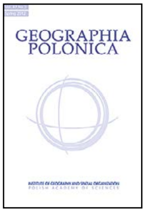

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FOSSIL LARGE MAMMALS FROM WIELKOPOLSKA: A STATE OF KNOWLEDGE

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Abstract

A number of 125 open-air localities from Wielkopolska documented presence of 18 species (3 carnivores, 4 proboscideans, 3 perissodactyls and 8 artiodactyls). Most of species are cold-adapted members of mammoth fauna from the Late Pleistocene, such as *Ursus arctos priscus*, *Mammuthus primigenius*, *Coelodonta antiquitatis*, *Equus ferus*, *Rangifer tarandus*, and *Bison priscus*. The few species like *Ursus arctos taubachensis*, *Palaeoloxodon antiquus* and *Stephanorhinus kirchbergensis* represent an older, thermophilic fauna dated to MIS 5e. The vast majority of bones are accidental finds, without a stratigraphic context. Most artiodactyls were found in alluvial sediments, in bogs or swamps, while carnivores are represented only by isolated remains.

Key words

open-air • biostratigraphy • taxonomy • Late Pleistocene • Eemian • proboscideans

Introduction

The remains of large animals, often found occasionally during earthworks or simply by accident, have aroused public interest since the dawn of time. Especially if they were bones of animals such as the woolly mammoth *Mammuthus primigenius* Blumenbach, 1799 or the woolly rhinoceros *Coelodonta antiquitatis* Blumenbach, 1799, which were remarkable for their size and massiveness. The oldest such information from Wielkopolska comes from the mid-19th century and were published individual finds as well as lists of remains of (Szafarkiewicz, 1863ab; Wahnschaffe, 1897, 1900ab, 1909; Beuschausen & Kühn, 1898; Maas, 1899, 1900; Chłapowski, 1904, 1905; Menzel, 1911; Hermann, 1911, 1913; Kiernik, 1911, 1912, 1913, 1914; Wolff, 1914; Sonntag, 1919). No monographs were published at the time.

These spectacular discoveries caused understandable surprise and curiosity, which was reflected in collecting and exhibiting such fossils in castle and church cabinets of curiosities. Years 1850-1939 were a period of intense industrialisation of Wielkopolska and thus significant intensification of earthworks related to the railway and road infrastructure, development of towns and villages, as well as a broad-based action of drainage and regulation of watercourses. Many of them were incomplete: fragments of skulls, mandibles, long bones, pelvis or ribs were further damaged during the extraction. Numerous remains, mainly of large cold-adapted proboscideans and ungulates like *M. primigenius* and *C. antiquitatis*, members of mammoth steppe fauna, were found in the course of these works. Relatively abundant were represented also wild horse *Equus ferus* Boddaert, 1785, moose *Alces alces* Linnaeus, 1758, giant deer *Megaloceros giganteus* Blumenbach, 1799, red deer *Cervus elaphus* Linnaeus, 1758, reindeer *Rangifer tarandus* Linnaeus, 1758, steppe wisent *Bison priscus* Bojanus, 1827 and aurochs *Bos primigenius* Bojanus, 1827. Because the vast majority of these finds are accidental, out of context, we are uncertain about their age for species such as *E. ferus*, *A. alces*, *C. elaphus*, and *B. primigenius* whether they are still Pleistocene or rather Holocene (Kowalski, 1959; Pawłowska, 2015ab).

The attached references are not a complete regional palaeontological bibliography at all, but include only the works cited in the article. Since this is the first broader study of this type for the region since the times of Lubicz-Niezabitowski (1926, 1929ab, 1938ab) and Kowalski (1959), all available materials were used from around the middle of the 19th century. Only recently some findings were summarised by Pawłowska (2015ab), mostly in broader, Polish context. Additionally, the material from one of the richest palaeontological sites in Wielkopolska, Krosinko, has been described in detail (Pawłowska, 2022).

This article is a palaeontological catalogue on the mammals of Wielkopolska. Despite the historical importance of Wielkopolska open sites there was no modern compilation of the mammalian remains from these sites, although there were revisions of individual groups and species. Because of the past disagreements between the original discoverers and the subsequent rivalry between private collectors. Additionally, the list of species allegedly found has greatly increased since the time of Lubicz-Niezabitowski (1926) or Kowalski (1959) (Pawłowska, 2015ab).

Material and methods

The paper presents current state of knowledge of large mammals (carnivores, proboscideans and ungulates) from Wielkopolska region (western Poland). This article is supplemented with database for a clearer overview of the present situation (Appendix available at https://rcin.org.pl/igipz/dlibra/publication/278543). It contains a full list of specific species and taxa, with the name of each discovery site, geographic coordinates, stratigraphic position of the specimens, species of accompanying fauna, and references. Possible information about the remains that were found in each site is also provided. Detailed descriptions are often missing, sometimes only quantitative data, e.g. NISP (Number of Identified Specimens) and MNI (Minimum Number of Individuals), are available. Unfortunately, some finds, especially from historical sites, have been subsequently destroyed or lost. Stratigraphic ages and radiocarbon dates, with indication of the laboratory number of the analysed sample, are also given when available.

The terminology for Quaternary glaciations and interglacials was that adopted by Marks et al. (2016). The geologic timescale and subdivisions were based on the Global chronostratigraphical correlation table for the last 2.7 million years v. 2022a released by the International Commission on Stratigraphy (https://stratigraphy.org/chart). For the MIS ages the benthic curve proposed by Lisiecki & Raymo (2005).

This paper does not attempt to verify the descriptions of the specimens, but instead provides a summary based on the sources available in the bibliography. Only part of the specimens was revisited so far and turned up certain of the specimens. Published sources were used to prepare a faunal list specified for each taxon, reconsidering the names of sites, which have in some cases been renamed, due to geographical updates. The current storage locations of the specimens have not been checked, but when available, was given. The year of discovery of each specimen is not known in all cases.

Wielkopolska is a historical region of Poland and the cradle of its statehood. The territorial scope of the region is difficult to define precisely because its borders are not based on any boundaries of geographical divisions. The borders of the region have changed over the centuries, therefore the current understanding of the territorial extent of Wielkopolska is not unambiguous. The swampy proglacial valley of the Barycz River was originally the border between Silesia and Wielkopolska. The western border is the lower Obra and the eastern border is the upper Warta and Noteć rivers. As a historical region, it covers an area of ca. 39,300 km^2, which is 12.6% of Poland's area (Fig. 1). In terms of physiography, the region belongs to two large spatial units separated by a line running through Leszno-Dolsk-Żerków-Konin. It marks the furthest extent of the last Baltic glaciation. To the north of this line there is the sub-province of the South Baltic Lake District, and to the south of the Central Polish Lowlands (Kondracki, 1998). The areas to the north are characterised by a very diverse early glacial relief, which was formed during the last Baltic glaciation. These are hilly and plain-moraine areas with a varied relief. Wide proglacial valleys and narrow gorge river valleys, numerous glacial troughs filled with lakes and sequences of hills and moraine hillocks often exceeding 100 m a.s.l. are characteristic elements of the landscape. The southern part of Wielkopolska is characterised by almost complete lack of lakes and less developed post-glacial forms. Here we have flat or

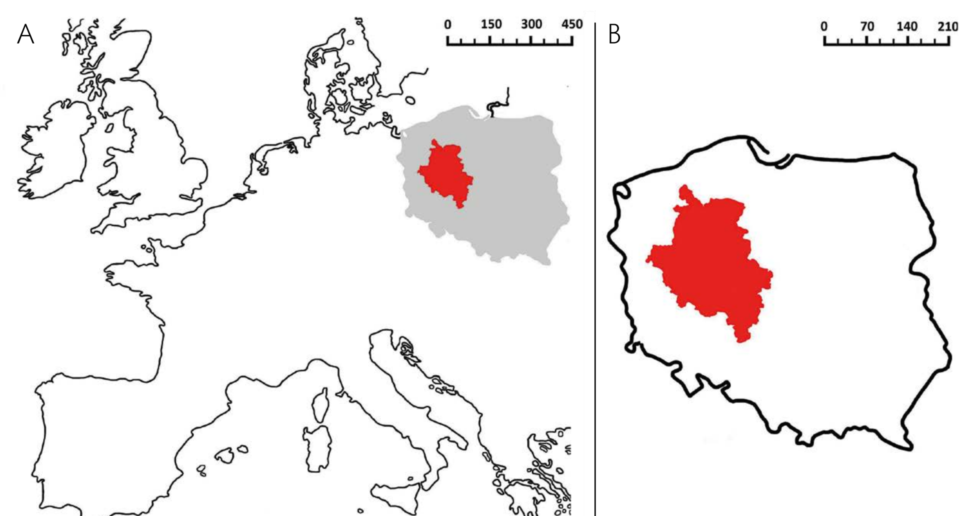

Figure 1. Location of Wielkopolska (Poland shaded gray, Wielkopolska shaded red) in Europe (A) and Wielkopolska (shaded red) in Poland (B)

slightly undulating moraine plains with small river valleys.

