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Chronology and distribution of Pleistocene woolly rhinoceros: A review of the archival data from Poland

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Abstract

This work provides a review of the state of knowledge of woolly rhinoceroses in Poland. We compile research results from the 19th century to the present day and consider the collected data not only quantitatively, but above all qualitatively. Here we present a list of 215 sites from Poland where the remains of the woolly rhinoceros have been found. Studies of woolly rhinos from Poland usually employ small samples. Our compilation of data also reveals that there is currently no basis for drawing conclusions regarding the geographical distribution pattern of the species in Poland. Only a small number of works have focused on matching the places where remains occurred with the geological conditions of the area and their depositional history. Moreover, the results show that the resolution of the radiocarbon dates that are currently published is insufficient to allow conclusions about the chronology of woolly rhinoceroses in Poland to be drawn. No works to date have dealt with any aspect of palaeopopulation research. The woolly rhinoceros is not present in Palaeolithic art in Poland. A summary of our knowledge of this taxon is the starting point for our multi-aspect research into this topic.

Key words: History, palaeogeography, taphonomy, Central Europe, WOOLRHINOPOLI Project

1. Introduction

Rhinoceroses are mammals belonging to the order Ungulates (Perissodactyla), in which the third toe is the most developed and carries the axis of the limb. The term "rhinoceros" covers a number of living and extinct species, with *Stephanorhinus etruscus*, *Stephanorhinus hundsheimensis*, the steppe rhino (*Stephanorhinus hemitoechus*), the forest rhino (*Stephanorhinus kirchbergensis*), and the woolly rhinoceros (*Coelodonta* species; Fig. 1) recognized from the fossil record of Pleistocene strata. The fifty-million-year history of this group of animals is now changing drastically with a population decline in the five living species of rhinoceroses — the white rhinoceros (*Ceratotherium simum*), the black rhinoceros (*Diceros bicornis*), the Indian rhinoceros (*Rhinoceros unicornis*), the Javan rhinoceros (*R. sondaicus*), and the Sumatran rhinoceros (*Dicerorhinus sumatrensis*) — which together number less than 30,000 individuals today.

Fossil members of rhinoceroses are known from Europe, Asia, North America, and Africa, and studies of their remains have shed light on intraspecies and interspecies distributional patterns, morphology, genetics, extinction, diet, and other issues.

One recently completed morphological study employed a Bayesian model to reveal the genus of *Stephanorhinus* as a monophyletic clade (Pandolfi, 2023). A consistent finding in morphological studies is that it is difficult to distinguish between fossil species using most skeletal elements, particularly postcranial elements, and this is particularly true in the genus *Stephanorhinus*. This has to do with the fact that interspecific variability often overlaps and includes polymorphic characters (Ballatore & Breda, 2019).

Fig. 1. Drawing of a woolly rhinoceros (WOOLRHINOPOLI Project).

Genetic investigation has shown that the extinct woolly rhinoceros is most closely related to the extant Sumatran rhinoceros (Orlando et al., 2003). Phylogenetic inference, based on a complete mitochondrial genome sequence of fossil *Stephanorhinus* from the Chondon River valley (Arctic Yakutia, Russia), has confirmed that of the extinct species, woolly rhinoceros, *Coelodonta* is most closely related to *Stephanorhinus* (Kirillova et al., 2017). A study of ancient DNA from eastern European sites further suggests that the effective population size of woolly rhinoceros increased at 29.7 ka BP and then remained stable until near extinction, ca 14 ka BP (Lord et al., 2020). The extinction of the *Stephanorhinus* species has also been studied, leading to the conclusion that *Stephanorhinus etruscus* went extinct at the Early–Middle Pleistocene (in Italy and the Iberian Peninsula) or the late Early Pleistocene (in Central Europe) (Pandolfi et al., 2017), while *Stephanorhinus hundsheimensis* became extinct in the late Middle Pleistocene–early Late Pleistocene (in Spain) (García-Fernández et al., 2023), *Stephanorhinus hemitoechus* at 41 ka BP (in Italy) (Pandolfi et al., 2017), and *Stephanorhinus kirchbergensis* at about the early Late Pleistocene — that is 120–104 ka BP (in Europe) or 13 ka BP (in China) (Shpansky, 2017).

