrence (6–7 m) and made it possible to examine the sediments in the stratigraphic sequence (Pawłowska et al., in press). Geological analysis revealed their occurrence in Pleistocene gravelly–sandy deposits of the braided river (Unit C; MIS 2) and Holocene peats (MIS 1).

In view of the hydrological conditions in the gravel pit, the faunal remains were excavated using a refueler suction pump and heavy equipment used on a daily basis for sediment extraction. This method of excavating the remains affected their completeness, as shown by the high frequency (c.50%) of modern fractures. Such specimens were
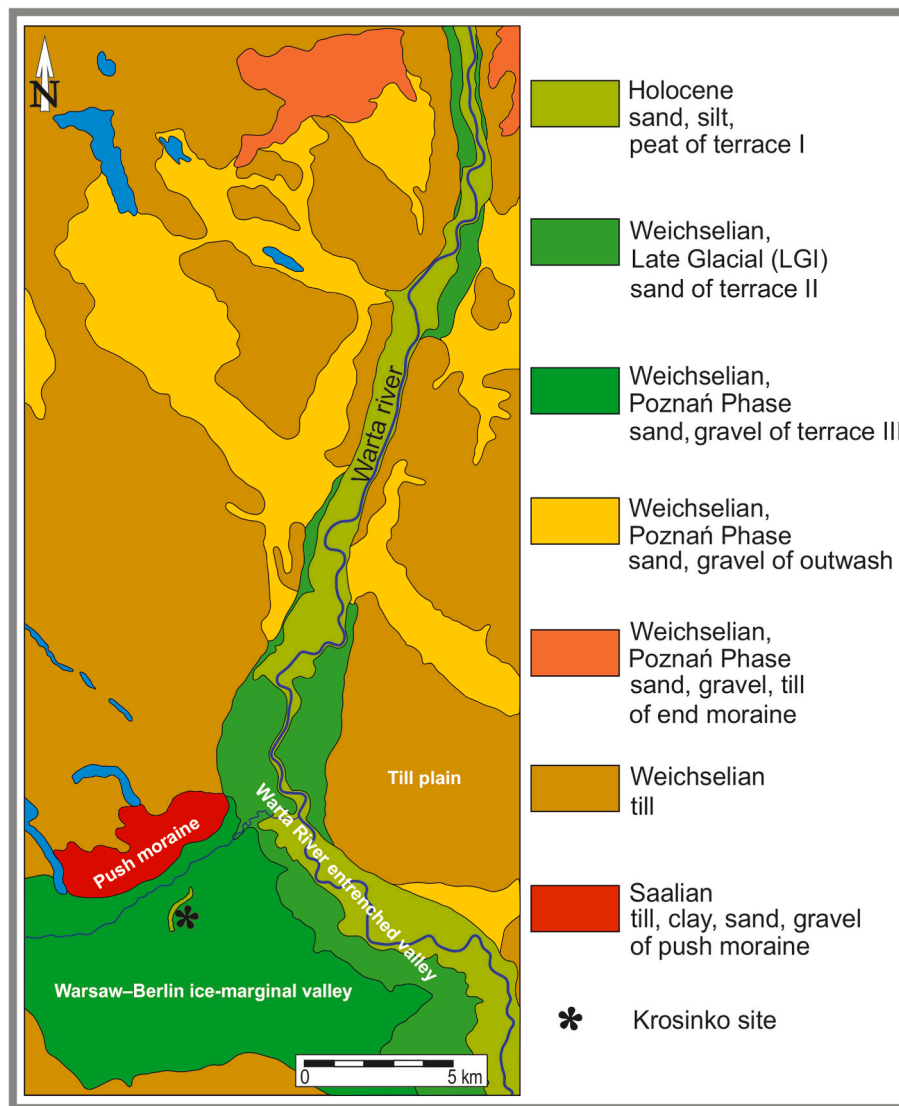
Fig. 3. Geological map of the study area with the location of Krosinko. Lakes are shown in blue. Based on Chachaj (1996), modified. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

reconstructed by combining fragments from a single element of a given taxon.

3.2. Palaeozoological method

The animal remains were examined using the comparative collection housed at the Institute of Geology at Adam Mickiewicz University and using key literature entries (Barone, 1972; Brown and Gustafson, 2000; Guérin, 1980; Heintz, 1970; Lister, 1996; Maglio, 1973; Prummel, 1988). Specimens belonging to the family Bovidae that did not display features of *Bos* or *Bison* (Balkwill and Cumbaa, 1992; Gee, 1993; Olsen, 1960; Sala, 1987; Stampfli, 1963) were designated as *Bos/Bison* due to their state of preservation. The remaining material was designated to taxon (species or genus).

3.3. Radiocarbon dating

Selected taxonomically diverse specimens were radiocarbon dated at the Poznań Radiocarbon Laboratory and in the Research Laboratory for Archaeology and the History of Art, Oxford University. In total twenty-one samples were radiocarbon dated, of which 13 dates are published here for the first time (Table 2). Radiocarbon dates were calibrated using

OxCal 20 software version 4.4, which works with IntCal20 (Reimer et al., 2020). The resulting dates were referenced to the Intimate event stratigraphy (Rasmussen et al., 2014), including the sequence of Greenland Stadials (GS) and Greenland Interstadials (GI) within the most recent glacial period. The GS and GI periods are the Greenland expressions of the characteristic Dansgaard–Oeschger events that represent cold and warm phases of the North Atlantic region, respectively (Rasmussen et al., 2014).

4. Results

4.1. Mammal remains

In the study of the Krosinko fauna, 261 items of mammalian remains from the Upper Pleistocene sediments (Fig. 5) and 10 items of mammalian remains from the Holocene sediments (Fig. 6) were found. These two subassemblages differ in the degree of fossilization and in the location where they were found in the gravel pit. The vast majority of remains that are fossilized (mainly due to permineralization by the precipitation of silica) were found in Pleistocene sediments. In contrast, sub-fossilized specimens come from Holocene peats. The faunal assemblages also differ in taxonomic composition, anatomical composition
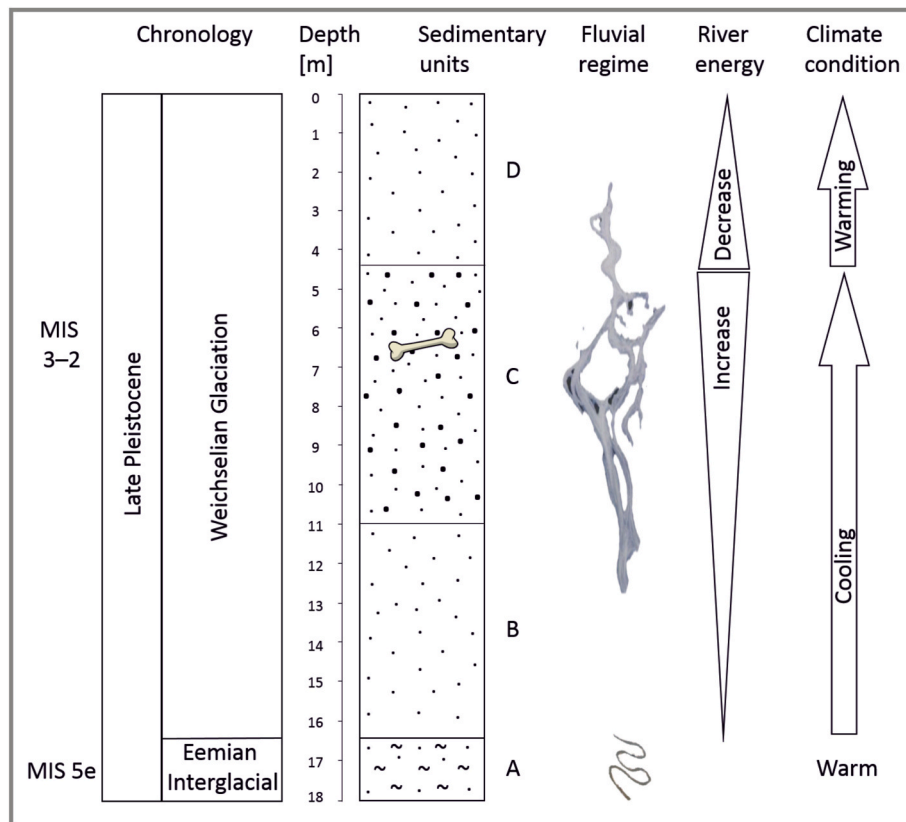
Fig. 4. Krosinko site, MIS 5e and MIS 3–2. Sedimentological succession in conjunction with fluvial regime change (from low-energy meandering river to high-energy braided river). Sediments of the units A–D are described in the text (from base to top: sandy silt (A), sand (B), gravelly sand (C), and sand (D)). A bone indicates depth of findings of mammals remains, along with flints and plant remains.

and degree of articulation of the elements.

4.1.1. Taxa distribution

The Pleistocene faunal assemblage is more taxonomically diverse than its Holocene counterpart, which may be indirectly related to sample size (n = 261 *vs* n = 10). The elements come from woolly mammoth (n = 70; 26.8% of the Pleistocene assemblage), woolly rhinoceros (n = 41; 15.7%), horses (n = 31; 11.9%), reindeer (n = 13; 5.0%), aurochs (n = 6; 2.3%), giant deer (n = 3; 1.1%), red deer (n = 3; 1.1%), cave lion (n = 3; 1.1%) (Fig. 7), fallow deer (n = 1; 0.4%), steppe bison (n = 1; 0.4%), and bear (n = 1; 0.4%) (Table 3). The dominant remains are thus those of woolly mammoth and woolly rhinoceros, with a fairly good proportion of horses. Aurochs and bison provide small contributions to the assemblage, although this may be a function of the poorly diagnostic elements of this group. Thus, the Bovidae proportion increases to 12.3% if we consider the combined proportion from aurochs, steppe bison and *Bos/Bison*.

The Holocene faunal assemblage includes remains of elk (n = 5) and red deer (n = 3) (Table 3).

4.1.2. Body part distribution

Mammalian skeletal elements from the Pleistocene assemblage represent all body parts (skull, axial, girdle, upper limb and lower limb). There are more isolated teeth, skull fragments, antlers, vertebrae, ribs and pelvises than other elements (Table 4). However, when looking at the distribution of skeletal elements for each taxon individually, the body part distribution is approximately even for woolly mammoths, woolly rhinos, horses and bovidae, in contrast to other species, where it is uneven (Table 4). Elements were not found in articulation, and no element displayed traces of articulation during material deposition.

The Holocene assemblage includes an elk skull with antlers,

mandible and ribs, as well as antlers, humerus and metacarpals belonging to red deer. Evidence of articulation was found between the mandible and the elk skull. All the elk elements are probably from a single individual.

4.2. Radiocarbon dating

The range of most of the dates is between 48 and 9 ka BP (Table 2), falling in MIS 3–MIS 1. However, two of the dates (>45,400 and > 48,300) are open dates with no lower limit, which may suggest that some material is older than MIS 3. Twenty dates indicate that the dated remains originate from the Late Pleistocene (MIS 3–2), and their stratigraphic range is associated with the Vistulian Glaciation, including the Last Glacial Maximum (LGM). Most dates from MIS 3 correspond to the Grudziądz Interglacial in the Polish chronostratigraphy. One date indicates Holocene age and relates to an elk skull.