Several major rivers flow through the region: Warta, Prosna, Obra, Widawka, Ner, Wełna and Noteć. These rivers are regulated in large sections and a significant number of palaeontological finds were made during works related to regulating, deepening, or cleaning these rivers. Throughout Wielkopolska, soils developed on post-glacial formations prevail, i.e. on clays of the youngest river sediments. moraines and clays of glacier melt water and glacial soils. Typical soil types in the region are loamy sands and sandy soils. Low accumulation terraces of proglacial valleys and river valleys are lined with river sands, peats or alluvial soils.

Results

General remarks

The fossil material from the vast majority of 125 open-air sites from Wielkopolska was probable accumulated through natural processes and there is no evidence of human activity (Fig. 2). It applies even to the recognised archaeological sites, where the accumulation of remains may be an outcome of natural or catastrophic death, slope or fluvial processes, activity of carnivores and some additional factors (Kaczmarek, 2004; Pawłowska, 2015ab, 2022). The detailed review of 125 open-air sites of Wielkopolska shows that the fossil theriofauna was dominated by large herbivores, members of the mammoth steppe fauna, dated at the Late Pleistocene. Among them, *M. primigenius* and *C. antiquitatis* greatly outnumbered the other forms, followed by *E. ferus*. Other ungulates, such as *R. tarandus*, *M. giganteus*, and *B. priscus*, co-occurred with them. Overall, proboscideans, perissodactyls and artiodactyls form the vast majority in the founded material, while single carnivores accompany them in some sites or are represented by isolated finds (Fig. 2).

However, the value of these materials varies greatly. This is especially true of those older, more or less until the 1950s. The only notable exception are the works of Lubicz-Niezabitowski (1912, 1926, 1929ab, 1932, 1934, 1935, 1938ab, 1948ab), who meticulously and successively described individual finds and catalogued finds from Wielkopolska. At that time, no regular excavations were carried out in the region, and descriptions of individual finds were usually brief and vague, based on data collected during the discoveries. Such treatment of finds, usually provided with a 1-2 sentence description, location, possibly date and finder's data, were then deposited in the museum. This method of dealing with found materials was used both during the Prussian partition and later, almost until the 1990s. A more numerous accumulation, a relatively good state of preservation and, above all, the ease of identification made them subject to a more detailed study. Such a situation makes it difficult, and most often even impossible, to draw conclusions about the occurrence, variability, palaeoecology or other aspects of the life of these extinct species. We can partially supplement this knowledge by using data from other, neighbouring regions, e.g. Silesia, where such finds are much more numerous and better studied (Marciszak et al., 2019b; Kropczyk & Marciszak, 2023). In such cases, data from other surrounding regions (Brandenburgia, Pomorze, Śląsk) can only be extrapolated. The lack of records of a number of species in older literature or, in general, their absence from the fossil record in Wielkopolska should be approached with some caution. Their absence does not necessarily mean a real lack of the species in the region. It is only the finds of the last dozen or so years that he tries to place in a geological context, although such activities usually come too late. Wielkopolska as a region has the fact that there are no caves in it, and almost all finds from open-air sites are accidental.

Some of the early papers contain puzzling discrepancies when compared with the faunas of other cave or open sites. In particular, two faunal assemblages appear to be represented: a warm interglacial fauna, and a cold-adapted glacial fauna, although deposits in particular sites are described as