The diet of fossil rhinoceros can be determined using various, often combined, methods including morphometry, microwear and mesowear analysis of teeth, isotopic studies, and analysis of organics in the form of food remains extracted from teeth. The dietary evolution of the two Middle to Late Pleistocene rhinoceros species *S. hemitoechus* and *S. kirchbergensis* in Central and Northwest Europe was traced by van Asperen & Kahlke (2015) using mesowear signal and morphometry. They showed a mixed feeder diet for both, comparable with that of extant mammal species in relatively open habitats. *S. kirchbergensis* consumed more or less browse in the diet depending on the quality of the habitat, while *S. hemitoechus* shifted from a mixed feeder to consuming more grass when necessary (van Asperen & Kahlke, 2015).

Ballatore (2016) has combined powder X-ray diffraction, carbon isotope geochemistry, tooth wear analysis, and biometry to perform a palaeoecological investigation of Pleistocene European Rhinoceroses (*Stephanorhinus*), also concluding that *Stephanorhinus* shows high specialization in browsing. Further work has also confirmed a mixed feeder diet for the forest rhino (from the Chondon River) through an analysis of food remains in the fossae of the cheek teeth, identified as *Larix*, *Vaccinium*, *Betula* spp., *Aulacomnium*, and dicotyledonous herbs and grasses (Kirillova et al., 2017). In addition, microwear analysis of teeth in this study further showed that, during the last months of its life, this individual fed predominantly on leaves and twigs (Kirillova et al., 2017). The study of the *Stephanorhinus kirchbergensis* find from the Chondon River also shows the validity of undertaking complex studies of rhino remains, which in this case combined genetic, dietary, and morphological analyses (morphometry, food remains from teeth, mesowear, and isotopes) to determine the taxonomic position, season, and age of death, as well as the discussed above diet of this individual.

Studies combining mesowear and isotope analysis have also confirmed a generally browse-dominated diet for *S. kirchbergensis* (Pushkina et al., 2020), as also other work (Stefaniak et al., 2021). This shows how different lines of evidence in *Stephanorhinus* research have led to the same consistent conclusions. However, the correlation between $\delta^{13}C$ and mesowear is not straightforward, because of the considerable variation in dietary specialisation within herbivorous mammals. For example, variation in feeding behavior among the *S. hemitoechus* and *S. kirchbergensis* species was induced by interspecific competition along with diversification of habitat within the range of each species' ecological tolerance. While their dietary flexibility enabled them to survive in a range of environments that were neither strictly steppe nor strictly forest, it does also cause difficulties in establishing the specific habitats and real dietary traits of the *Stephanorhinus* palaeopopulation (van Asperen & Kahlke, 2015).

The woolly rhinoceros (*C. antiquitatis* Blumenbach 1799) has been demonstrated to be a specialised grazer on the basis of the high mesowear signal resulting from dental analysis. This points to abrasion-dominated diets and open grassland habitats (Pushkina et al., 2020).

Although the woolly rhinoceros provides the most evidence for the presence of fossil rhinos in Europe, there is still in many respects no synthesis for this taxon. Here, we will focus on woolly rhinoceros outlining the current state of knowledge, especially from the perspective of its spatial and temporal occurrence in Poland, by closely scrutinized the results to date on woolly rhino remains. It will prove extremely valuable to compile for the first time the scopes of various types of research into the woolly rhinoceros in Poland, by tracking geographical, chronological, demographic, genetic, and taphonomic datasets to reconstruct its natural history, as well as social aspects of its history.

1.1. Woolly rhinoceroses

1.1.1. Emergence and evolution of the genus *Coelodonta*

The fossil record of the genus *Coelodonta* goes back to 3.7 Ma BP and was established on the basis of the remains of *Coelodonta thibetana*, found in Tibet (Zanda Basin) in the Pliocene strata (Deng et al., 2011). Between 2.5 and 1.0 Ma BP the genus is represented by the remains of *Coelodonta nihowanensis*, found at many localities in China.