The dated Pleistocene remains are from the woolly mammoth (n = 3), woolly rhinoceros (n = 3), horses (n = 3), giant deer (n = 1), red deer (n = 1), reindeer (n = 3), a steppe bison (n = 1), aurochs (n = 2), a bear (n = 1), a cave lion (n = 1), and a mammal (n = 1). The mammoths range between 43 and 31 ka BP and the woolly rhinoceri fall between 48 and 38 ka BP. Horse bone dating yielded very clustered dates of 48 and 47 ka BP. The skull of the giant deer has an open dating, being >45 ka BP. The single date for red deer is 38 ka BP, while those for reindeer range between 36 and 26 ka BP. Of the elements belonging to Bovidae, both the steppe bison and aurochs bones were dated to 35 ka BP and 34 and 38 ka BP, respectively. Dating of the bear humerus yielded a date of 32 ka BP, and the cave lion mandible received a date of >48 ka BP.

Table 2

Results of radiocarbon dating of taxonomically diverse mammal samples from Krosinko. GID: General identification number; cal BP: calibrated years before the present; MIS: Marine isotope stage; LGM: Last Glacial Maximum. The hyphen means that dates extend out of range.

GID number	Taxon	Element	14C years BP	Cal BP	Lab No.	References	MIS	Chronology
KR/211.F3	Eurasian elk (Alces alces)	Skull with antler	9185 ± 40	8542–8293	OxA-26791	This study	MIS 1	Holocene
KR/111.F122	Reindeer (Rangifer tarandus)	Antler	26,460 ± 240	29,151–28268	OxA-26786	This study	MIS 2	LGM
KR/111.F193	Reindeer (Rangifer tarandus)	Antler	28,500 ± 300	31,720–29887	Poz-23774	Lorenc and Pawłowska, 2010	MIS 2	
KR/111.F29	Woolly mammoth (Mammuthus primigenius)	Pelvis	31,160 ± 390	34,317–32757	OxA-26801	Pawłowska (2015)	MIS 3	
KR/111.F153	Bears (Ursus sp.)	Humerus	32,000 ± 450	35,525–33451	OxA-26803	This study	MIS 3	
KR/111.F192	Woolly mammoth (Mammuthus primigenius)	Loose tooth	32,500 ± 400	36,422–34130	Poz-23424	Lorenc and Pawłowska, 2010	MIS 3	
KR/111.F104	Aurochs (Bos primigenius)	Mandible	34,300 ± 600	38,812–35665	OxA-26794	This study	MIS 3	Vistulian Glaciation
KR/111.F179	Mammals	Rib	34,400 ± 550	38,840–35868	OxA-26784	This study	MIS 3	
KR/111.F101	Steppe bison (Bison priscus)	Skull with horncore	35,150 ± 700	39,809–37155	OxA-26795	This study	MIS 3	
KR/111.F128	Reindeer (Rangifer tarandus)	Antler	36,550 ± 750	40,421–38387	OxA-26787	This study	MIS 3	
KR/111.F191	Aurochs (Bos primigenius)	Skull	38,000 ± 900	41,836–39187	Poz-22688	Lorenc and Pawłowska, 2010	MIS 3	
KR/111.F134	Red deer (Cervus elaphus)	Radius	38,300 ± 1000	42,128–39375	OxA-26792	This study	MIS 3	
KR/112.F3	Woolly rhinoceros (Coelodonta antiquitatis)	Humerus	38,500 ± 900	42,125–39672	Poz-53988	This study	MIS 3	
KR/111.F37	Woolly mammoth (Mammuthus primigenius)	Loose tooth	43,800 ± 1900	52,369–41386	OxA-26788	Pawłowska (2015)	MIS 3	
KR/111.F139	Giant deer (Megaloceros giganteus)	Skull with antler	>45,400	–	OxA-26793	Croitor et al. (2014)	MIS 3	Late Pleistocene
KR/111.F77	Woolly rhinoceros (Coelodonta antiquitatis)	Radius	46,500 ± 2600	–	OxA-26802	This study	MIS 3	
KR/111.F178	Equids (Equus ferus)	Thoracic vertebra	47,000 ± 2800	–	OxA-26785	This study	MIS 3	
KR/111.F190	Equids (Equus ferus)	Metatarsal II/IV	47,000 ± 3000	–	Poz-22678	Lorenc and Pawłowska, 2010	MIS 3	
KR/111.F24	Equids (Equus ferus)	Loose tooth	48,200 ± 3200	–	OxA-26789	This study	MIS 3	
KR/111.F71	Cave lion (Panthera spelaea spelaea)	Mandible	>48,300	–	OxA-26790	Marciszak et al. (2021)	MIS 3	
KR/111.F85	Woolly rhinoceros (Coelodonta antiquitatis)	Femur	48,400 ± 32	–	OxA-26804	This study	MIS 3	

5. Discussion

Field studies revealed a new site, Krosinko, in western Poland that provided a large faunal assemblage. The location of the site is in keeping with the significant lack of palaeontological studies of Quaternary fauna from this region of Poland, and thus takes on a significance for the North European Plain. Generally, radiocarbon dating allows two sub-assemblages: to be distinguished – Pleistocene and Holocene – but the wide range of available dates suggest that the older assemblage may be more complex in nature.

5.1. Krosinko fauna in the broader context

5.1.1. Pleistocene fauna

5.1.1.1. Elephantidae and Rhinocerotidae. In the Pleistocene faunal assemblage from Krosinko, remains of woolly mammoth and woolly rhinoceros dominate over other identified taxa such as horses, giant deer, red deer, fallow deer, reindeer, steppe bison, aurochses, bears and cave lions. This contrasts with the remains of elk and red deer, which were the only remains found in the Holocene peats (MIS 1). Krosinko is one of the 265 sites of Pleistocene age in Poland at which the occurrence woolly mammoths has been recognized since the early 19th century (Pawłowska, 2015). These sites are distributed throughout Poland, with a noticeable concentration along rivers and their tributaries.

The woolly rhinoceros, as a complementary species of the Pleistocene fauna of Poland, is equally abundantly found at palaeontological sites. However, there is no synthetic compilation of its geographical variation that would verify the approximately one hundred sites known in the 1960s (Kowalski, 1959), and the temporal variation has never been studied.

The Pleistocene faunal biodiversity displayed from Krosinko, with the dominance of woolly mammoth and woolly rhinoceros, reflects the structure of the *Mammuthus–Coelodonta* faunal complex. The term *Mammuthus–Coelodonta* Faunal Complex means more or less cold-adapted Pleistocene large-mammal assemblages with similar or identical faunistic structures known from transregional expansion in Eurasia (Kahlke, 1999, 2014). This term is a modification of the previous terms "*primigenius–antiquitatis* fauna" for Asian cold-adapted mammal assemblages of Late Pleistocene age (Pei, 1957) and "*Mammuthus–Coelodonta* fauna" (Chow et al., 1959). The various animal species are included in the Middle Pleistocene faunal complex and the Late Pleistocene faunal complex, respectively, which is related to, among other things, the evolution of the fauna at that time. For example, in the mammoth lineage, the steppe mammoth (*Mammuthus trogontherii* Pohlig, 1885; Eurasia: *c.* 600–200 ka BP) is a direct ancestor of the woolly mammoth (*Mammuthus primigenius* Blumenbach, 1799; Eurasia: *c.* 500–4 ka BP) (Maglio, 1973; Lister and Sher, 2001; Lister et al., 2005). Generally, however, it can be stated that these are animals of the genera *Mammuthus* (mammoth), *Coelodonta* (rhinoceros), *Equus* (horse), *Bos* (aurochs), *Bison* (bison), *Ovibos* (muskox), *Rangifer* (reindeer), *Megaloceros* (deer), *Alces* (elk), *Saiga* (saiga), *Ursus* (bear), *Panthera* (lion), *Crocuta* (hyena), *Lynx* (lynx), *Canis* (wolf) and *Alopex* (fox), and so associated with both the steppe and tundra.

A crucial ecological factor in the formation of this complex was the formation of the Eurasian steppe–tundra (MIS 12; marine isotope stage), a biome that no longer exists today, but that enabled species of Arctic tundra origin to disperse towards the south and south-west as species of steppe origin spread into northern and western regions. Evidence of their co-occurrence (*Mammuthus, Coelodonta, Rangifer*) found at the Bad Frankenhausen (Thüringen) site (460 ka BP) marks the first appearance of the structure of the *Mammuthus–Coelodonta* faunal complex (Kahlke, 1999, 2014). During the peak of the LGM, the mammoth steppe stretched from the Iberian Peninsula across Eurasia into Alaska and Canada (to Yukon) and served as the main source of protein for
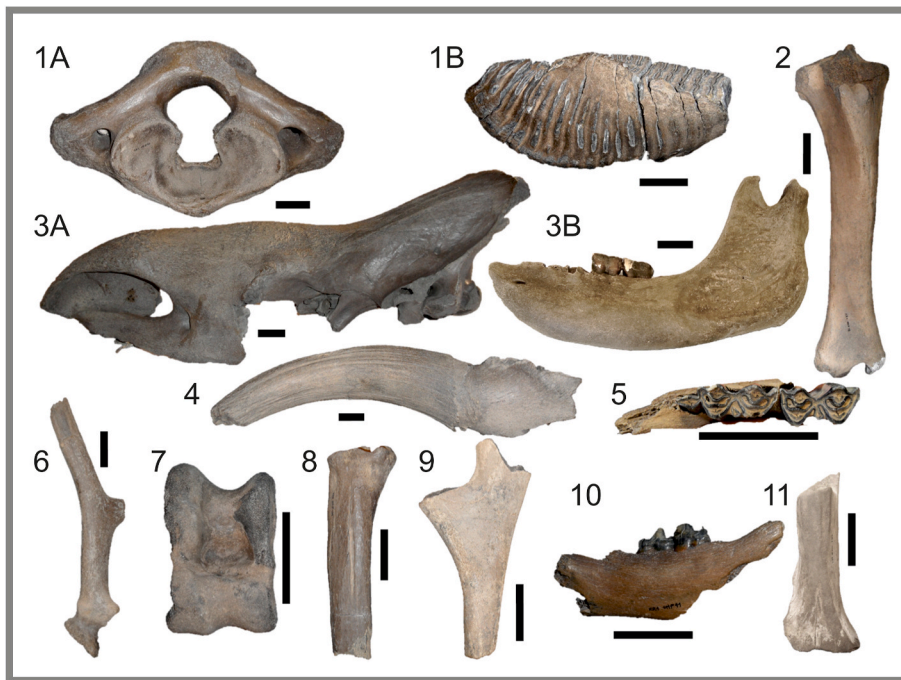
Fig. 5. Representatives of the main animal groups in Krosinko (≥MIS 3–2). 1: Woolly mammoth (*Mammuthus primigenius*; 1 A: atlas, 1 B: lower third molar); 2: horse (*Equus ferus*; tibia); 3: woolly rhinoceros (*Coelodonta antiquitatis*; 3 A: skull, 3 B: mandible); 4: steppe bison (*Bison priscus*; horncore and skull); 5: aurochs (*Bos primigenius*; mandible with M2–3); 6: reindeer (*Rangifer tarandus*; antler); 7: giant deer (*Megaloceros giganteus*; astragalus); 8: red deer (*Cervus elaphus*; radius); 9: fallow deer (*Dama dama*; antler); 10: cave lion (*Panthera spelaea spelaea*; mandible with premolar 4–molar 1); 11: bear (*Ursus*; humerus). Scale bar = 5 cm. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)
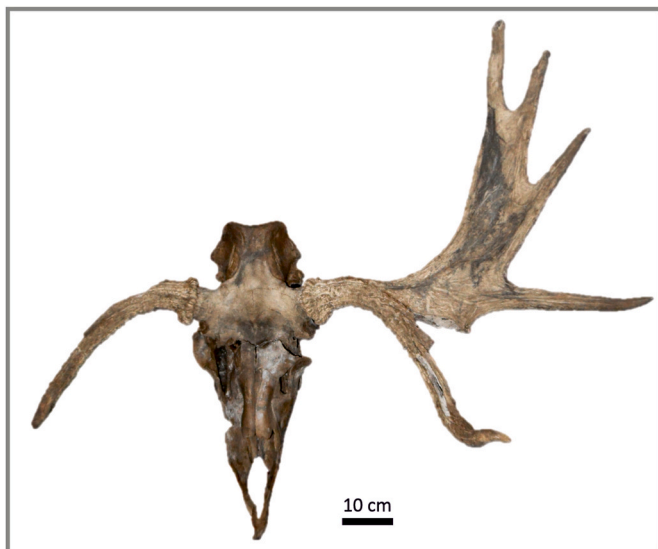