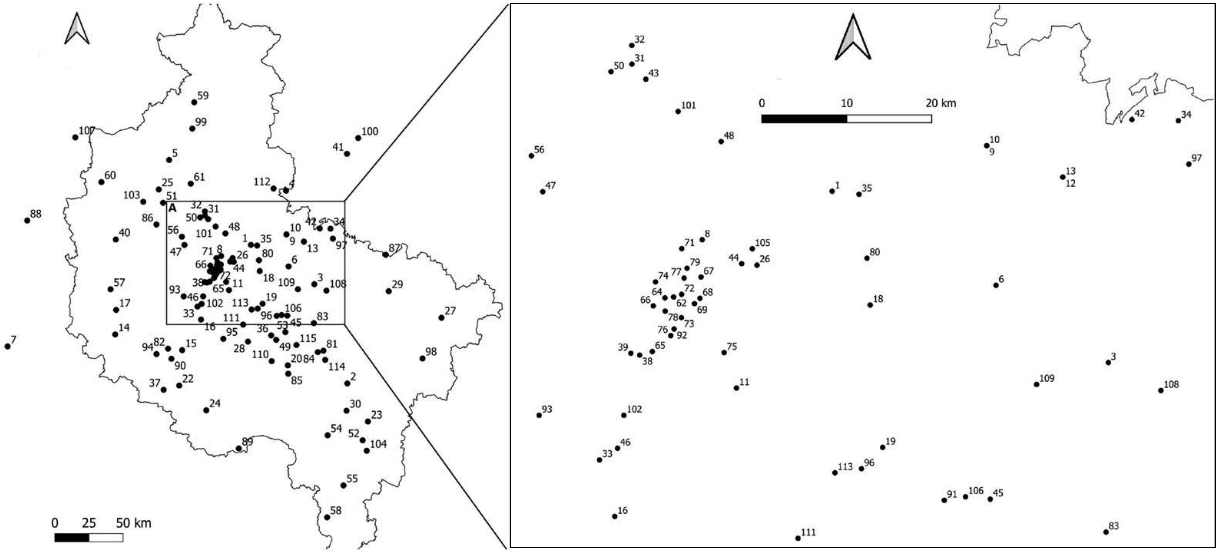

Figure 2. Location of open–air sites with mammal remains in Wielkopolska: 1 – Bednary, 2 – Bogusław, 3 – Broniszewo, 4 – Brudzyń, 5 – Czarnków, 6 – Czerniejewo, 7 – Czerwieńsk, 8 – Czerwonak, 9 – Dębnica, 10 – Dobromierz, 11 – Gądki, 12 – Gniezno, 13 – Gołaszyn, 14 – Gościeszyn, Obra river, 15 – Gryżyna, 16 – Grzybno, 17 – Jabłonna, 18 – Iwno, 19 – Jankowo, 20 – Jarocin, 21 – Jarocin vicinity, 22 – Kąkolewo, 23 – Kalisz-Piwonice, 24 – Karzec, 25 – Klempicz, 26 – Kobylnica, 27 – Koło, 28 – Konarzyce, 29 – Konin, Brown Coal Mine, 30 – Kotowiecko, 31 – Kowanowo, 32 – Kowanówko, 33 – Krosinko, 34 – Kruchowo, 35 – Krześlice, 36 – Krzykosy, 37 – Leszno, 38 – Luboń, 39 – Luboń–Żabikowo, 40 – Lubosz, 41 – Łabiszyn, Noteć river, 42 – Łukaszewko, 43 – Łukowo, 44 – Mechowo (Wierzenica-Mechowo), 45 – Miłoław, 46 – Mosina, 47 – Mrowino, 48 – Murowana Goślina, 49 – Nowe Miasto nad Wartą, 50 – Oborniki, 51 – Obrzycko, 52 – Ołobok, Prosna river, 53 – Orzechowo, Warta river, 54 – Ostrów Wielkopolski, 55 – Ostrzeszów, 56 – Pamiątkowo, 57 – Paproć, 58 – Perzów, 59 – Piła-Koszyce (Kuźnica Pilska), 60 – Piłka, 61 – Połajewo, 62 – Poznań, 63 – Poznań vicinity, 64 – Poznań-Brama Bydgoska, 65 – Poznań-Dębiec, 66 – Poznań-Dębiec/Górczyn, 67 – Poznań-Główna, 68 – Poznań-Malta, 69 – Poznań-Malta (Dolina Świętojańska), 70 – Poznań-Malta (Młyn Świętojański), 71 – Poznań-Naramowice, 72 – Poznań-Ostrów Tumski, 73 – Poznań-Rataje, 74 – Poznań-Sołacz, 75 – Poznań-Spławie, 76 – Poznań-Starołęka, 77 – Poznań-Szelągowska (Poznań-Szeląg), 78 – Poznań-Wilda, 79 – Poznań-Wilczy Młyn, 80 – Poznań-Żegrze Promno, 81 – Prosna river near Gizałki, 82 – Przysieka Stara, 83 – Pyzdry, 84 – Robaków, Prosna river, 85 – Rogówek, 86 – Rudki, 87 – Siedlimowo, 88 – Skwierzyna-Oberski Młyn, 89 – Szkaradowo, 90 – Spławie, 91 – Starkówiec Piątkowski, 92 – Starołęka, 93 – Stęszew, 94 – Śmigiel, 95 – Śrem, 96 – Środa Wielkopolska, 97 – Trzemeszno, 98 – Turek vicinity, 99 – Ujście, 100 – Wałownica, 111– Warta River near Oborniki, 112 – Warta River near Puszczykowo, 113 – Warta River near Wronki, 114 – Wielowieś, 115 – Wierzenica, 116 – Winnagóra, 117 – Wołogoszcz, 118 – Wólka, 119 – Września, 120 – Zalesie, 121 – Zaniemyśl, 122 – Żabiczyn, 123 – Żabikowo, 124 – Żegocin, 125 – Żerków

homogenous. It was clear that further minor revisions, without a complete and broad survey of the material, could add little to our knowledge, therefore every collection that could be traced so far was examined, as was the whole of pertinent literature.

Radiocarbon dating

Among 28 radiocarbon dates, 26 documented presence of Late Pleistocene species during MIS 3, and they mostly concentrated between +50-35 kya BP (Tab. 1). Some dates are open and their values exceed the method range, which may suggest that some specimens are older than MIS 3. Most dates from MIS 3 correspond to the Grudziądz Interglacial in the Polish chronostratigraphy, and they are dated before the Last Glacial Maximum (LGM). So far those dates indicated also, that most large mammals like *P. spelaea*, *M. primigenius*, *C. antiquitatis*, robust form of *E. ferus*, *M. giganteus*, *R. tarandus*, and *B. priscus*, mostly forms lived on the open grasslands, disappeared in Wielkopolska before the LGM. The noteworthy is the late occurrence of *M. primigenius* from Kawęczyn (ca. 210.2-19.5 kya BP) (Tab. 1; Nadachowski et al., 2011, 2018). More thermophilus faunal elements like *A. alces* or *B. primigenius* were probably not present during the coolest phases of the Late Pleistocene, and they entered Wielkopolska after LGM. What more, in most records subfossil nature of their state of preservation indicates a younger, Holocene age. Additionally, two dates indicate presence of *A. alces* during the early Holocene (Pawłowska, 2015b, 2022).

Two main hypotheses try to explain decreasing of large herbivores, and as affect, also carnivores, in Wielkopolska. In first, population fluctuations resulted from human exploitation, while in the other, those species were not significantly affected by human activity, and fluctuations in their populations were caused by environmental changes. It can be propose that like in the case of *M. primigenius*, Late Palaeolithic societies exploited large herbivores more intensively when the species were abundant. During other periods of scarcity or disappearance of particular species under the climatic circumferences, hunter-gatherers turned to other species (Nadachowski et al., 2011, 2018).

Palaeobiological and palaeoenvironmental context of finds

Based on palaeontological data, it is possible to assume that Wielkopolska played an important role as a corridor for migrating animals which moved from east to west and in the opposite direction. The flat, vast area without any major natural barriers was perfect for the migration of large herbivore herds and the carnivores that followed them. The fossil mammal fauna was dominated by large herbivores, members of the mammoth steppe fauna. The mammoth steppe is regarded as one of the most extensive biomes, with cold, dry climate and plant biomass dominated by palatable high-productivity grasses, herbs and willow shrubs (Zimov et al., 2012). The animals were adapted to surviving in low temperatures, but not to moving in deep, loose snow. The large, massive and short-legged *C. antiquitatis* or *O. moschatus*, not being adapted to deep snow, avoided areas with permanent, thick snow cover.

In postglacial times the cold, dry climate changed to a warmer and wetter one which, among other things, resulted in a much greater snowfall which hindered movement and reduced food supply. As a result, the main members of the mammoth steppe fauna: *M. primigenius*, *C. antiquitatis*, *B. priscus* and *M. giganteus*, disappeared. Other species, like *R. tarandus* or *O. moschatus*, retreated to the north and east, while still other, most flexible forms like *E. ferus* or *U. arctos* significantly changed their morphology. Both species evolved into more generalised, smaller forms of slighter build which needed smaller food resources than their Late Pleistocene relatives (Marciszak et al., 2019b).

In respect to the depositional environment two types of localities prevailed: those in which the bones were buried under or within

Table 1. The list of radiocarbon dates obtained for remains of large mammals from Wielkopolska open-air sites. The calibration for dates was made with the OxCal software (version OxCal 4.3). Presented calibrated date with 95.4% probability

Species	Site	Bone	Lab. no.	Uncal. kya BP	Cal. kya BP	Source
Ursus cf. *arctos*	Krosinko	humerus	OxA-26803	32.000 ± 450	38.537-38.044	Pawłowska, 2022
Panthera spelaea spelaea	Oborniki	mc 5	Poz-96211	40.000 ± 1000	45.276-44.803	Marciszak et al., 2021
	Krosinko	mandible	OxA-26790	>48.300		Marciszak et al., 2021
Mamuthus primigenius	Kawęczyn	molar	Poz-28221	14.620 ± 80	20.138-19.452	Nadachowski et al., 2011
	Krosinko	pelvis	OxA-26801	31.160 ± 390	37.867-37.211	Pawłowska, 2015a
	Krosinko	tooth	Poz-23424	32.500 ± 400	39.035-38.400	Lorenc & Pawłowska, 2010
	Pyzdry	radius	OxA-26709	40.000 ± 1200	45.276-44.803	Pawłowska, 2015a
	Krosinko	m3	OxA-26788	43.800 ± 1900	48.579-47.610	Pawłowska, 2015a
Coleodonta antiquitatis	Krosinko	humerus	Poz-53988	38.500 ± 900	44.516-44.252	Pawłowska, 2022
	Spławie	skull	Poz-31458	39.000 ± 1000	44.733-44.421	Stefaniak et al., 2023
	Krosinko	tooth	OxA-26788	43.800 ± 1900	48.579-47.610	Pawłowska, 2015b
	Jóźwin	skull	Poz-34505	44.000 ± 1400	48.739-47.822	Stefaniak et al., 2023
	Krosinko	radius	OxA-26802	46.500 ± 2600	51.666-50.026	Pawłowska, 2022
	Września	skull	Poz-38122	47.000 ± 4000	52.104-50.487	Stefaniak et al., 2023
	Krosinko	femur	OxA-26804	48.400 ± 3200	54.324-51.995	Pawłowska, 2022
Equus ferus	Krosinko	thoracic	OxA-26785	47.000 ± 2800	52.404-50.847	Pawłowska, 2022
	Krosinko	metatarsal 2/4	Poz-22678	47.000 ± 3000	52.104-50.487	Lorenc & Pawłowska, 2010
	Krosinko	tooth	OxA-26789	48.200 ± 3200	54.257-51.823	Pawłowska, 2022
Bos primigenius	Krosinko	mandible	OxA-26794	34.300 ± 600	41.665-41.175	Pawłowska, 2022
	Krosinko	skull	Poz-22688	38.000 ± 900	44.345-44.085	Lorenc & Pawłowska, 2010
Bison priscus	Krosinko	skull	OxA-26795	35.150 ± 700	42.590-41.884	Pawłowska, 2022
Megaloceros giganteus	Krosinko	skull	OxA-26793	>45.400		Croitor et al., 2014
Alces alces	Krosinko	skull	OxA-26791	9185 ± 40	12.531-12.143	Pawłowska, 2022
	Żabikowo	skull	Poz-53724	9450 ± 50	13.060-12.438	Pawłowska, 2015b
Cervus elaphus	Krosinko	skull	OxA-26792	38.300 ± 1000	44.440-44.188	Pawłowska, 2022
Rangifer tarandus	Krosinko	antler	OxA-26786	26.460 ± 240	32.960-32.341	Pawłowska, 2022
	Krosinko	antler	Poz-23774	28.500 ± 300	35.090-34.095	Lorenc & Pawłowska, 2010
	Krosinko	antler	OxA-26787	36.550 ± 750	43.760-43.210	Pawłowska, 2022

alluvial deposits associated mainly with the last glaciation and those in which the remains were found near or in the lower layers of loess cover. Both site types are correlated with the period of MIS 3.