Coelodonta seems to have arrived in Europe in the early Middle Pleistocene, around 500–400 ka, as shown by finds of *Coelodonta tologoijensis*, a species of rhino with more evolved features, at localities in Germany (Bad Frankenhausen), Russia, and Mongolia (Nalaikha). However, some authors have claimed that finds from Germany should be assigned to *C. antiquitatis praecursor* (Uzunidis, 2022). Finds from the Kuznetsk Basin (Russia) recorded as *C. cf. tologoijensis* indicate an initial westward expansion of this group of rhinoceroses into southwest Siberia (Kahlke & Lacombat, 2008).

Woolly rhinoceros (*Coelodonta antiquitatis*) comparable to *C. tologoijensis* spread westward and entered Central Europe and, in several cases, Western Europe, during all of the subsequent Middle to Late Pleistocene cold stages (around 470–350 ka), as a result of preferable environmental conditions — namely, extended phases of low temperature and aridity (Kahlke & Lacombat, 2008). By the end of the Pleistocene (until ca. 40 ka; Stuart & Lister, 2012) the woolly rhinoceros was widely distributed geographically in Eurasia.

1.1.2. Environment and diet

The natural environment is the complex of physical, chemical, and biotic factors (such as climate, soil, and living things: i.e. Wolfhagen et al., 2020) that act upon an organism or an ecological community, which ultimately determine its form and survival. Despite the fact that animals are embedded in specific environments, they possess some ecological flexibility to adapt when that environment changes.

For the woolly rhinoceros, the natural habitat was the steppe-tundra, a biome that formerly existed but which has no analogue in today's landscapes as its characteristic vegetation no longer exists. One of the earliest large species of herbivore to appear there was the steppe mammoth (*Mammuthus trogontherii*), recognized in Poland at fifteen sites (Pawłowska, 2015a), including Bełchatów, where cultural traces on a rib, likely left by *Homo heidelbergensis* (indirect evidence given the lack of human remains), constitute the oldest butchery marks from Poland (Pawłowska et al., 2014; Pawłowska, 2017a) and one of a relatively few from Eurasia (Pawłowska, 2017a).

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 megafauna, which are a subset of the largest terrestrial species in a community or an ecosystem. However, environments in the Quaternary varied by the presence of subenvironments which included refugia, ecological niches that are closely related to the latitude. Environmental fluctuations during the Pleistocene were driven by climate, by alternating cycles of cold and warming in relation to glacial and interglacial periods, which in turn occurred in response to the development and disappearance of ice sheets in Europe (Hrynowiecka et al., 2022). These dynamic environmental changes affected the spatial range of fauna in the Pleistocene in Europe, including that of the woolly rhinoceros.

The main adaptations of the woolly rhinoceros to the extremely cold, harsh conditions that prevailed on the mammoth steppe included its long, thick hair, horns that supported recovering food from the snow cover, and genetic mutations that allowed a type of receptor in the skin for sensing warm and cold temperatures (Fortelius, 1983; Lord et al., 2020). The woolly rhinoceros fed on green plants, mostly grass with shrubs and woody vegetation in the winter diet, as part of seasonal changes, as shown by isotopic signatures (Tiunov & Kirillova, 2010). A study of the stomach contents of frozen rhinoceroses revealed that the last meals of those individuals contained cereal grain (grasses) and sedge (Vereshchagin & Baryshnikov, 1992). It is assumed that the low grass density and lack of suitable habitat prevented it from crossing the Bering Strait to the American continent (Boeskorov, 2001; Prothero, 1993). As a result, the remains of the woolly rhinoceros are known only in Europe and Asia.

1.1.3. Fossil records

Woolly rhinoceros fossils are fairly common and have been discovered in a range from western Europe to northeastern Siberia. Their absence in specific locations seems to indicate that they did not reach north–central Siberia or North America.

Extinct rhinos from Germany, the Czech Republic, Slovakia, Ukraine, and Belarus, Lithuania, all of which are neighbors of Poland have been the subject of many studies. Geraads et al. (2021) provide for the first time a comprehensive database of fossil rhinos of the old world Neogene and Quaternary, showing that representatives of this group were present in many localities: at 268 sites in Germany (with references to almost 60 works), at 208 sites in the Czech Republic (with references to almost 20 works), at 34 sites in Slovakia (with references to almost 70 works), at 32 sites in Ukraine (with references to almost 20 works), at 2 sites in Belarus (with references to 1 work), and at 1 sites in Lithuania (with references to 2 works). They also showed the distribution pattern of fossil rhinos in Central Europe corresponding to the woolly mammoth, which is comprehensible given the general ecological requirements of these herbivores.