Fig. 6. Krosinko site. Skull of elk (*Alces alces*; MIS 1).

megafauna. The relationship of animals and this ecosystem was dependent. The mammoth steppe provided food indirectly for carnivores and directly for herbivores, who grazed, trampled vegetation and fertilized the landscape, maintaining ecosystem productivity (Zimov et al., 2012). A diverse set of megaherbivore and megacarnivore species lived within this biome, and there was significant ecosystem faunal and floral homogeneity. One of the earliest large species of herbivore to appear in the steppe–tundra area was the steppe mammoth (*Mammuthus trogontherii*), recognized in Poland at fifteen sites (Pawłowska, 2015), including Bełchatów, where cultural traces on a rib, likely left by *Homo heidelbergensis* (indirect evidence given the lack of human remains), are the oldest butchery marks from Poland (Pawłowska et al., 2014a; Pawłowska, 2017). More recently research, conducted by author reveals the presence of steppe mammoth at one more site (Władysławów), which expands to sixteen the number of Polish locations. Unfortunately,

this biome disappeared at the end of the Pleistocene, which correlates with the extinction of many megafauna species.

5.1.1.2. Equidae. The group with the third-greatest number of remains (n = 31) in the Krosinko assemblage is that of horses (*Equus* sp.). Horse remains have been recognized at about eighty Polish sites (Kowalski, 1959; Woroncowa-Marcinowska et al., 2017) mainly distributed across the south-west and north of the country. For the central Poland, Krosinko is one of only two other sites (Poznań and Oborniki) known from earlier studies (Kowalski, 1959). Isotopic studies of the mammoth steppe using carbon and nitrogen isotopic compositions of megafauna collagen indicated that woolly mammoths had a distinct diet, likely comprising decayed plants, and that some horses shared this dietary niche (Drucker et al., 2015; Schwartz-Narbonne, 2016). Taphonomic factors aside (Pawłowska, 2010), this could justify the frequent co-occurrence of horse and mammoth remains, both in this assemblage from Krosinko and in assemblages from other sites.

5.1.1.3. Bovidae. Differential diagnosis of aurochs and bison is more easily made based on rock paintings depicting animal features such as horns and coatings than based on fossil material. This is due to the morphological similarity of many skeletal elements (e.g. Balkwill and Cumbaa, 1992; Gee, 1993; Olsen, 1960; Sala, 1987; Stampfli, 1963). There is also no consensus among researchers as to the features distinguishing *Bos* from *Bison*. This results in an overabundance of remains classified in the family Bovidae or the *Bos/Bison* group in the taxonomic distribution of many collections, including that of Krosinko. Future studies of differences in the collagen protein sequence may be helpful. Several remains from Krosinko, however, are definitely from steppe bison and aurochs. The steppe bison is known from 44 sites scattered all over Poland (with the exception of mountainous areas), whereas aurochs have been found at 63 sites (Kowalski, 1959). However, there always remains a margin of error in these data given the absence of a revision of the taxonomic assignments of all remains. It seems that steppe bison shared environments with horses in the Late Pleistocene, incorporating forbs and grasses into their diets, as demonstrated by dental microwear texture analysis and mesowear analyses from Alaska (Kelly et al., 2021). This is unexpected, in that the separation of food
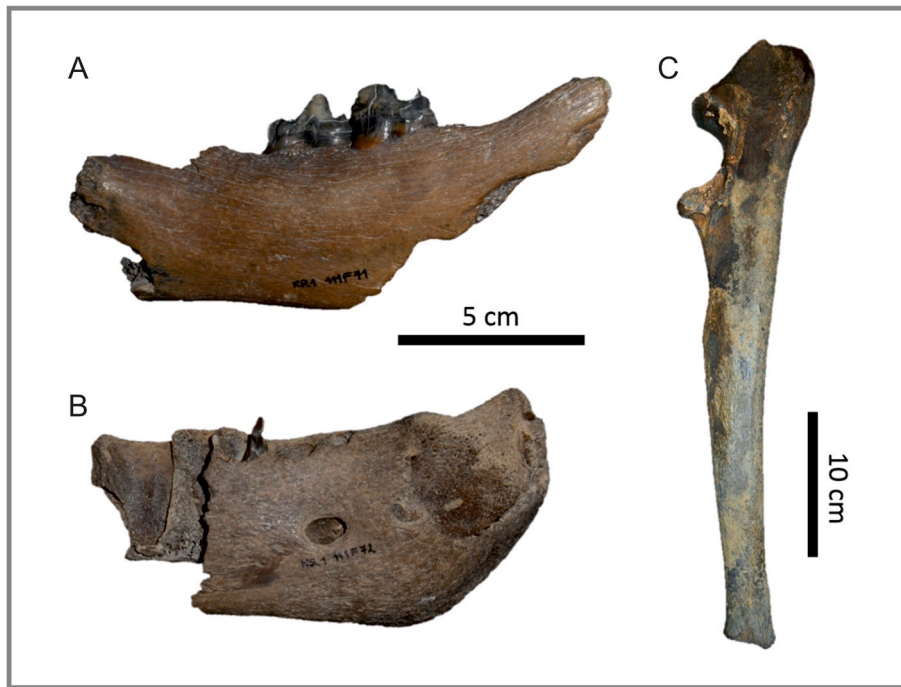
Fig. 7. Mandibles (A: lingual and B: buccal views) and ulna bone (C: lateral view) of the cave lion (*Panthera spelaea spelaea*).

Table 3
Krosinko site, Central Europe. Composition and taxa proportions of the faunal assemblages (at least MIS 3–1). NISP: number of identified specimens; MIS: Marine isotope stage.

Age	Taxon	NISP	% NISP
Holocene (MIS 1)	Eurasian elk (*Alces alces*)	5	
	Mammals	2	
	Red deer (*Cervus elaphus*)	3	
Pleistocene (MIS 3–2)	Woolly mammoth (*Mammuthus primigenius*)	70	26,8
	Woolly rhinoceros (*Coelodonta antiquitatis*)	41	15,7
	Equids (*Equus*)	31	11,9
	Cervidae	6	2,3
	Giant deer (*Megaloceros giganteus*)	3	1,1
	Red deer (*Cervus elaphus*)	3	1,1
	Fallow deer (*Dama dama*)	1	0,4
	Reindeer (*Rangifer tarandus*)	13	5,0
	Steppe bison (*Bison priscus*)	1	0,4
	Aurochs (*Bos primigenius*)	6	2,3
	Bos/Bison	25	9,6
	Ruminantia (Bovidae/Cervidae)	5	1,9
	Carnivora	1	0,4
	Bears (*Ursus* sp.)	1	0,4
	Cave lion (*Panthera spelaea spelaea*)	3	1,1
	Unidentified mammals	51	19,5
Total Pleistocene		261	100,0
Total		271	

resources facilitates the co-occurrence of competing megaherbivore species in a shared geographic range, leading to high local and regional diversities in communities of Late Pleistocene megafauna (Kelly et al., 2021). These studies have also shown that Late Pleistocene bison (and also horses) incorporated more forbs from the mammoth steppe in their diets than do modern grazers, and thus had less abrasive diets.

5.1.1.4. Cervidae. Among deer, the taxonomic distribution in the Krosinko assemblage indicates the presence of giant deer, red deer, fallow deer and reindeer.

In Poland, giant deer remains have been found mainly in the south of the country and are known for about 25 sites (Kowalski, 1959; Stefaniak, 2015). Giant deer from Krosinko were very large, as indicated by the comparison of element measurements against other specimens in Eurasia, and particularly against the largest specimens from Ireland (Croitor et al., 2014). The skull is noteworthy (Fig. 8), with its measurements revealing that it belonged to a very large individual giant deer rivalling the largest specimens from Ireland: the frontal breadth of the skull from Krosinko corresponds to the maximal limit of variation range of the sample from Ireland reported in 1994 by Lister (Croitor et al., 2014). In contrast to the Krosinko outcomes, most species findings from Eastern Europe are characterized by "normal" larger body size.

Among other cervids, the compilation by Kowalski (1959) shows that significantly more sites in Poland feature the reindeer of remains (n = 119) than of red deer (n = 42) or fallow deer (n = 4). In this context, however, the fallow deer antler fragment from Krosinko provides added value to the biogeography of the taxon in Central Europe, being the only one from the north–central part of Poland.

The bone collagen isotopic signatures showed that mainly reindeer, but also giant deer, were the prey of the extinct cave lion *Panthera spelaea* (Bocherens et al., 2011), which is discussed next.

5.1.1.5. Felidae. The cave lion belongs to the family Felidae, one of two groups of predators found in the Krosinko assemblage. Synthesis of the cave lion distribution in Poland shows that Krosinko is one of eighteen open-air sites that, along with 42 cave sites, are recorded in Poland (Kowalski, 1959; Marciszak et al., 2021). Furthermore, Krosinko is one of two sites, alongside Kowanówko (Lubicz-Niezabitowski, 1938), marking the maximum northerly range of occurrence of the cave lion in Poland. While the remains of adult male individuals predominate in all Polish cave lion assemblages, the mandibles from Krosinko are from females.

5.1.1.6. Ursidae. The second group of carnivores is that of bears, represented in the Krosinko assemblage by an element of a bear (*Ursus* sp.). This adds to the list of 56 Polish sites (Kowalski, 1959) where remains of this genus have been found.