Taxonomic overview of findings

Carnivores

Remains of only three carnivores (*Canis lupus*, *Ursus arctos* and *Panthera spelaea*) are mentioned from Wielkopolska. The carnivores are represented by isolated remains, with an overwhelming majority constituted by herbivores, and apart *P. spelaea*, have never been the subject of more detailed studies. Among them fossil material of *P. spelaea*, after detail morphometrical studies (Lubicz-Niezabitowski, 1938ab; Kowalski, 1959; Barycka, 2008; Pawłowska, 2015b, 2022; Marciszak et al., 2021) showed to represent a nominative chronosubspecies *Panthera spelaea spelaea* Goldfuss, 1810. Occurrence of this advanced form is characterised for the Late Pleistocene (MIS 6/5-2) (Marciszak et al., 2021). Partially preserved mandibles from Kowanówko (large male) and Krosinko belonged to morphologically advanced individuals, with narrow p4 shorter than m1, and narrow m1 without zigzag enamel and lingual bulge and with considerably reduced talonid.

In cave lion biochronology especially noteworthy are dwarf specimens from Krosinko and Oborniki (Pawłowska, 2015b, 2022; Marciszak et al., 2021). Even as for lionesses, there are really small (Fig. 3; Marciszak et al.,

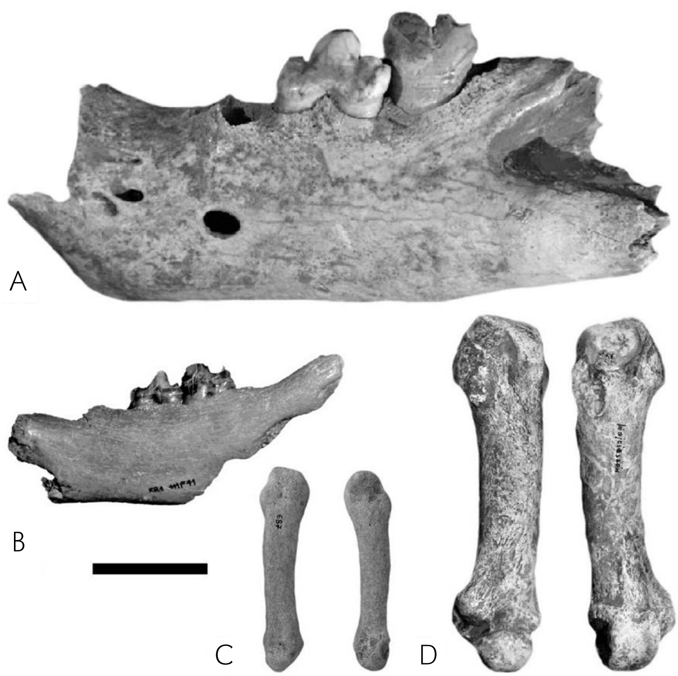

Figure 3. Example of great sexual and temporal variability of the Pleistocene lion *Panthera spelaea* from Poland

Males of a steppe lion *Panthera spelaea fossilis* von Reichenau, 1906: A – left mandible from Wschodnia Cave (MIS 9), D – right metacarpal 5 from Południowa Cave (MIS 19-17). Both specimens are from Sudety Mts (Silesia, SW Poland)
Females (lionesses) of a cave lion *Panthera spelaea spelaea* from Wielkopolska (example of dwarf individuals): B – left mandible from Krosinko (MIS 3), C – left metacarpal 5 from Oborniki (MIS 3). All individuals show to the same scale, scale bar 50 mm. Photo A. Marciszak (A, B, D) and K. Pawłowska (C)

2023a). A general decrease in size in the cave lion evolution was found. During the period 48-45 kya BP, much smaller individuals appeared, comparable with medium-sized extant lions, as was noted for lionesses from Krosinko and Oborniki (Marciszak et al., 2021, 2023a). Populations of *P. spelaea* rapidly declined, and their genetic variability was dramatically reduced, which caused a genetic bottleneck (Barnett et al., 2009, 2016). It is the ecological response of the local, surviving populations to harsh environmental conditions and declination in prey abundance (Marciszak et al., 2014, 2019bc, 2021).

The carnivoran body size is a great advantage in conflicts between carnivorans, and large adult males almost always dominate their competitors (Eaton, 1979; Diedrich, 2021). In this respect, the smaller body size of the last lions might result in their being more vulnerable to attacks by other carnivores and less effective in conflicts with them. It is especially important in case of flat and extensive areas as Wielkopolska, where there are no caves or other shelters, where the lion could hide from a possible attack. Such small stature lioness Krosinko and Oborniki would have rather little chance of defending its prey against its two main competitors, whose remains also have been found in small numbers in Wielkopolska. A partially preserved, massive m1 and great metatarsal 5 from Mechowo testify possible presence of robust steppe (cave) wolf *Canis lupus spelaeus* Goldfuss, 1823, a specific wolf ectomorph, characteristic for the open grasslands (Marciszak et al., 2021, 2023b). From Mechowo, Oborniki, Rososzyca or Żerków came few bones of immense steppe brown bear *Ursus arctos priscus* sensu lato, the largest carnivore of Middle-Late Pleistocene palaeocommunities (Marciszak et al., 2019a). Among finds of this form the noteworthy are maxilla fragment and distal epiphysis of a left humerus from one of the numerous gravel pits near Żerków and a partially preserved right mandible near Rososzyca of a huge bear. After examination it turned out to be a steppe brown bear, a rare but characteristic element of the Late Pleistocene faunas of Eurasia. The width of the distal base is 145 mm and is almost half the width of the large male brown bear *Ursus arctos arctos* Linnaeus, 1758, living recently in Poland (Fig. 4). The specimen is currently deposited in one of the private collections. The remains of this form are known from several finds in Wielkopolska (Maas, 1899;

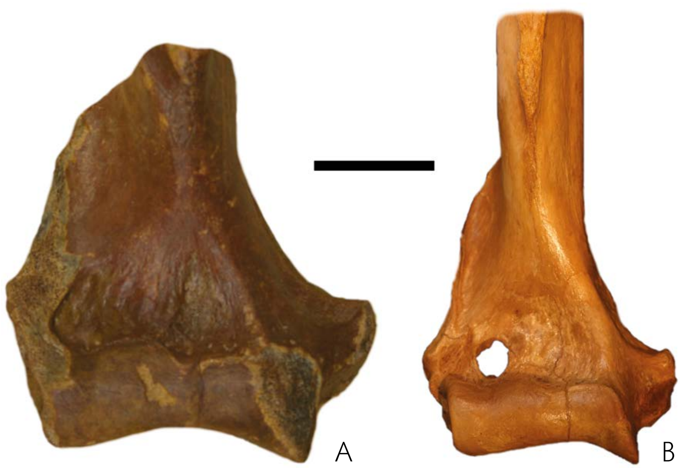

Figure 4. Comparison of the left humerus of a Late Pleistocene steppe brown bear *Ursus arctos priscus* (A) and a Holocene brown bear *Ursus arctos arctos* (B) from Wschodnia Cave. Both individuals are adult males, the width of the distal base is 145 mm (A) and 100 mm (B), respectively. Scale 50 mm

Wahnschaffe, 1909; Hermann, 1913; Sonntag, 1919; Marciszak et al., 2019a). Unfortunately, the attempts to dating those relics so far failed.