Despite its considerable spatial distribution, the degree of preservation of remains of *C. antiquitatis* varies, with skeletal elements without articulation predominating. One exception is the complete specimen of a woolly rhinoceros individual, along with soft tissues, which was preserved in the fossil record thanks to favorable ozokerite (earth wax) and rock salt as fossilization conditions that are abundant in the area of the find in Starunia, Ukraine (Kubiak, 1994; Kowalski, 2000; Kubiak & Drygant, 2005). Well-preserved remains also have been found in permafrost in Russia (Belyaev et al., 2023; Boeskorov et al., 2011).

2. Material and methods

The material for the study consists of the remains of woolly rhinoceroses found at Polish sites. The list of sites that these remains were recovered from is based on works published since the nineteenth century. For all archival sites, basic data (mainly the location) have been verified and in some cases have been corrected against Stefaniak et al. (2023) in order to make them useful in the synthesis. To this end, a new system for specifying sites is proposed here, as was done in our earlier synthesis of sites with mammoth remains (Pawłowska, 2015a). This means, among other things, separating the name and context of site, giving the district in the subheading of the name of site, and the county and voivodship as separate data. This allows a standardised way of determining site location. Sites with the woolly rhinoceros remains are given in the order of the authors who discovered or first described them, as such paper brought new value to the field. We did not include papers that merely duplicate data.

3. Results and discussion

Like the woolly mammoth, woolly rhinoceros is part of the *Mammuthus–Coelodonta* faunal complex, a term that refers to cold-adapted Pleistocene large mammal assemblages with similar or identical faunistic structures, known for their transregional expansion in Eurasia (Kahlke, 2014). The Middle Pleistocene and Late Pleistocene faunal complexes include various animal species, which are associated with the evolution of the fauna during those times. The faunal complex is, generally speaking, made up of animals associated with both the steppe and tundra.

The woolly rhinoceros is a common species found in Upper Pleistocene assemblages in Poland, as demonstrated by numerous Pleistocene faunal assemblages (see Appendix 1). It is therefore surprising that there has been little attention paid to research into the remains of this species from Polish contexts. To overcome this, a multiproxy study has been conducted on the rhinoceros remains, along with other taxa, from Krosinko in Wielkopolska, which included taxonomic, taphonomic, radiocarbon, genetic, and social aspects (Pawłowska, 2022, 2023; Pawłowska et al., 2022). The results of these earlier studies, along with the history of research on the woolly rhinoceros in Poland, will be presented in terms of geographic, chronological, demographic, genetic, and taphonomic evidence, as well as artistic representation. This site, along with others (such as Sitkówka) have also contributed to syntheses already compiled for Central Europe (Puzachenko et al., 2022).

3.1. Geographic and historic evidences

The oldest palaeontological discoveries of woolly rhinoceros sites date back to the nineteen century (Table 1). Although Stefaniak et al. (2023) states that the first summary paper was published in 1884 by A. Slósarski, who reported on the skull and mandible of a woolly rhinoceros found near Kamieńczyk in 1815, in fact the first paper that dealt with the synthesis of Pleistocene fauna was by Staszic (1815) with the telling title "First treatise on...". This work described one of the first rhinoceros finds from Poland, which was a mandible found in 1810 near Kamieńczyk, where the Liwiec River reaches the Bug River (Staszic, 1815) (Fig. 2).

The results of these studies from the turn of the century were summarised by Kowalski (1959), who gave a list of almost a hundred sites (Kowalski, 1959) and provided a distribution of these sites for Poland. The sites are distributed almost all over the country, mainly along rivers and their tributaries. This list of Polish sites with woolly rhinoceros remains includes the results of seminal works of Lubicz-Niezabitowski (1913, 1926, 1929, 1938), a summary of which has been presented by Pawłowska (2015b), along with findings and evaluations of specimens held in collections. Later studies of the Pleistocene fauna added more sites with evidence of the occurrence of woolly rhinoceros to the general list, or made use of data from these all authors (Kubiak, 1969, 1989; Kubiak & Dziurdzik, 1973; Kuc et al., 2005; Kubiak, 2009; Kuc et al., 2012; Borsuk-Białynicka, 1973). The monograph of Borsuk-Białynicka provided a morphometric study of skulls from Poland, Russia, and the Czech Republic.