Table 4

Krosinko (Central Europe), faunal remains of Late Pleistocene age. Anatomical differentiation of remains of individual taxa in the Pleistocene subassemblage. MP: *Mammuthus primigenius* (woolly mammoth); CA: *Coelodonta antiquitatis* (woolly rhinoceros); E: Equids; MG: *Megaloceros giganteus* (giant deer); CE: *Cervus elaphus* (red deer); DD: *Dama dama* (fallow deer); RT: *Rangifer tarandus* (reindeer); BPr: *Bison priscus* (steppe bison); BP: *Bos primigenius* (aurochs); B/B: *Bos/Bison*; U: *Ursus* sp. (bear); PSS: *Panthera spelaea spelaea* (cave lion); NISP: number of identified specimens.

| Element/Taxa	MP	CA	E	Cervidae	MG	CE	DD	RT	BPr	BP	B/B	Ruminantia	Carnivora	U	PSS	Total NISP	% NISP
Skull	2	5	1		1			2	1	1	2					**15**	7,1
Loose tooth	23	3	5							1	1					**33**	15,7
Mandible	2	1								1	1	2			2	**9**	4,3
Antler				3			1	11								**15**	7,1
Atlas	1		2								2					**5**	2,4
Axis											1					**1**	0,5
Other vertebrae	1	6	4	1							2		1			**15**	7,1
Rib	7	1	2							2	1					**13**	6,2
Scapula	3	1									3					**7**	3,3
Humerus	1	2		1						1	1			1		**7**	3,3
Radius		3	2			1				1	1	1				**9**	4,3
Ulna		2													1	**3**	1,4
Carpal	2	1														**3**	1,4
Metacarpal	1		2			1					2					**6**	2,9
Pelvis	7	3	1													**11**	5,2
Femur	3	4									1	1				**9**	4,3
Patella		2														**2**	1,0
Tibia		2	3								2					**7**	3,3
Fibula	1															**1**	0,5
Astragalus	1		2		1						1					**5**	2,4
Calcaneus						1										**1**	0,5
Other tarsals	1															**1**	0,5
Metatarsal		2	3	1	1						2					**9**	4,3
Phalanges		1	4								2					**7**	3,3
Scapula or pelvis	1															**1**	0,5
Long bone	5															**5**	2,4
Indeterminate	8	2														**10**	4,8
Total	70	41	31	6	3	3	1	13	1	6	25	5	1	1	3	**210**	100,0
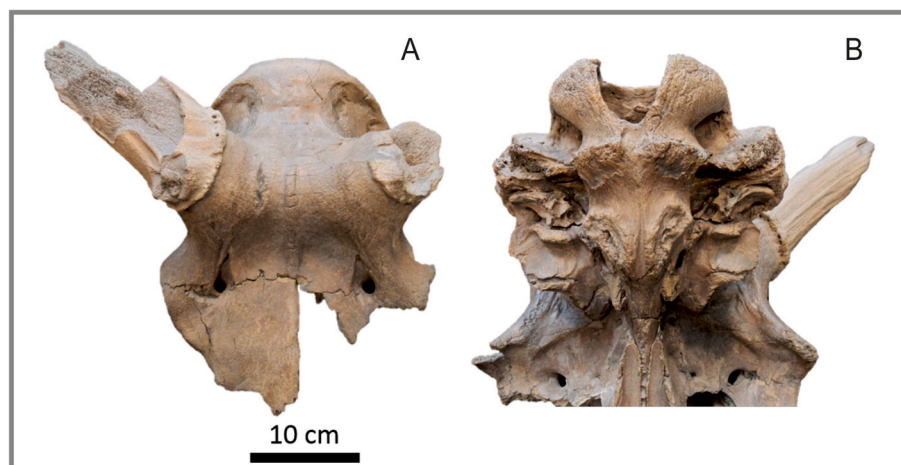
Fig. 8. Krosinko site. The skull of a giant deer (*Megaloceros giganteus*) in dorsal (A) and ventral (B) views.

5.1.2. Holocene fauna

The results indicate the presence of only elk and red deer remains from the Holocene peats that complete the sedimentary succession at Krosinko, which constitutes a record of the presence of a lake. The small total of remains (n = 10) is due to the lack of large-scale peat exploitation in this area, as is the case for sandy sediments. The radiocarbon date obtained in this study (9185 ± 40 BP; OxA-26791) is within the range of the presence of elk in Poland, which is reported by Kowalski (1959) as being from the Pleistocene to the postglacial. In total, sixty Polish sites have been recognized so far (Kowalski, 1959; Stefaniak et al., 2014).

5.1.3. Body-part distribution of Krosinko fauna

The results obtained from the Pleistocene faunal analysis (at least MIS 3–2) indicate that the body-part distribution for individual taxa is random, not displaying any characteristic pattern such as the dominance of one element over others. The anatomical diversity of the remains indicates a natural accumulation. The fact that bones were not found in articulatory or anatomical order, and that evidence was not found suggesting that they had been articulated at deposition stage, indicates that they were reworked during deposition. This is consistent with the results of geological studies, which clearly imply a significant palaeo-environmental dynamic (Pawłowska et al., in press). Further research focused on detailed taphonomic studies should shed more light on their depositional history, though this is beyond the scope of this work.

In the case of the Holocene remains (MIS 1), the presence of articulated elk skeletal elements indicates that they originate from a single individual (MNI = 1) and that any post-depositional processes that

might have disturbed the bone setting had a negligible influence.

5.2. Palaeoclimate conditions in Central Europe

Environmental conditions, including palaeoclimatic conditions, can be reconstructed from various data sets, of which faunal analysis – enhanced by the results of lithological analysis and microtextural analysis of quartz grains (Pawłowska et al., in press) – was used here.

The prevalence of woolly mammoth and woolly rhinoceros over other taxa in the Krosinko assemblage indicates harsh environmental conditions in the Late Pleistocene. These species, particularly the mammoth, preferred the cold and dry conditions that characterized the mammoth steppe where they occurred. At the same time, the absence of roe deer and beavers suggests that temperate species did not colonize the area from glacial refugia, and thus that there was not yet sufficient climate change with land deglaciation.

The palaeoclimatic conditions towards the south of Central Poland are inferred from fauna composition to be consistent with the reconstruction of palaeoenvironmental conditions based on lithological analysis and the microtexture analysis of quartz grains. These results, indicating the significant proportion of RM (round matt grains) and EM/RM (grains with dull edges and corners) grains, showed that Unit C – in which megafaunal bones were found along with plant remains and flints – was accumulated during a period of severe climatic conditions of periglacial features, with strong influence from aeolian processes (Pawłowska et al., in press). Simultaneously, the presence of an active layer in the permafrost at this time, as determined by the presence of cracked grains and the frequency and very advanced degree of frost microtexture development, further confirmed the dry and cold climate conditions, with frequent transitions through 0 °C.

The existence of permafrost during the Late Pleistocene is well known in Central Europe, as its extent reached as far south as 48–49°N (Duchkov, 2006). Under these conditions of periglacial and *in-situ* frost weathering at Krosinko, cryoturbation marks (pseudoretouch, scratches, cracks and pitting) and frost cracks (flaws, cracks, concentric circles) developed (Chambers, 2005; Chu et al., 2015), as recorded on the flints (Pawłowska et al., in press).

The periglacial climate inferred by the faunal and sedimentological analysis is consistent with the type and palaeoregime of the river, which was determined to be braided and high-energy (Pawłowska et al., in press). Such fluvial systems functioned on ice sheet forelands supplied by meltwaters from the north and by rivers from the south.

5.3. Radiocarbon chronology, habitats and biogeography of Pleistocene fauna

5.3.1. General notes on the radiocarbon age

The spatial and temporal distribution of fauna in the Pleistocene in Europe was not uniform. Individual settlement patterns by species shed light on the differences between species. We observe the reduction in abundance, range decline and population fragmentation to local refugia, where the last populations became extinct or survived. In the last interglacial period, the limits of the ranges changed at different rates – not only in different species, but also within a single species over different parts of its range (Plasteeva et al., 2020). This has to do with the different subenvironments the animals may have preferred, and with the presence of refugia that provided opportunities to survive adverse conditions. For cold-adapted fauna, periglacial conditions were not a problem, unlike for temperate species. Climatic changes entailed environmental changes, as best exemplified by the woolly mammoth and the woolly rhinoceros, which display different patterns. While woolly mammoth existed in Europe at the end of the Late Pleistocene, with a pattern of retreats northward, the woolly rhinoceros disappears from the fossil record *c.* 14 ka BP (Lorenzen et al., 2011; Stuart and Lister, 2012). Previous studies have shown that, prior to the Last Glacial Maximum (LGM), most species occupied consistent isotopic niches on the

mammoth steppe, suggesting consistent diets or habitats (Schwartz-Narbonne, 2016). These patterns of isotopic niches altered during the LGM, and these patterns were not restored in the Holocene (Schwartz-Narbonne, 2016). These changes suggest that the ecosystem suffered severe disturbance during the LGM, prior to the extinction of many taxa at the end of the Pleistocene. Bison, horse, muskox and reindeer are species that managed to survive the decline of the mammoth steppe.

Radiocarbon dating results indicate that the Krosinko assemblage composition is complex, and it contains faunal remains of variable age. Given the radiocarbon dating performed on some of the recovered remains, at least some of these animals lived during MIS 3, MIS 2, and MIS 1. The presence of open dates suggests that some of them are even earlier. The variation in radiocarbon age of the remains confirms the presence of two subassemblages: one Pleistocene (at least MIS 3–2) and one Holocene (MIS 1: 9.1 ka BP). This mixed assemblage is not contemporaneous, even within the Pleistocene range, as indicated by radiocarbon dates (48.4 ka BP–26.4 ka BP). Considering depth of occurrence (6–7 m) of the assemblage in the geological sequence, the remains constitute a single horizon of up to ~1 m thickness. A quite compact assemblage was thus possibly deposited as the effect of one geological event at *c.* $26{,}460 \pm 240$ BP or later, as can be inferred from the latest available radiocarbon date applying the concept of "residual material" (Ramsey, 2008). The wide range of radiocarbon dates probably reflects the chronological distributions differing to various degrees between species, most probably resulting from changing climate and environment preferences. Alternatively, it suggests the bones may come from numerous variable original sources. This implies that the assemblage does not represent a single biocenosis, nor even a single taphocenosis. Each species will thus be discussed individually.

5.3.2. Elephantidae and Rhinocerotidae

The results of radiocarbon dating of the woolly mammoth remains (*Mammuthus primigenius*) from Krosinko, supplemented with those from other Polish sites, were used to reconstruct the time and place of extinction of the woolly mammoth in Poland (Pawłowska, 2015). The radiocarbon dates indicate that woolly mammoths occurred in Poland between about 54 and 30 cal ka BP (with a predominance of dates between 35 and 30 cal ka BP), which correlates with MIS 3 and is consistent with the existing state of knowledge. From previous radiocarbon studies (Nadachowski et al., 2011), it was apparent that mammoth occurrence in Poland was discontinuous, with two defined gaps: each gap occurred between a different pair of events linked with cold climate in Central Europe, i.e. between H5 and H4 (43.2–40.6 cal ka BP) and between H4 and H3 (34.8–32.0 cal ka BP). Radiocarbon dating has also made it possible to demonstrate the presence of mammoths between H4 and H3 (32.6 and 32.5 cal ka BP) using the example of two other sites in Poland, thus shifting the range of this gap. Thus, new radiocarbon dates that extend and verify the existing data have led to the conclusion that, to date, there is no evidence for the occurrence of mammoths in Poland between 43.2 and 40.6 cal ka BP, or between 34.8 and 32.6 cal ka BP. The radiocarbon dates support the conclusions of Ukkonen et al. (2011) on the occurrence of woolly mammoth in the circum-Baltic region – namely, that (i) the mammoth was widespread in northern and north-eastern Europe during MIS 3; and (ii) that the widest distribution of mammoths occurred around 30 ka. This taxon was closely associated with the steppe.