Steppe brown bear is not a separate species or even a subspecies, but a specific ecomorph adapted to living in specific environmental conditions. The brown bear is one of the most adaptable large mammals and the range of its steppe form is a good example of this. It was similar to today's Kodiak bear *Ursus arctos middendorffi* Merriam, 1896, but it was even larger. Adult males reached a length of 2.5-3 m, 1.5-1.6 m in shoulder height and a weight of 800-1000 kg. When standing upright, it could measure more than 3.5 m, which made it the largest carnivore of the Late Pleistocene of Eurasia. Apart from its much larger size, it differed from the extant brown bear in having a more massive build, wider teeth and a different diet composition (Marciszak et al., 2019a).

Its large size played an important role in obtaining food. They were partly related to the influence of temperature and climate, where, according to Bergman's rule, larger individuals live in climates with a more severe climate regime. However in the case of this bear large individuals are also known from interglacial and interstadial periods. It seems that their large size was also related to a high-protein diet, obtained by these large bears in two ways: by hunting and by taking prey from other carnivores. They wandered across vast open areas in search of prey and food, also taking advantage of seasonal abundance (fish, berries). Their size was a significant advantage when confronted with other carnivores. After smelling the carcass of an animal killed by another carnivore (lion, hyena, wolf, human), the bear moved towards the source of the smell and then took over the prey. Its stature and size alone caused virtually every Late Pleistocene carnivore, even the most hungry or desperate one, to give way. However, in case of any resistance, the strongly muscled front limbs, armed with 15 cm claws, were the final argument. Additionally, the abundance of large herds of herbivores provided the necessary amount of food for such a large carnivore to survive. After the retreat of the ice sheet, the fauna was rebuilt, and instead of open grassy areas, dense forests appeared, inhabited by numerous small and medium-sized species living in scattering. The world around large, carnivore steppe brown bears has changed and it turned out that the environment offers much more favourable conditions for smaller, more versatile and ecologically plastic forms. This was also true of the brown bear, where the large, carnivorous steppe brown bear, requiring large amounts of food, was replaced by the smaller, more omnivorous brown bear, which survives to this day (Marciszak et al., 2019a). Few isolated relics like those from brown coal mine near Konin documented presence of older, more thermophilic form *Ursus arctos taubachensis* Rode, 1935, dated to MIS 5e.

Proboscideans

Proboscidean remains have been found in Wielkopolska from 1874 onwards (Kowalski, 1959; Kaczmarek, 2004). Among them locations such as Poznań-Szelągowska, Poznań-Wilda and Turek have provided bones and teeth over a number of years (Pawłowska, 2015ab). At least 49 localities documented occurrence of four species in Wielkopolska (Tab. 2). However, it should be noted here that from this number, straight-tusked elephant *Palaeoloxodon antiquus* Falconer & Cautley, 1847 is represented by three sites, while the occurrence of tetralophodont gomphothere *Tetralophodon longirostris* Kaup, 1832, the steppe mammoth *Mammuthus trogontherii* Pohlig, 1885 was recorded only from a single find. All the others represent *M. primigenius* the most common and best-known proboscidean species in overall. There are, however, still many isolated teeth and bones from sites that are not precisely known. In such cases the location given is just Wielkopolska, with no exact data. It is also likely that there are unstudied materials in many private or small local (church, school) museums and collections

Table 2. Occurrence of large mammals in Wielkopolska open-air sites

Species	Sites
Canis lupus cf. *spelaeus*	Mechowo
Ursus arctos priscus/taubachensis	Konin, Krosinko (cf.), Mechowo, Rososzyca, Żerków
Panthera spelaea spelaea	Kowanówko, Krosinko, Mechowo, Szkaradowo
Tetralophodon longirostris	Oborniki
Palaeoloxodon antiquus	Konin, Oborniki
Mammuthus trogontherii	Oborniki
Mammuthus primigenius	Bogusław, Kąkolewo, Kalisz-Piwonice, Klempicz, Konarzyce, Konin, Kowanowo, Krosinko, Krzykosy, Leszno, Luboń, Luboń-Żabikowo, Łukowo, Mechowo, Nowe Miasto nad Wartą, Oborniki, Obrzycko, Piła-Koszyce, Poznań-Brama Bydgoska, Poznań-Dębiec, Poznań-Dębiec/Górczyn, Poznań-Główna, Poznań-Malta, Poznań-Malta (Dolina Świętojańska, Młyn Świętojański), Poznań-Ostrów Tumski, Poznań-Rataje, Poznań-Sołacz, Poznań-Spławie, Poznań-Starołęka, Poznań-Szelągowska, Poznań-Wilda, Promno, Pyzdry, Skwierzyna-Oberski Młyn, Spławie, Stęszew, Śmigiel, Środa Wielkopolska, Trzemeszno, Turek, Wałownica, Warta River, Wołogoszcz, Wólka, Zalesie, Zaniemyśl, Żabikowo, Żerków
Stephanorhinus kirchbergensis	Konin, Oborniki
Coelodonta antiquitatis	Bogusław, Czarnków, Dobromierz, Gołaszyn, Jankowo, Jarocin, Karzec, Kobylnica, Konin, Kowanowo, Kowanówko, Krosinko, Leszno, Luboń, Luboń-Żabikowo, Mechowo, Mosina, Oborniki, Ostrzeszów, Perzów, Poznań, Poznań vicinity, Poznań-Czerwonak, Poznań-Dębiec, Poznań-Główna, Poznań-Malta, Poznań-Rataje, Poznań-Starołęka, Poznań-Szelągowska, Poznań-Wilda, Poznań-Wilczy Młyn, Poznań-Zegrze, Prosna river, Pyzdry, Spławie, Starołęka, Stęszew, Śrem, Turek, Wierzenica, Września, Zalesie, Żabikowo, Żerków
Equus ferus	Brudzyń, Czerniejewo, Dębnica, Krosinko, Oborniki, Orzechowo, Poznań-Dębiec, Poznań-Główna, Poznań-Szelągowska, Przysieka Stara, Pyzdry, Śrem, Turek, Ujście, Zalesie, Żerków
Alces alces	Bednary, Gościeszyn, Grzybno, Koło, Kotowiecko, Krosinko, Krześlice, Lubosz, Łabiszyn, Łukaszewko, Miłosław, Mrowino, Nowe Dwory, Połajewo, Poznań-Główna, Poznań-Wilda, Prosna river, Rogówek, Środa Wielkopolska, Warta River, Wielowieś, Żabiczyn, Żabikowo, Żegocin
Megaloceros giganteus	Krosinko, Oborniki, Pamiątkowo, Pyzdry, Robaków, Turek, Żabikowo, Żegocin
Cervus elaphus	Jabłonna, Krosinko, Kruchowo, Nowe Dwory, Ołobok, Orzechowo, Poznań, Poznań vicinity, Poznań-Główna, Poznań-Szelągowska, Pyzdry, Rudki
Rangifer tarandus	Gądki, Gniezno, Krosinko, Murowana Goślina, Oborniki, Poznań vicinity, Poznań-Naramowice, Pyzdry, Turek, Zalesie, Żerków
Capreolus capreolus	Mechowo, Poznań
Ovibos moschatus	Pyzdry
Bison priscus	Czerwieńsk, Gryżyna, Iwno, Konin, Krosinko, Mechowo, Oborniki, Orzechowo, Poznań, Poznań-Szelągowska, Pyzdry, Turek, Zalesie
Bos primigenius	Broniszewo, Iwno, Kobylnica, Konin, Kowanówko, Krosinko, Ostrów Wielkopolski, Paproć, Piłka, Poznań, Poznań-Główna, Poznań-Malta, Poznań-Szelągowska, Piłka, Siedlimowo, Starkówiec Piątkowski

not included in any inventory. Such finds could not be included here. There are known to the authors and in the future will be taken into consideration during preparing revision of this species from Wielkopolska.

From Oborniki gravel pit, one of the most abundant sites (in fact complex sites) from Wielkopolska, came the only Miocene faunal element *T. longirostris* (Chłapowski, 1905; Menzel, 1911; Wolff, 1914; Krause, 1925; Schroeder, 1930; Kowalski, 1959, 1960). The exact age of this isolated find (right M3) is not known. Since Oborniki abundant fauna is mostly correlated with the Late Pleistocene (Lubicz-Niezabitowski, 1926; Kowalski, 1959, 1960; Pawłowska, 2015ab), the age is uncertain. This gomphothere was widespread in Europe during Vallesian (11.6-9 mya) and Turolian (9-5.3 mya) (Lazaridis & Tsoukala, 2014). *T. longirostris* is considered to be an indicator for forested environments sustaining fluvial systems. Lack of contemporary fauna and incomplete stage of preservation make the more precise analysis difficult. Even if the layer from which such a find comes is geologically more closely dated, it is still difficult to determine the age of the mammal assemblage, because it usually consists of specimens lying on a secondary deposit (Kowalski, 1959, 1960). However, already Chłapowski (1905) and some later authors mentioned their relatively large size and more advanced and specialized than those of the other gomphotheres. The characteristics of the species and evolutionary trends indicate a possible a Late Miocene age (MN 11-12, 9-7 mya).

Similar problem is with the determination of the exact age of another proboscidean also found in Oborniki, namely *M. trogontherii* (Chłapowski, 1905). Males of this giant mammoth, exceeding in size even *P. antiquus*, might reaching more than 4.5 m at the shoulder and 15 t weight, as was obtained from great humerus 146 cm long and an associated pelvis from Mosbach 2 (Germany, MIS 15-13) (Larramendi, 2016). On average males reaching 4 m at the shoulder height. *M. trogontherii* appeared in Europe ca. 0.9-0.8 mya, and its occurrence in Eurasia is characterised by complex diachronous mosaic pattern. European populations of this species experienced a persistent size reduction towards the end of the Middle Pleistocene, between MIS 11 and MIS 7. Smaller mammoths with *M. primigenius* type molar morphology displaced those of *M. trogontherii* type in Europe over the course of the late Middle Pleistocene (MIS 11 to the MIS 7/6 boundary) (Lister, 2022). It was result of a protracted highly complex pattern that likely reflects regional migration and introgression (Lister & Sher, 2015). In such context, the single record of *M. trogontherii* from Oborniki can only be very provisionally dated on the Middle Pleistocene.

The most impressive find of *P. antiquus* is 50 years old, particularly large tusker from the found 24.02.1984 in a brown coal mine "Jóźwin" in Konin (Fig. 5; Fedorowicz & Olszak, 1988; Gorczyca, 1988; Jakubowski, 1988, 1996; Stankowski, 1988; Lorek, 1988; Maćkowiak, 1988; Frydrychowicz, 2021). Based on the length of long bones (humerus 128.7 cm long, ulna 108.3 cm long, radius 100.2 cm long, femur 142.9 cm long, tibia +88 cm long), was estimated at about 405-410 cm tall at the shoulders and estimate to weigh about 11.5-12 tonnes (Jakubowski, 1988, 1996; Larramendi, 2016). This puts it in the ranks of the largest individuals ever found, comparable in size with the immense tuskers from Viterbo (Italy), Montreuil (France) or Taubach (Germany) (Larramendi, 2016). A strong sexual dimorphism was characterised for this species, with males being substantially larger than females, which reached a height of about 3 m and weight of 5.5 t (Larramendi et al., 2017).

The earliest appearance of *P. antiquus* in Europe is dated on 0.8-0.75 mya in Italy and slightly later also in England. During his long lasted European evolution, its morphology remained relatively static, unlike *M. primigenius* (Lister, 2004). In Wielkopolska all three records are correlated with Eemian interglacial (MIS 5e, 130-115 kya), which well corroborated with the perception of this species as a member of thermophilic, interglacial faunas. The finds mostly come from lake deposits and

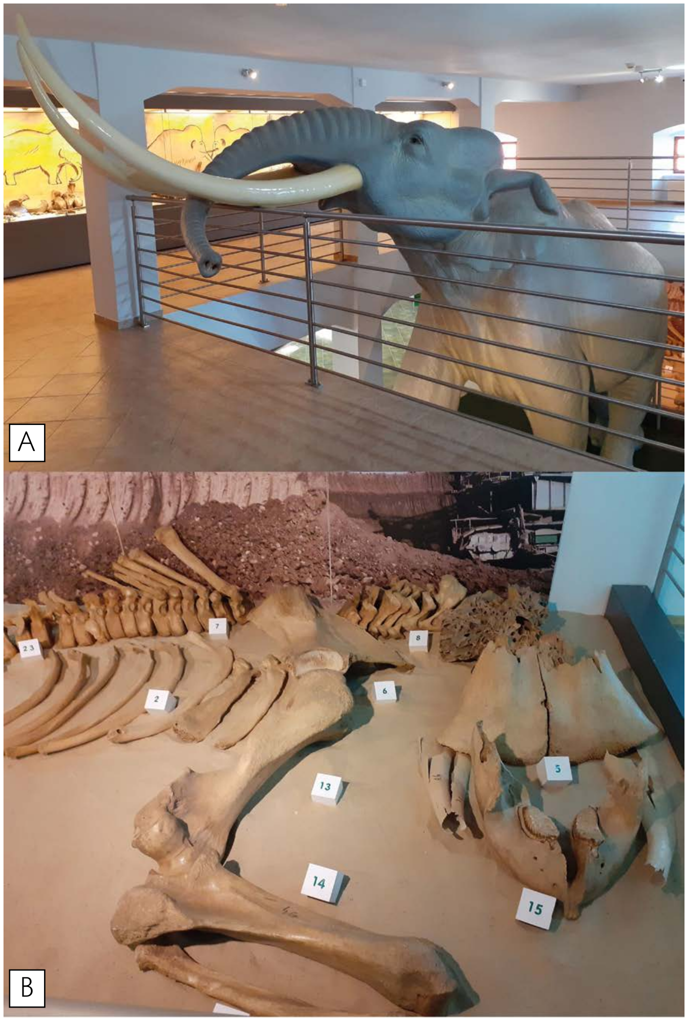

Figure 5. Model (A) and skeleton (B) of a forest elephant *Palaeoloxodon antiquus* from the Brown Coal Mine "Konin" on the exhibition at the Regional Museum in Konin (photo D. Frydrychowicz)

fluvial sediments, which additionally confirmed their interglacial character. Dental microwear studies suggest that the diet was highly variable according to the local conditions, with a predominance browsing over grazing to nearly totally browsing (Saarinen & Lister, 2016; Rivals et al., 2019). *P. antiquus* vanished from most territory of Europe (also from Poland) at the end of MIS 5e, and their records younger than MIS 5d are rare (Stuart, 2005). Some remnant populations survived probably to the end of MIS 3 (29-28 kya) in the southern Iberian Peninsula. Its extinction is likely to be due to climactic deterioration in association with human pressure, especially direct hunting (de Carvalho et al., 2020; Gaudzinski-Windheuser et al., 2023).

Remains of *P. antiquus* at numerous sites across Eurasia are associated with stone tools and many bones bear cut and percussion marks indicative of butchery. However, in the case of most sites, it is unclear whether the elephants were hunted or were scavenged (Konidaris & Tourloukis, 2021; Gaudzinski-Windheuser et al., 2023). A find of almost complete skeleton of a tusker from Konin, partially destroyed during excavation, it offers an unusual opportunity to study the possible cause of death of this individual. However, detail studies showed, that there are no reliable sings on bones, which would allow to determine the reasons that caused its death. Contrary to that, in some sites like two Eemian, German localities Lehringen and Neumark Nord, bones hold some clear sings of interactions with human (Konidaris & Tourloukis, 2021; Gaudzinski-Windheuser et al., 2023). In case of Konin tusker, we can hardly talk about a carnivore attack as a possible cause of death either. With its enormous size, this adult male was virtually out of range of attack from any contemporary carnivore, including such immense species like *U. a. taubachensis*, *P. s. fossilis*, or *Homotherium latidens latidens* Owen, 1846. In this particular case, the most likely cause of death was drowning in a swamp while searching for food on the shore or while drinking water.