There is still debate about the process of extinction of the woolly rhinoceros (*Coelodonta antiquitatis*) in Eurasia, particularly regarding whether it was simultaneous (isochronous) or gradual across parts of Europe (anisochronous) (Lorenzen et al., 2011; Stuart and Lister, 2012). This has to do with radiocarbon studies, which remain insufficient, leading to gaps (such as *c.* 40–34 ka BP) in the pattern of dates in certain areas, indicating temporary absences of *C. antiquitatis* (Stuart and Lister, 2012). The three radiocarbon dates of the Krosinko woolly rhinoceros, which range between 48.4 and 38.5 ka BP, do not resolve the nature of

extinction but have great chronostratigraphic significance. The radiocarbon date of 38,500 ± 900 BP (Table 2) falls exactly in the previously defined temporal absence of the woolly rhinoceros in Europe. This allows us to limit the range of the woolly rhino's gap in Europe to 40 to 38 ka BP. This also shows how further radiocarbon dating of woolly rhinoceros remains is necessary to better understand the pattern of the European distribution of this species. The general pattern for Eurasia deducible from published radiocarbon dates shows that the woolly rhinoceros ranged from >49 to *c*. 15 ka BP, with the species becoming extinct in European Russia at 19.4–15.1 ka BP, and in Britain at *c*. 35 ka BP (GI-7) (Stuart and Lister, 2012). From the perspective of Polish chronology, the radiocarbon dates of woolly rhinos from Krosinko indicate their presence during the Grudziądz Interglacial of the Vistulian Glaciation (MIS 3). The temporal variability of the occurrence of the woolly rhinoceros in Poland has never been studied, and individual radiocarbon dates indicate that it was present *c*. 28.4 ka BP (Szczecin: Stuart and Lister, 2012), 20.8 ka BP (Deszczowa Cave: Nadachowski et al., 2009; Stuart and Lister, 2012), 17.8 and 16.1 ka BP (Jasna Cave: Stuart and Lister, 2012). Even earlier work has reported that rhinoceros remains have generally been found in layers dated to Riss – which nonetheless needs to be verified – and to Würm, which would correspond to MIS 8–3 (2?) (Kowalski, 1959). However, a systematic and synthetic study of the remains of this species needs to be carried out to shed light on the occupation patterns of Poland in the context of the rest of Europe, and to resolve questions of morphological variation in specific subenvironments.

5.3.3. Equidae

The two radiocarbon dates for horse (*Equus ferus*) bones are closely clustered at 48 and 47 ka BP. This is consistent with previous results of relative dating of horse remains from Poland (MIS 8, 5d–2), which mainly point to the Weichselian Glaciation (Riss, Würm: Cyrek et al., 2010; Kowalski, 1959). However, radiocarbon dating series are lacking, as is the case with the other taxa discussed here. Horses are a common species in both glacial and interglacial faunal assemblages in Eurasia. They prefer grassland or steppe areas, which does not mean that they are ecologically or geographically restricted to these habitats (Woodward, 1991), but are rather associated with a wide range of Pleistocene and Holocene environments (Azzaroli, 1992). In the Holocene, wild horses survived in the steppe zone (Plasteeva et al., 2020). Their ecological plasticity has in part to do with their ability to thrive in areas where other ungulates fail to flourish. This prevalence is associated with the use of habitat containing thick, fibrous vegetation – a resource which other ungulates (such as ruminants) avoid due to the prohibitive amount of energy and processing time involved – due to distinctive digestive anatomy and physiology (Kaagan, 2000). Many authors have emphasized the role of climate in the evolution of the horse, especially during the transition from Pleistocene to Holocene, with its severe changes in climate (Uerpmann, 1990). For this reason, the Pleistocene ranges of widespread wild horses in Eurasia were fragmented along with decreasing abundance in the Early Holocene. Isotope studies also record changes, such as depletion in horse $\delta^{13}C$ at the start of the Holocene, as is also seen in cattle and red deer as a result of changing plant $\delta^{13}C$ values due to an increase in atmospheric CO_2 concentration (Stevens and Hedges, 2004).

5.3.4. Bovidae

The radiocarbon dates for representatives of the family Bovidae—35 ka BP for steppe bison (*Bison priscus*) and 38 and 34 ka BP for aurochs (*Bos primigenius*)—fall in the Middle Weichselian glaciation or the Grudziądz Interstadial in Polish stratigraphy (MIS 3).

The radiocarbon data of the steppe bison skull with horncore (39.8–37.1 cal ka BP) falls in GI-9–GI-8c. Given this taxon's dominance during the colder periods of the Late Pleistocene, with their association with open environments (steppe–tundra), this date should be associated with GS-9. On the other hand, recent palaeo-ecological studies indicate

that this species also lived under interstadial conditions, leading to the conclusion that ancient bison adapted to different degrees of palaeomobility, according to the prevailing palaeo-ecological conditions and climate (Funck et al., 2020). The fossil record of the taxon in Poland begins with the Middle Pleistocene, although it is known from only one cave (Biśnik: MIS 7–Cyrek et al., 2010, later revised by Krajcarz et al., 2014 to MIS 6/5e). Its distribution throughout Poland falls within MIS 5d–2, based on the fossil record in the absence of radiocarbon chronology, although excluding mountainous areas in the south (Würm: Kowalski, 1959). This is related to the development of the steppe bison during this time (Würm) at the expense of *Bison priscus schoetensacki*, associated with forest biotopes, which became rarer (Palacio et al., 2017). During the Middle and Late Weichselian, the steppe bison (*B. priscus*) alternated in its occupation of Western Europe with the European bison (*Bison bonasus*) as a result of climate-induced environmental changes, as shown by studies of ancient mitogenomes from throughout Europe, the Caucasus and Siberia, and reinforced by evidence from cave paintings (Chauvet cave, France, 36 ka) (Massilani et al., 2016). The Late Pleistocene European steppe bison originated from northern Eurasia, whereas the modern wisent population emerged from a refugium in the southern Caucasus after the Last Glacial Maximum (Massilani et al., 2016). At the same time, the steppe bison was disappearing from the fossil record in Poland, as seen by the lack of its remains in postglacial strata (Kowalski, 1959). This is confirmed on a European scale. Only *B. bonasus* in Europe survived the effects of the climate changes in the Holocene, associated with temperate climate and forested vegetation, as specified by fossil records and DNA study; however, this survival was at the expense of reductions in its genetic diversity (Massilani et al., 2016). The northern steppe bison population persisted locally in southern Yukon into the middle Holocene (5400 years ago: Zazula et al., 2017).

Radiocarbon dates for aurochs (41.8–39.1 cal ka BP and 38.8–35.6 cal ka BP) fall into GS-11–GS-9 and GS-9–GS-8. These dates should be associated with GI-10 and GI-9, and thus with moderate climatic conditions, as this taxon requires. During cold intervals, the aurochs probably retreated, though in the absence of a radiocarbon chronology for this species in Poland this is difficult to confirm at the moment. The fossil record suggests that aurochses occurred in Poland in the Pleistocene (MIS 5d–2) and Holocene (MIS 1), with the last representative of the species dying in 1627 (Würm, Holocene: Kowalski, 1959). During the Pleistocene, the spread of the aurochs was considerable in Europe, with no evidence from Ireland or of crossing the Bering Strait. The lower abundance of aurochs finds in the Pleistocene than in the Holocene (Wright, 2013) also seems to apply to Poland. This may be the result of the reduction in its range during the numerous Pleistocene glacial periods (Wright, 2013). On the other hand, it could also be explained by a potential increase in abundance during the early Holocene (Mesolithic and Neolithic) in response to increasingly favourable mild and humid conditions after the end of the last Ice Age (Van Vuure, 2005). Nonetheless, its dependence on temperate climate and on open forests, widespread during the Holocene Climatic Optimum, has been confirmed (Degerbøl and Fredskild, 1970) and is associated with the distribution in Europe. This reason, along with the great genetic variation of Italian aurochses, leads to the assumption that the species may have retreated to refugia, perhaps on the Apennine Peninsula, during the Last Glacial Maximum (Mona et al., 2010). Central and northern areas in Europe were recolonized after the last glaciation by eastern immigrants originating from regions in Eastern Asia that hosted temperate forests with large areas of grassland during the last glaciation (Mona et al., 2010). In the Holocene, aurochses are common and took on symbolic meaning for people, as shown by evidence from the Middle East, including Çatalhöyük. In Neolithic Çatalhöyük, highly selected elements of aurochses (which were hunted using obsidian tools [Pawłowska, 2014]), were used to decorate houses and were included in feast and other deposits (Pawłowska, 2020).

5.3.5. Cervidae

The radiocarbon date for the skull of the giant deer (*Megaloceros giganteus*) (>45 ka BP) is an open date and may correspond to MIS 3, when the giant deer was very common in the higher and middle latitudes of Europe, or may be far beyond MIS 3. Giant deer preferred mixed semi-open habitats that allowed both grazing and browsing, as demonstrated by the relatively narrow distribution of *M. giganteus* in Eurasia and the palaeoecological data, as two independent lines of evidence (Lister and Stuart, 2019). In Poland, giant deer remains occur only in the Pleistocene strata (Kowalski, 1959; Pawłowska et al., 2014b), which is consistent with the results from Krosinko, with their complete absence so far in the postglacial period. However, this species survived until around 6900 radiocarbon year BP (Holocene) in western Siberia (Stuart et al., 2004). The pattern of distributional changes showing that it disappeared from the eastern areas of Eurasia correlates chronologically with the spread of closed forest, while its extinction in western Europe remains strongly linked to the deterioration of the climate and the replacement of a productive mixed habitat with a tundra-like landscape in the Younger Dryas (Late Glacial Interstadial: LGI) (Lister and Stuart, 2019).

The dating of the red deer (*Cervus elaphus*) radius bone from Krosinko to 38 ka BP (42.1–39.3 cal ka BP) points to MIS 3 (GI-10 or GI-9), which falls within the time frame of the species' occurrence in Poland (MIS 11/9: Pawłowska et al., 2014a; MIS 8: Cyrek et al., 2010; MIS 5d–2; Würm: Kowalski, 1959) and in Europe (MIS 14–1). The pattern of European inhabitation is discontinuous in the central part (LGM), when deer occupied the refugia of southern Europe, as indicated by three deeply divergent mitochondrial DNA lineages (the western European, eastern European and Mediterranean groups) that split during the last glaciation as a result of isolation (Skog et al., 2009). The western and eastern European lineages could be linked to Iberian and Balkan refugia, respectively, while the Mediterranean one might originate from a refugium in Sardinia, Spain or Africa (Skog et al., 2009). This is related to the habitat requirements of red deer, which was and is associated with woodlands. Their development in LGI (Bölling) restores the occurrence of the taxon in Central Europe. This species is usually present in deciduous forests, although it is also known from coniferous forests and open habitats. Similarly, giant deer is a mixed feeder, alternately browsing and grazing according to the available habitat (Gordon, 2003). Its successful recolonization in the late European Pleistocene led to its prevalence in the Holocene (MIS 1), and this is also apparent in the assemblage recovered from the Krosinko peats.

Radiocarbon dates from Krosinko indicate the presence of reindeer (*Rangifer tarandus*) in Central Poland between 36 and 26 ka BP, which correlates with the Middle and Late Weichselian glaciation (MIS 3–2). The oldest date (40.4–38.3 cal ka BP) corresponds to the GS-10–GS-9 stadial, and the others (31.7–29.8 cal ka BP and 29.1–28.2 cal ka BP) to the GS-5.2–GS-5.1 and GS-5.1–GS-4 stadials. These results are consistent with the climatic requirements of the reindeer, which is a cold-hardy species. Its abundance declined during warming, as is well illustrated by an example from France (Grotte XVI), where episodes of summer warming between about 36,000 and 12,000 radiocarbon years ago led to a decline in the relative abundance of reindeer (Grayson and Delpech, 2005). Also, because of climate links, reindeer, along with saiga antelope, spotted hyena and arctic fox, underwent significant distributional changes in their range during the Pleistocene to Holocene shift (Sommer, 2020). This has implications for their distribution in Poland during the Pleistocene by displaying a characteristic pattern of retreating further and further north as the climate warms (transition to MIS 1; LGI). Climate projections show that a temperature rise of 4–7.5 °C in the far north would lead to high mortality in reindeer populations, and this mortality may be accompanied by a significant retreat of the southern limit of their distribution (Grayson and Delpech, 2005). The oldest reindeer remains from Poland are known from a single site (Bełchatów coal mine) and are dated to MIS 11/9 (Pawłowska et al., 2014a). The fossil record of other reindeer remains discovered in Poland ranges from MIS 8–6 through 5d–2 (for cave findings) to MIS 1 (for mostly Mesolithic sites of northern Poland) (Riss, Würm and postglacial: Kowalski, 1959).

5.3.6. Felidae

Radiocarbon dating of the mandible of a cave lion (*Panthera spelaea spelaea*) from Krosinko gave a date >48.3 ka BP (falls in or far beyond MIS 3). This dating, alongside the radiocarbon dating of material from other Polish sites, has shown the presence of this taxon between 150 and 28 ka BP (Marciszak et al., 2021). Generally, the cave lion (*Panthera spelaea*) has been recorded in Poland at sites dated in the range 750–28 ka. This predator was predominantly associated with open habitats that characterized cool stages, but it may also have occurred in the more open woodland that developed in interstadials (Stuart and Lister, 2011). This is strongly confirmed by the recent discovery of a partial skeleton of a cave lion in Torca del Leónthe (Iberia) dated to GI-11, which was a warming event in which a mature forest developed under humid and temperate conditions at this site (Álvarez-Lao et al., 2020). Isotope study has pointed to an individualistic prey choice for cave lions, with some individuals more oriented to reindeer and others to young cave bears, significantly without competition from cave hyenas, which display different isotopic signatures (Bocherens et al., 2011). During its history, the cave lion went through a demographic bottleneck during MIS 3, as shown in DNA analysis by a decline in effective population size around 47 cal ka BP, followed by an increase most likely around 18 cal ka BP (Ersmark et al., 2015). This change is correlated with the appearance of dwarf and gracile specimens in Poland from MIS 3 (Marciszak et al., 2021). The species recovered shortly before its extinction which, according to Stuart and Lister (2011), occurred around 14 cal ka BP. The process of decline of the Pleistocene lion was approximately synchronous across Poland, but the species vanished much earlier than in other European areas (Marciszak et al., 2021). The reason for the extinction of the cave lion has to do with climate change, with forces of ecosystem change leading to the collapse of the mammoth steppe ecosystem (Stuart and Lister, 2011). This change, moreover, affected many taxa.

5.3.7. Ursidae

A bear (*Ursus* sp.) from Krosinko with a radiocarbon date of 32 ka BP stratigraphically matches the Middle Weichselian Glaciation or Grudziądz Interstadial (MIS 3), and also corresponds with the stratigraphic range of the occurrence of bears in Poland, including both *U. speleaus* and *U. arctos* (from MIS 8 to MIS 2; Riss–Würm: Kowalski, 1959).

6. Conclusions

The study of the Krosinko findings led to the reconstruction of the faunistic structure from the Late Pleistocene to Holocene (at least MIS 3–1). The two subassemblages differed both taxonomically and taphonomically. The Pleistocene assemblage included woolly mammoth, woolly rhinoceros, horse, giant deer, red deer, fallow deer, reindeer, steppe bison, aurochs, bear and cave lion, while the Holocene was represented by elk and red deer. The range of fossilization of the material is extreme, ranging from very high in the Pleistocene assemblage to little, if any, (sub-fossilization) in the Holocene assemblage.

The Pleistocene faunal assemblage, in which woolly mammoth and woolly rhinoceros dominate, reflects the structure of the *Mammuthus–Coelodonta* faunal complex. Representatives of this complex preferred the dry and cold conditions that characterized the palaeoenvironmental conditions at Krosinko, and thus in Central Europe in the Late Pleistocene. In addition, this area was characterized by permafrost, which also covered much of Europe. These palaeoenvironmental features are associated with the mammoth steppe, a biome that functioned from Eurasia to Canada. The diversity of this steppe influenced the faunal distribution in the range of taxa and groups of taxa. The biogeography of the Krosinko fauna, combined with radiocarbon chronology (21 dates), was thus conducted separately for each taxon. This approach was necessary because of the individual

response of taxa to changing environmental conditions in response to those of climate. These changes, combined with reductions in herbivores, led to the disappearance of the mammoth steppe and to the near or total extinction of the faunal species inhabiting it.

Relating the Krosinko results to European evidence showed the dynamics of colonization of Eurasia by different Pleistocene fauna, their habits and adaptations, and the history of migration, population replacement and extinction in Eurasia. The fossil record, radiocarbon chronology and DNA study form common lines of evidence for a long-term process of species extinction, preceded by range reduction and even by long existence in terminal refugia accompanied by a loss of genetic variation and adaptive flexibility (Lister and Stuart, 2008). However, some species, such as woolly mammoth, horse, giant deer, steppe bison and muskoxen, survived the Late Pleistocene extinction event and could be described as species with a high degree of ecological flexibility.

Further research should focus on the taphonomic evaluation of the Krosinko faunal material, in order to reconstruct the depositional history in detail and to determine whether there are non-fluvial factors responsible for their shape and deposition. In particular, it would be valuable to assess the contribution of humans, and its character, on the assemblage by evaluating marks present on the remains (natural *vs* anthropic). No less important is the need to revise the remains of Bovidae to separate them into *Bos* and *Bison*, in order to perform a series of radiocarbon dating for most taxa, excluding the woolly mammoth and cave lion, and so to establish their precise chronology in Poland and to relate them to patterns of settlement, withdrawal and extinction in Eurasia.

Author contributions

KP designed and performed the research, the analysis of the results, prepared the manuscript, and responses for reviewers.

Data availability

Data (the faunal material) presented in this manuscript is stored as a private collection. Access to the specimens is available by request to the author.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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References

Álvarez-Lao, D.J., Álvarez-Vena, A., Ballesteros, D., Garcia, N., Laplana, C., 2020. A cave lion (*Panthera spelaea*) skeleton from Torca del León (NW Iberia): micromammals indicate a temperate and forest environment corresponding to GI-11 (MIS 3). Quat. Sci. Rev. 229, 106123. https://doi.org/10.1016/j.quascirev.2019.106123.

Azzaroli, A., 1992. Ascent and decline of monodactyl equids: a case for prehistoric overkill. Ann. Zoöl. Fenn. 28, 151–163.

Balkwill, D., Cumbaa, S.L., 1992. Guide to the identification of postcranial bones of *Bos taurus* and *Bison bison*. Canadian Museum of Nature.

Barone, R., 1972. Anatomie comparée des mammifères domestiques. Tome 1. Ostéologie. Vigot Freres, Paris.

Bocherens, H., Drucker, D.G., Bonjean, D., Bridault, A., Conard, N.J., Cupillard, C., Germonpré, M., Höneisen, M., Münzel, S.C., Napierala, H., Patou-Mathis, M., Stephan, E., Uerpmann, H.-P., Ziegler, R., 2011. Isotopic evidence for dietary ecology of cave lion (*Panthera spelaea*) in North-Western Europe: prey choice, competition and implications for extinction. Quat. Int. 245 (2), 249–261. https://doi.org/10.1016/j.quaint.2011.02.023.

Brown, C.L., Gustafson, C.E., 2000. A Key to Postcranial Skeletal Remains of Cattle/Bison, Elk, and Horse. Washington State University Laboratory of Anthropology, Pullman.

Chachaj, J., 1996. Detailed Geological Map of Poland, Scale 1 : 50,000, Sheet 507 Mosina. Polish Geological Institute, Warszawa.

Chambers, J.C., 2005. Like a rolling stone? The identification of fluvial transportation damage signatures on secondary context bifaces. Lithics: The Newsletter of the Lithic Studies Society 24, 66–77.

Chow, M., Chang, Y.P., Hu, C.K., Liu, H.I., Hsu, Y.H., Chou, P.H., Lee, Y.C., Hsien, H.H., 1959. Pleistocene Mammalian Fossils from the Northeastern Provinces. Institute of Vertebrate Paleontology, Academia Sinica, Beijing (in Chinese, with English summary).

Chu, W., Thompson, Ch, Hosfield, R., 2015. Micro-abrasion of flint artifacts by mobile sediments: a taphonomic approach. Archaeol. and Anthropol. Sci. 7, 3–11. https://doi.org/10.1007/s12520-013-0157-0.

Croitor, R., Stefaniak, K., Pawłowska, K., Ridush, B., Wojtal, P., Stach, M., 2014. Giant deer *Megaloceros giganteus* Blumenbach, 1799 (Cervidae, mammalia) from Palaeolithic of Eastern Europe. Quat. Int. 326–327, 91–104. https://doi.org/10.1016/j.quaint.2013.10.068.

Cyrek, K., Socha, P., Stefaniak, K., Madeyska, T., Mirosław Grabowska, J., Sudoł, M., Czyżewski, Ł., 2010. Palaeolithic of Biśnik cave (southern Poland) within the environmental background. Quat. Int. 220 (1–2), 5–30. https://doi.org/10.1016/j.quaint.2009.09.014.

Degerbøl, M., Fredskild, B., 1970. The Urus (*Bos primigenius* Bojanus) and Neolithic Domesticated Cattle (*Bos taurus domesticus* Linne) in Denmark. The Royal Danish Academy of Science and Letters, Copenhagen.

Drucker, D.G., Vercoutere, C., Chiotti, L., Nespoulet, R., Crépin, L., Conard, N.J., Münzel, S.C., Higham, T., van der Plicht, J., Lázničková-Galetová, M., Bocherens, H., 2015. Tracking possible decline of woolly mammoth during the Gravettian in Dordogne (France) and the Ach Valley (Germany) using multi-isotope tracking (13C, 14C, 15N, 34S, 18O). Quat. Int. 359, 304–317.

Duchkov, A.D., 2006. Characteristics of permafrost in Siberia. In: Lombardi, S., Altunina, L.K., Beaubien, S.E. (Eds.), Advances in the Geological Storage of Carbon Dioxide. Springer, Dordrecht, pp. 81–91.

Ersmark, E., Orlando, L., Sandoval-Castellanos, E., Barnes, I., Barnett, R., Stuart, A., Lister, A., Dalén, L., 2015. Population demography and genetic diversity in the Pleistocene cave lion. Open Quat. 1 (4), 1–14. https://doi.org/10.5334/oq.aa.