In Poland it is commonly, that *M. primigenius* remains recovered from Palaeolithic archaeological sites deposited by humans or carnivores in situ in cultural layers, usually in well-recognized stratigraphic contexts. Contrary to that, in Wielkopolska remains of *M. primigenius* were mostly found in sand and gravel pits, during road and engineering constructions, cartographic and regulatory river works (Pawłowska, 2015ab). They are mainly isolated teeth, tusk fragments or molars, sometimes also postcranial elements were found. Those isolated finds recovered from gravel pits, from river banks, or in glacial, fluvioglacial, or loess sediments, sometimes transported either by the flow of streams or meltwaters from the retreating glaciers or by advancing ice sheets. In these cases, we have to take into account that remains were shifted from the place of deposition, like erratic, and the transport distance in most cases is not known (Nadachowski et al., 2018). However, taphonomy studies of mammoth bones have demonstrated that the final deposition of the remains from the original death site occurred in most cases less than 10 km away (Ukkonen et al., 1999) in Finland and less than 50 km away in Sweden (Ukkonen et al., 2007). The only possible accumulation of remains of *M. primigenius* in stratigraphic context with Palaeolithic tools is Poznań-Szelągowska (Lubicz-Niezabitowski, 1929a; Pawłowski, 1929; Szafer & Trela, 1929; Chmielewski, 1975). However, there is no general agreement about this statement, and because now most of the site area is destroyed and built-up, it is almost impossible to testify that information (Kaczmarek, 2004).

Due to the fact that *M. primigenius* material is stored in numerous museums and private collections in Wielkopolska and is particularly abundant, we decided to exclude many uncertain findings from this paper. Some of the bones and teeth need verification for the possible occurrence of *P. antiquus* or *M. trogontherii* among the very abundant remains of *M. primigenius*. It requires particular attention and examining of the whole material before the final publication. It can be only said, that the morphology and size of *M. primigenius* individuals from Wielkopolska do not differ from those obtained from other Polish and European localities. They were distinctly smaller than *P. antiquus* and *M. trogontherii*, and dimensionally comparable with the extant African elephant *Elephas africana* Blumenbach, 1797. Males were 2.7-3.5 m tall the shoulder and weight up to 8.5 t, while females reached 2.6-2.9 m in shoulder heights and weighed up to 4 t (Larramendi, 2016).

Widespread during the Late Pleistocene *M. primigenius* started to decrease during MIS 2, where population fluctuations and range expansions and reductions were highly dynamic (Nadachowski et al., 2018 and references therein). The results of AMS dating of its remains from Wielkopolska indicate that the species occurred in Poland between about 54 and 30 call kya BP, with a predominance of dates between 35 and 30 call kya BP (Pawłowska, 2015ab, 2022). This correlates with MIS 3 and is consistent with the existing state of knowledge (Nadachowski et al., 2018). It well collaborated with the radiocarbon dates obtained from other Polish sites, with some possible discontinuous during that period (Nadachowski et al., 2018). *M. primigenius* became extinct in most of Europe by ca. 14 kya, except for core areas such as the far northeast of Europe, where they survived until the beginning of the Holocene. No significant correlation was found between the distribution of *M. primigenius* in Europe and human activity (Nadachowski et al., 2018).

Perissodactyls

Two Eemian sites (Konin and Oborniki) confirmed occurrences of *Stephanorhinus kirchbergensis* Jäger, 1839 in Wielkopolska, in total number of 13 localities from Poland (Hermann, 1911, 1913; Lubicz-Niezabitowski, 1926; Kowalski, 1959; Pawłowska, 2015a; Sobczyk et al., 2020; Stefaniak et al., 2021ab, 2023). Although the exact age of Oborniki specimen is not fully confirmed, is more likely, that it is also dated on Eemian (MIS 5e). Geological and palaeobotanical analyses showed, that Konin specimen lived during the warmest stages of the Eemian Interglacial (Sobczyk et al., 2020; Stefaniak et al., 2021ab). One of the most impressive record of this species is an almost complete skeleton of the individual (including the skull, mandible, axial skeleton with forelimbs and right hind limb) found in Gorzów Wielkopolski. Historically relevant to Śląsk, is located in the nearby of historical borders of Wielkopolska (Sobczyk et al., 2020; Stefaniak et al., 2021ab, 2023).

This large species was somewhat less robust and has proportionally more elongated limbs that *C. antiquitatis*. It was comparable in size with the largest specimens of the white rhinoceros *Ceratotherium simum* Burchell, 1817. Males, which were larger than females, were 350-400 cm long, 170-200 cm high and weight up to 3-3.5 t, with the average of 2.5 t. It two horns, especially the first one, were shorter and more rounded in cross section. Morphologically it strongly resembles extant black rhinoceros *Diceros bicornis* Linnaeus, 1758. It was a forest and forest-steppe dweller which fed on leaves, shoots, as well as low-growing plants (Stefaniak et al., 2021b, 2023).

S. kirchbergensis was predominantly present in Europe during interglacial, and together with *U. a. taubachensis*, *P. antiquus*, and *Hippopotamus amphibius* Linnaeus, 1758 formed a core of thermophilic fauna, characteristic of warm periods (von Koenigswald & Heinrich, 1999; von Kolfschoten, 2000; Pushkina, 2007). The material of *S. kirchbergensis* from Wielkopolska do not have any signs, that could document human activity. However from sites like Taubach (Germany, MIS 5e) remains of this species with cut marks are known. Among them a strong dominance of young subadults individuals have been found, while adults rhinoceros are rare. It has been suggested exploitation on site by Neanderthals (Bratlund, 1999).

The timing of *S. kirchbergensis* disappearance is unclear. The species went extinct from Europe at the onset of the cold phases of MIS 4. It was widely distributed throughout Asia and all the way north to northern Siberia at ca. 40 kya. The latest dated remains of come from China and are dated on MIS 2, which may have been the last refugium for the species (Pang et al., 2017; Stefaniak et al., 2023).

Much more commonly found in Wielkopolska is found *C. antiquitatis*, traditionally regarded as a habitant of open grasslands and member of steppe mammoth fauna. Among 185 Polish records of this species, 148 are from open-air sites, while only 37 came from caves (Stefaniak et al., 2023). In this number 45 localities came from Wielkopolska. All finds from this region were without anatomical position and mostly without stratigraphical context. They are represented include mostly skulls, isolated teeth, elements of the axial skeleton, and limb bones (Fig. 6). Although in general perception the occurrence of *C. antiquitatis* is correlated with the Late Pleistocene, the species appeared in Poland much earlier, already during MIS 13-12 (Berto et al., 2021; Kot et al., 2022; Stefaniak et al., 2023).

The species was inhabitant of the open areas of the mammoth steppe, well adapted to keep warm. Compared to *S. kirchbergensis*, it was slightly smaller and especially

Figure 6. Skull of a wholly rhinoceros *Coelodonta antiquitatis* from the Brown Coal Mine "Konin" on the exhibition at the Regional Museum in Konin (photo D. Frydrychowicz). Scale bar 100 mm

lower, with proportionally longer head and body and shorter legs. Males were 320-360 cm long, 140-160 cm high and weight 1.7-2.5 t (Boeskorov, 2012). Two horns differ considerably metrically and morphologically, with the anterior one long up to 150 cm, strongly flattened laterally. The second is no longer than 50 cm and more triangular (Boeskorov et al., 2011).

Unfortunately, the stratigraphic information of finds of *C. antiquitatis* from Wielkopolska are unclear, and few radiocarbon dates documented presence of the species during MIS 3 (Pawłowska, 2022). In Poland obtained so far dates indicate that the species became extinct before the great global warming at 14.7 kya, at the Greenland Stadial 2a (GS-2a)/ Greenland Interstadial 1 (GI-1) transition (Stefaniak et al., 2023 and references therein). The youngest, obtained so far from Poland AMS date (16,460 ± 90 BP, 20,126-19,583 call. BP, Poz-82384) came Silesian site Skarszyn, located less than 50 km from the southern border of Wielkopolska (Marciszak et al., 2019a). Such young date suggests that, given the short distance from Wielkopolska, this species could have been present in this area even in the period of MIS 2.