Funck, J., Heintzman, P.D., Murray, G.G., Shapiro, B., McKinney, H., Huchet, J.B., Bigelow, N., Druckenmiller, P., Wooller, M.J., 2020. A detailed life history of a Pleistocene steppe bison (*Bison priscus*) skeleton unearthed in Arctic Alaska. Quat. Sci. Rev. 249, 106578. https://doi.org/10.1016/j.quascirev.2020.106578.

Gee, H., 1993. The distinction between postcranial bones of *Bos primigenius* Bojanus, 1827 and *Bison priscus* Bojanus, 1827 from the British Pleistocene and the taxonomic status of *Bos* and *Bison*. J. Quat. Sci. 8 (1), 79–92. https://doi.org/10.1002/jqs.3390080107.

Gordon, I.J., 2003. Browsing and grazing ruminants: are they different beasts? For. Ecol. Manag. 181 (1–2), 13–21. https://doi.org/10.1016/S0378-1127(03)00124-5.

Grayson, D.K., Delpech, F., 2005. Pleistocene reindeer and global warming. Conserv. Biol. 19 (2), 557–562. https://doi.org/10.1111/j.1523-1739.2005.00267.x.

Guérin, C., 1980. Les rhinoceros (Mammalia, Perissodactyla) du Miocene terminal au Pleistocene superieur en Europe occidentale: comparison avec les especes actuelles. Documents du Laboratoire de Géologie de la Faculté des Sciences de Lyon 79, 1–1182.

Heintz, E., 1970. Les Cervidés villafranchiens de France et d'Espagne. Memoires du Museum National D'Histoire Naturelle Nouvelle Serie, Serie C, Sciences de la Terre.

Hrynowiecka, A., Żarski, M., Jakubowski, G., Nadachowski, A., Pawłowska, K., Pawłowski, D., Szymanek, M., Nast, D., 2018. Eemian and Vistulian (Weichselian) paleoenvironmental changes: A multi-proxy study of sediments and mammal remains from the Ławy paleolake (Eastern Poland). Quat. Int. 467, 131–146. https://doi.org/10.1016/j.quaint.2016.10.033.

Kaagan, L.M., 2000. The Horse in the Late Pleistocene and Holocene Britain. University College London, London.

Kahlke, R.D., 1999. The History of the Origin, Evolution and Dispersal of the Late Pleistocene *Mammuthus–Coelodonta* Faunal Complex in Eurasia (Large Mammals). Fenske Companies, Rapid City.

Kahlke, R.D., 2014. The origin of Eurasian Mammoth Faunas (*Mammuthus–Coelodonta* Faunal Complex). Quat. Sci. Rev. 96, 32–49. https://doi.org/10.1016/j.quascirev.2013.01.012.

Kelly, A., Miller, J.H., Wooller, M.J., Seaton, C.T., Druckenmiller, P., DeSantis, L., 2021. Dietary paleoecology of bison and horses on the mammoth steppe of eastern Beringia based on dental microwear and mesowear analyses. Palaeogeogr. Palaeoclimatol. Palaeoecol. 572, 110394. https://doi.org/10.1016/j.palaeo.2021.110394.

Kowalski, K., 1959. Katalog ssaków plejstocenu Polski [A Catalogue of the Pleistocene Mammals of Poland]. PAN, PWN, pp. 1–267 (in Polish with English and Russian introduction).

Krajcarz, M.T., Bosák, P., Šlechta, S., Pruner, P., Komar, M., Dresler, J., Madeyska, T., 2014. Sediments of Biśnik cave (Poland): lithology and stratigraphy of the Middle Palaeolithic site. Quat. Int. 326, 6–19. https://doi.org/10.1016/j.quaint.2013.10.017.

Kubiak, H., 2001. Remains of fossil elephants in Poland. In: Cavarretta, G., Gioia, P., Mussi, M., Palombo, M.-R. (Eds.), Proceedings of the 1st International Congress "The World of Elephants", pp. 115–118. Rome.

Librado, P., Der Sarkissian, C., Ermini, L., Schubert, M., Jónsson, H., Albrechtsen, A., Fumagalli, M., Yang, M.A., Gamba, C., Seguin-Orlando, A., Mortensen, C.D.,

Petersen, B., Hoover, C.A., Lorente-Galdos, B., Nedoluzhko, A., Boulygina, E., Tsyganova, S., Neuditschko, M., Jagannathan, V., Thèves, C., Alfarhan, A.H., Alquraishi, S.A., Al-Rasheid, K.A.S., Sicheritz-Ponten, T., Popov, R., Grigoriev, S., Alekseev, A.N., Rubin, E.M., McCue, M., Rieder, S., Leeb, T., Tikhonov, A., Crubézy, E., Slatkin, M., Marques-Bonet, T., Nielsen, R., Willerslev, E., Kantanen, J., Prokhortchouk, E., Orlando, L., 2015. Tracking the origins of Yakutian horses and the genetic basis for their fast adaptation to subarctic environments. Proc. Natl. Acad. Sci. Unit. States Am. 112 (50), E6889–E6897. https://doi.org/10.1073/pnas.1513696112.

Lister, A.M., 1994. The evolution of the giant deer, *Megaloceros giganteus* (Blumenbach). Zool. J. Linn. Soc. 112, 65–100.

Lister, A.M., 1996. The morphological distinction between bones and teeth of fallow deer (*Dama dama*) and red deer (*Cervus elaphus*). Int. J. Osteoarchaeol. 6 (2), 119–143. https://doi.org/10.1002/(SICI)1099-1212(199603)6:2<119::AID-OA265>3.0.CO;2-8.

Lister, A.M., Sher, A.V., 2001. The origin and evolution of the woolly mammoth. Sci 294, 1094–1097. https://doi:10.1126/science.1056370.

Lister, A.M., Sher, A.V., van Essen, H., Wei, G., 2005. The pattern and process of mammoth evolution in Eurasia. Quat. Int. 126–128, 49–64. https://doi.org/10.1016/j.quaint.2004.04.014.

Lister, A.M., Stuart, A.J., 2008. The impact of climate change on large mammal distribution and extinction: evidence from the last glacial/interglacial transition. C. R. Geosci. 340 (9–10), 615–620. https://doi.org/10.1016/j.crte.2008.04.001.

Lister, A.M., Stuart, A.J., 2019. The extinction of the giant deer *Megaloceros giganteus* (Blumenbach): new radiocarbon evidence. Quat. Int. 500, 185–203. https://doi.org/10.1016/j.quaint.2019.03.025.

Lorenc, M., Pawłowska, K., 2010. Pierwsze radiowęglowe (14C) datowania kości ssaków ze żwirowni w Krosinku (Wielkopolska) [First radiocarbon dating of mammal bones from the gravel pit at Krosinku (Wielkopolska)]. Przegląd Geol. 58 (11), 1103–1106 (in Polish with English abstract).

Lorenzen, E.D., Nogués-Bravo, D., Orlando, L., Weinstock, J., Binladen, J., Marske, K.A., Ugan, A., Borregaard, M.K., Gilbert, M.T.P., Nielsen, R., Ho, S.Y.W., Goebel, T., Graf, K.E., Byers, D., Stenderup, J.T., Rasmussen, M., Campos, P.F., Leonard, J.A., Koepfli, K.-P., Froese, D., Zazula, G., Stafford, T.W., Aaris-Sørensen, K., Batra, P., Haywood, A.M., Singarayer, J.S., Valdes, P.J., Boeskorov, G., Burns, J.A., Davydov, S.P., Haile, J., Jenkins, D.L., Kosintsev, P., Kuznetsova, T., Lai, X., Martin, L.D., McDonald, H.G., Mol, D., Meldgaard, M., Munch, K., Stephan, E., Sablin, M., Sommer, R.S., Sipko, T., Scott, E., Suchard, M.A., Tikhonov, A., Willerslev, R., Wayne, R.K., Cooper, A., Hofreiter, M., Sher, A., Shapiro, B., Rahbek, C., Willerslev, E., 2011. Species-specific responses of Late Quaternary megafauna to climate and humans. Nature 479 (7373), 359–364. https://doi.org/10.1038/nature10574.

Lubicz-Niezabitowski, E., 1938. O kilku ciekawszych szczątkach kopalnych zwierząt ssących Polski [Ueber einige bemerkenswerte fossile Reste aus gestorbener Saugetiere Polens]. Kosmos 63 (4), 431–438 (191–198) (in Polish with German summary).

Maglio, V.J., 1973. Origin and evolution of the elephantidae. Trans. Am. Phil. Soc. 63 (3), 1–149.

Marciszak, A., Lipecki, G., Pawłowska, K., Jakubowski, G., Ratajczak-Skrzatek, U., Zarzecka-Szubińska, K., Nadachowski, A., 2021. The Pleistocene lion *Panthera spelaea* (Goldfuss, 1810) from Poland – a review. Quat. Int. 605, 213–240. https://doi.org/10.1016/j.quaint.2020.12.018.

Massilani, D., Guimaraes, S., Brugal, J.P., Bennett, E.A., Tokarska, M., Arbogast, R.M., Baryshnikov, G., Boeskorov, G., Castel, J.-C., Davydov, S., Madelaine, S., Putelat, O., Spasskaya, N.N., Uerpmann, H.-P., Grange, T., Geigl, E.M., 2016. Past climate changes, population dynamics and the origin of *Bison* in Europe. BMC Biol. 14 (1), 1–17. https://doi.org/10.1186/s12915-016-0317-7.

Mona, S., Catalano, G., Lari, M., Larson, G., Boscato, P., Casoli, A., Sineo, L., Patti, C.D., Pecchioli, E., Caramelli, D., Bertorelle, G., 2010. Population dynamic of the extinct European aurochs: genetic evidence of a north-south differentiation pattern and no evidence of post-glacial expansion. BMC Evol. Biol. 10 (1), 1–13. https://doi.org/10.1186/1471-2148-10-83.

Nadachowski, A., Żarski, M., Urbanowski, M., Wojtal, P., Miękina, B., Lipecki, G., Ochman, K., Krawczyk, M., Jakubowski, G., Tomek, T., 2009. Late Pleistocene Environment of the Częstochowa Upland (Poland) Reconstructed on the Basis of Faunistic Evidence from Archaeological Cave Sites. Institute of Systematics and Evolution of Animals Polish Academy of Sciences, Kraków.

Nadachowski, A., Lipecki, G., Wojtal, P., Miękina, B., 2011. Radiocarbon chronology of woolly mammoth (*Mammuthus primigenius*) from Poland. Quat. Int. 245 (2), 186–192. https://doi.org/10.1016/j.quaint.2011.03.011.

Olsen, S.J., 1960. Post-cranial Skeletal Characters of *Bison* and *Bos*. Papers of the Peabody Museum of Archaeology and Ethnology. Harvard University, Cambridge.

Palacio, P., Berthonaud, V., Guérin, C., Lambourdière, J., Maksud, F., Philippe, M., Plaire, D., Stafford, T., Marsolier-Kergoat, M.-C., Elalouf, J.M., 2017. Genome data on the extinct *Bison schoetensacki* establish it as a sister species of the extant European bison (*Bison bonasus*). BMC Evol. Biol. 17 (1), 1–11. https://doi.org/10.1186/s12862-017-0894-2.

Pawłowska, K., 2010. The usefulness of a taphonomic approach for studies of Pleistocene mammals. Geologos 16 (3), 183–189. https://doi.org/10.2478/v10118-009-0012-z.