Remains of *Equus ferus* from Wielkopolska were found in 18 localities, and never where subject of more detail studies (Kaczmarek, 2004; Pawłowska, 2015ab, 2022). Previous authors only provisionally mentioned their presence or sometimes gave a very short description. Most of the finds are of unclear stratigraphic position, and obtained AMS dates documented presence of this species during MIS 3 (Kaczmarek, 2004; Pawłowska, 2015b, 2022). Horses were only preliminarily studied during this work, since some new finds are still coming to light and more can be expected.

The material of *E. ferus* from Wielkopolska known so far seem to be homogeneous. Most of the remains belonged to medium and large-sized individuals with dental morphology typical of caballoid horses. The most postcranial elements are large and robust. Among them also specimens smaller and more slightly build than a medium-sized extant horse have been recorded. Similar data were presented by German researchers, where for example Maas (1899) from Mechowo mentioned presence of a huge, robust caballoid horse. According to some earlier researchers (Maas, 1899; Wahnschaffe, 1909; Hermann, 1913; Kowalski, 1959), some finds might be older than the Late Pleistocene. But the age is very uncertain, and many *E. ferus* remains from Wielkopolska are quite young, of a Holocene age (Kaczmarek, 2004; Pawłowska, 2015b, 2022).

Artiodactyls

Though the most represented family in species number, artiodactyls are however less informative than the other large mammals from Wielkopolska open-air sites. There exist numerous pre-war records of cervids, mostly found in alluvium sediments or peat and represented by antlers or their fragments. In some cases, skull fragments, isolated teeth or single bones of postcranial skeleton were found. All the cervid remains are metrically and morphologically indistinguishable from modern species. Wielkopolska must have been occupied by the *C. elaphus* in spring when stags shed their antlers, since most of the antler bases found were naturally shed. Their rounded bases show that they were not broken off. The fact indicates the season of the year when the remains were deposited. The possible Late Pleistocene records of *C. elaphus* may suggest that the species migrated into Wielkopolska only during woodland interstadials or it may have adapted to treeless herb vegetation, possibly in the form of a distinct ecotype (Pawłowska, 2015b, 2022).

Another well represented artiodactyl is *Alces alces*, a species whose material comprised mainly antlers and their fragments and sometimes also calvaria. This is partly due to the species being probably quite common in lowland Wielkopolska, and partly to its particularly robust and compact skull structure. The remains of *A. alces* have been described from peatlands, lake and river sediments, and are almost exclusively of Holocene age, as was showed by e.g. skull from Żabikowo, where date gave an age of 9450 ± 50 BP (10,799-10,561 call BP, Poz-53724) (Pawłowska, 2015b). Wielkopolska is characterised by relatively frequent finding of almost complete skeletons of *A. alces*, like those from Poznań-Główna, Krześlice or Łukaszewko (Lubicz-Niezabitowski, 1929b, 1932). There are characterised by particularly large size, robust build, and antlers formed as shovels. Metrically those individuals were considerable larger than extant European moose and comparable in stature with great Alaskan moose *Alces alces gigas* Miller, 1899. This applies especially for the bull from Łukaszewko, with antlers spacing of 162.5 cm, while in the record sized European bulls the spacing diameter do not exceed 140-150 cm (Fig. 7; Lubicz-Niezabitowski, 1929b, 1932; Kaczmarek, 2004).

Bovids are represented by two big and massive species, the cold-adapted *Bison priscus* and the more thermophilus *Bos primigenius*, both tending to inhabit open grasslands. Their

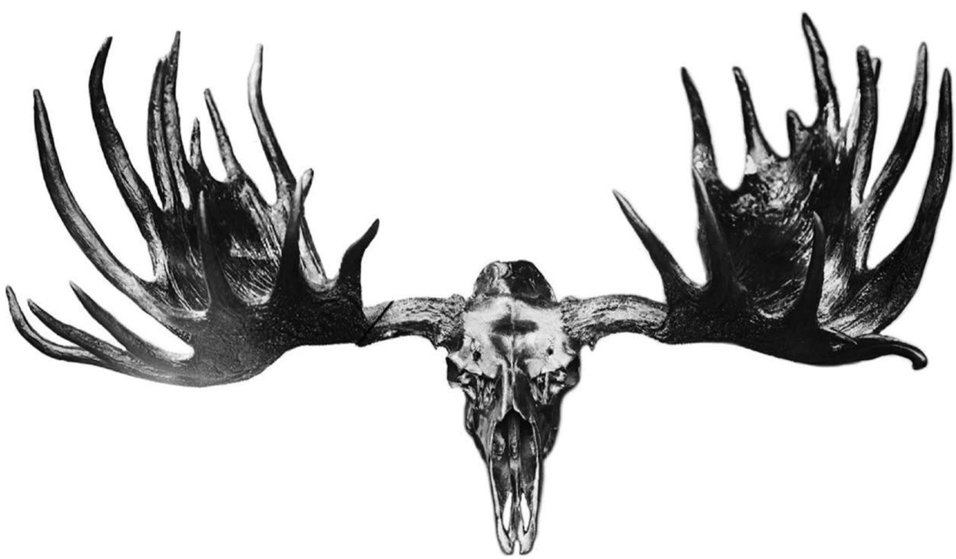

Figure 7. The skull of a moose bull *Alces alces* from Łukaszewko near Trzemeszno (photo W. Rakowski, from the collection of the Institute of Agricultural and Forest Environment of the Polish Academy of Sciences. According to Sita, 2019, changed)

remains, mainly skulls and isolated bones, come from the fluvial depositional context like sands and gravels (Pawłowska, 2015b, 2022). The noteworthy is also a single record of northern, cold-adapted *Ovibos moschatus* from vicinity of Pyzdry, dated on MIS 3 (Stefaniak, 2015; Stefaniak et al., 2020, 2021ab).

Conclusions

In the first, extensive revision of the fauna of open-air sites from Wielkopolska 18 mammal species have been recorded, the presence of which was documented from 125 sites. Among 18 species were 3 carnivores, 4 proboscideans, 3 perissodactyls and 8 artiodactyls. The fossil theriofauna was dominated by large herbivores, members of the mammoth steppe fauna, dated at the Late Pleistocene (MIS 5d-2). Recorded from 49 localities *Mammuthus primigenius* and *Coelodonta antiquitatis*, found in 45 sites, greatly outnumbered the other forms, followed by *E. ferus*. Other ungulates, such as *Megaloceros giganteus*, *Rangifer tarandus*, and *Bison priscus*, co-occurred with them. Few sites like Konin and Oborniki documented occurrence of more thermophilus faunal elements like *Palaeoloxodon antiquus*, *Stephanorhinus kirchbergensis* and *Ursus arctos taubachensis*, dated on the last interglacial (Eemian, MIS 5e). Numerous remains of *Alces alces*, *Cervus elaphus*, *Bos primigenius* do not usually have an exact age, and in many cases the subfossil nature of their state of preservation indicates a younger, Holocene (MIS 1) age of the finds. The sole find of *Tetralophodon longirostris* from Oborniki is the only Miocene faunal record from Wielkopolska.

The fossil material from the vast majority of open-air sites from Wielkopolska represent single, inarticulate finds such as skulls, teeth, long bones. Among ungulates, a large share of skulls and their fragments is noteworthy, including such impressive finds as the skull of a moose bull *Alces alces* from Łukaszewko. Only single finds like the skeleton of immense tusker of *Palaeoloxodon antiquus* from Brown Coal Mine in Konin were found articulated within the stratigraphic context. Majority of the bones were accumulated through natural processes and there is no evidence of human activity. It applies even to the recognised archaeological sites, where the accumulation of remains may be an outcome of natural or catastrophic death, slope or fluvial processes, activity of carnivores and some additional factors.

Editors' note:
Unless otherwise stated, the sources of tables and figures are the author's, on the basis of their own research.
The References include the items listed both in the article and in the Appendix.

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