Pawłowska, K., 2014. The smells of Neolithic Çatalhöyük, Turkey: Time and space of human activity. J. Anthropol. Archaeol. 36, 1–11. https://doi.org/10.1016/j.jaa.2014.07.001.

Pawłowska, K., 2015. Elephantids from Pleistocene Poland: State of knowledge. Quat. Int. 379, 89–105. https://doi.org/10.1016/j.quaint.2015.05.014.

Pawłowska, K., 2017. Large mammals affected by hominins: paleogeography of butchering for the European Early and Middle Pleistocene. Quat. Int. 438, 104–115. https://doi.org/10.1016/j.quaint.2017.03.043.

Pawłowska, K., 2020. Time of change: cattle in the social practices of Late Neolithic Çatalhöyük. Archaeol. and Anthropol. Sci. 12 (2), 1–18. https://doi.org/10.1007/s12520-019-00961-x.

Pawłowska, K., Greenfield, H., Czubla, P., 2014a. "Steppe" mammoth (*Mammuthus trogontherii*) remains in their geological and cultural context from Bełchatów (Poland): A consideration of human exploitation in the Middle Pleistocene. Quat. Int. 326–327, 448–468. https://doi.org/10.1016/j.quaint.2013.08.047.

Pawłowska, K., Stefaniak, K., Nowakowski, D., 2014b. Healed antler fracture in a giant deer (*Megaloceros giganteus*) from the Pleistocene of Poland. Palaeontol. Electron. 17 (1), 9. https://doi.org/10.26879/448, 23A.

Pawłowska, K., Zieliński, T., Woronko, B., Sobkowiak-Tabaka, I., Stachowicz-Rybka, R., in press. Integrated environmental records in Late Pleistocene Poland: The paleofluvial regime and paleoclimate inferred from Krosinko site. Quat. Int.

Pei, W.-C., 1957. The zoogeographical divisions of Quaternary mammalian faunas in China. Vertebr. Palasiat. 1, 9–24.

Plasteeva, N.A., Gasilin, V.V., Devjashin, M.M., Kosintsev, P.A., 2020. Holocene distribution and extinction of ungulates in northern Eurasia. Biol. Bull. 47 (8), 981–995. https://doi.org/10.1134/S1062359020080105.

Prummel, W., 1988. Distinguishing Features on Postcranial Skeletal Elements of Cattle, *Bos primigenius f. taurus*, and Red Deer, *Cervus elaphus*. Institut für Haustierkunde Neue Universität, Kiel.

Ramsey, C.B., 2008. Deposition models for chronological records. Quat. Sci. Rev. 27 (1–2), 42–60. https://doi.org/10.1016/j.quascirev.2007.01.019.

Rasmussen, S.O., Bigler, M., Blockley, S.P., Blunier, T., Buchardt, S.L., Clausen, H.B., Cvijanovic, I., Dahl-Jensen, D., Johnsen, S.J., Fischer, H., Gkinis, V., Guillevic, M., Hoek, W.Z., Lowe, J.J., Pedro, J.B., Popp, T., Seierstada, I.K., Steffensena, J.P., Svensson, A.M., Vallelonga, P., Vinther, B.M., Walker, M.J.C., Wheatleyj, J.J., Winstrup, M., 2014. A stratigraphic framework for abrupt climatic changes during the Last Glacial period based on three synchronized Greenland ice-core records: refining and extending the INTIMATE event stratigraphy. Quat. Sci. Rev. 106, 14–28. https://doi.org/10.1016/j.quascirev.2014.09.007.

Reimer, P.J., Austin, W.E.N., Bard, E., Bayliss, A., Blackwell, P.G., Bronk Ramsey, C., Butzin, M., Cheng, H., Edwards, R.L., Friedrich, M., Grootes, P.M., Guilderson, T.P., Hajdas, I., Heaton, T.J., Hogg, A.G., Hughen, K.A., Kromer, B., Manning, S.W., Muscheler, R., Palmer, J.G., Pearson, C., Plicht, J. Van Der, Reimer, R.W., Richards, D.A., Scott, E.M., Southon, J.R., Turney, C.S.M., Wacker, L., Adolphi, F., Büntgen, U., Capano, M., Fahrni, S.M., Fogtmann-Schulz, A., Friedrich, R., Köhler, P., Kudsk, S., Miyake, F., Olsen, J., Reinig, F., Sakamoto, M., Sookdeo, A., Talamo, S., 2020. The IntCal20 Northern Hemisphere radiocarbon age calibration curve (0–55 cal kBP). Radiocarbon 62, 725–757. https://doi.org/10.1017/RDC.2020.41.

Rutkowski, E., 1967. Czwartorzęd wysoczyzny północnokonińskiej. Pr. Inst. Geol. 48, 5–81.

Sala, B., 1987. *Bison schoetensacki* Freud. from Isernia la Pineta (early Mid-Pleistocene, Italy) and revision of the European species of *Bison*. Palaeontogr. Ital. 74, 113–170.

Schwartz-Narbonne, R.E., 2016. Reframing the mammoth steppe: examining mammoth steppe ecology using carbon and nitrogen isotopic compositions of megafauna collagen. Electronic Thesis and Dissertation Repository 3495. https://ir.lib.uwo.ca/etd/3495.

Skog, A., Zachos, F.E., Rueness, E.K., Feulner, P.G.D., Mysterud, A., Langvatn, R., Lorenzini, R., Hmwe, S.S., Lehoczky, I., Hartl, G.B., Stenseth, N.C., Jakobsen, K.S., 2009. Phylogeography of red deer (*Cervus elaphus*) in Europe. J. Biogeogr. 36 (1), 66–77. https://doi.org/10.1111/j.1365-2699.2008.01986.x.

Sommer, R.S., 2020. Late Pleistocene and Holocene history of mammals in Europe. In: Hackländer, K., Zachos, F.E. (Eds.), Mammals of Europe – Past, Present, and Future. Springer, pp. 83–98.

Stampfli, H.R., 1963. Wisent *Bison bonasus* (Linné, 1758), Ur, *Bos primigenius* Bojanus, 1827, und hausrind, *Bos taurus* Linné. In: Boessneck, J., Jequier, I.P., Stampfli, H.R. (Eds.), Seeberg Burgäschisee-Süd. Die Tierreste. Acta Bernensia 2 (3), 117–196.

Stankowski, W., 1988. Pozycja stratygraficzna szkieletu słonia leśnego w świetle analizy geologicznej stanowiska Jóźwin 1984 (doniesienie wstępne)[Stratigraphic position of the forest elephant skeleton in the light of geological analysis of the Jóźwin site 1984 (preliminary report)]. Muzeum Okręgowe w Koninie Zeszyty Muzealne 2, 95–102 (in Polish).

Stankowski, W., Tobolski, K., 1982. Osady torfowe i limniczne wieku eemskiego z odkrywki Kazimierz kopalni węgla brunatnego w Koninie [Peat and limnic sediments of Eemian age from the Kazimierz outcrop of the Konin lignite mine]. Badania Fizjogr. nad Pol. Zachodnią 34, 171–178 (in Polish).

Stefaniak, K., 2015. Neogene and Quaternary Cervidae from Poland. Institute of Systematics and Evolution of Animals Polish Academy of Sciences, Kraków.

Stefaniak, K., Pawłowska, K., Ratajczak, U., Robličková, M., Gumiński, W., Wojtal, P., 2014. Middle and late Pleistocene elks (*Cervalces* Scott, 1855 and *Alces* Gray, 1821) from Poland: palaeoenvironmental and palaeogeographic implications. Ann. Soc. Geol. Pol. 84 (4), 341–362.

Stevens, R.E., Hedges, R.E., 2004. Carbon and nitrogen stable isotope analysis of northwest European horse bone and tooth collagen, 40,000 BP–present: palaeoclimatic interpretations. Quat. Sci. Rev. 23 (7–8), 977–991. https://doi.org/10.1016/j.quascirev.2003.06.024.

Stuart, A.J., 2015. Late Quaternary megafaunal extinctions on the continents: a short review. Geol. J. 50 (3), 338–363. https://doi.org/10.1002/gj.2633.

Stuart, A.J., Kosintsev, P.A., Higham, T.F., Lister, A.M., 2004. Pleistocene to Holocene extinction dynamics in giant deer and woolly mammoth. Nature 431, 684–689. https://doi.org/10.1038/nature02890, 7009.

Stuart, A.J., Lister, A.M., 2011. Extinction chronology of the cave lion *Panthera spelaea*. Quat. Sci. Rev. 30 (17–18), 2329–2340. https://doi.org/10.1016/j.quascirev.2010.04.023.

Stuart, A.J., Lister, A.M., 2012. Extinction chronology of the woolly rhinoceros *Coelodonta antiquitatis* in the context of late Quaternary megafaunal extinctions in northern Eurasia. Quat. Sci. Rev. 51, 1–17. https://doi.org/10.1016/j.quascirev.2012.06.007.

Uerpmann, H.-P., 1990. Die Domestikation des Pferdes im Chalkolithikum West-und Mitteleuropas. Madrider Mitteilungen 31, 109–153.

Ukkonen, P., Aaris-Sørensen, K., Arppe, L., Clark, P.U., Daugnora, L., Lister, A.M., Lõugas, l., Seppä, H., Sommer, R.S., Stuart, A.J., Zupiņš, I., 2011. Woolly mammoth (*Mammuthus primigenius* Blum.) and its environment in northern Europe during the last glaciation. Quat. Sci. Rev. 30 (5), 693–712. https://doi.org/10.1016/j.quascirev.2010.12.017.

Van Vuure, C., 2005. Retracing the Aurochs: History Morphology and Ecology of an Extinct Wild Ox. Pensoft, Sofia.

Woodward, S.L., 1991. Late Pleistocene North American equids: why a widespread large mammal may be sparsely represented in early archaeological sites. In: Purdue, J.R., Klippel, W.E., Styles, B.W. (Eds.), Beamers, Bobwhites, and Blue-Points: Tributes to the Career of Paul W. Parmalee. Illinois State Museum Scientific Papers, 23, pp. 261–272.

Woroncowa-Marcinowska, T., Pawłowska, K., Żarski, M., Urban, J., 2017. Zespoły plejstoceńskiej fauny (zbiory Muzeum Geologicznego PIG-PIB) w ujęciu stratygraficznym, geologicznym i tafonomicznym. [The Pleistocene mammal assemblages from the Geological Museum of PGI-NRI; a stratigraphical, geological and taphonomic approach]. Przeglad Geol. 65 (1), 53–62 (in Polish with English abstract).

Wright, E., 2013. The History of the European Aurochs (*Bos primigenius*) from the Middle Pleistocene to its Extinction: an Archaeological Investigation of its Evolution, Morphological Variability and Response to Human Exploitation. Doctoral dissertation. University of Sheffield.

Zazula, G.D., Hall, E., Hare, P.G., Thomas, C., Mathewes, R., La Farge, C., Martel, A.L., Heintzman, P.D., Shapiro, B., 2017. A middle Holocene steppe bison and paleoenvironments from the versleuce meadows, whitehorse, Yukon, Canada. Can. J. Earth Sci. 54 (11), 1138–1152. https://doi.org/10.1139/cjes-2017-0100.

Zimov, S.A., Zimov, N.S., Tikhonov, A.N., Chapin III, F.S., 2012. Mammoth steppe: a high-productivity phenomenon. Quat. Sci. Rev. 57, 26–45. https://doi.org/10.1016/j.quascirev.2012.10.005.