Since 1973, rhinos have not disappeared from the Polish research agenda, and have been the subject of publications (Karaszewski, 1980; Król, 1998; Kaczmarek 2004; Wiszniowska et al., 2005; Wojtal, 2007; Woroncowa-Marcinowska et al., 2013; Pawłowska, 2015b; Woroncowa-Marcinowska et

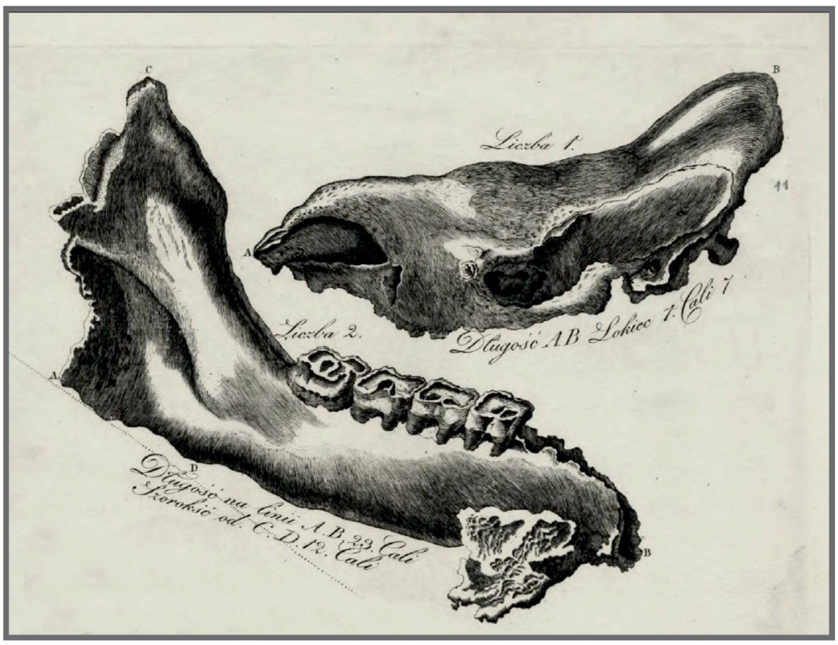

Fig. 2. Mandible (lower specimen) and skull (upper) of a woolly rhinoceros found in 1810 and 1815, respectively in Kamieńczyk site: the first illustration of fossil rhinos from Poland (modified from Staszic, 1815).

al., 2017; Hrynowiecka et al., 2018; Marciszak et al., 2019; Jach & Wojtal, 2021; Geraads et al., 2021; for more see Appendix 1) and many research projects, especially joint projects conducted by Adam Mickiewicz University, Poznań with Polish museums. These works have resulted in the discovery of a new sites, especially in Wielkopolska (Krosinko, Oborniki, Pyzdry, Spławie, Turek: Pawłowska, 2009a, 2009b, 2010, 2015a, 2015b, 2017b, 2022, 2023; Pawłowska et al., 2022), but also in Małopolska (Siedliszowice: Pawłowska, 2012). Notable among these works is a monograph (Woroncowa-Marcinowska et al., 2013) discussing the remains of Pleistocene fauna, including fossil rhinoceroses, in their geological, historic, and chronological context, which had not been done previously on such a scale. This work also yielded an opportunity to examine the forest elephant described by Stankowski (1989), which revealed its physical condition by identifying pathologies (Pawłowska et al., forthcoming) and its depositional history from the final moments of its life (Stankowski, 1989; Pawłowska, 2009a, 2009b). Also, the find was placed among all other finds of forest elephants from Poland (Pawłowska, 2015a).

Recognition of Polish evidence for woolly rhinoceros' distribution was recently expanded to 157 sites by Geraads et al. (2021) who presented an update of Kowalski's synthesis, along with the revision of some site names, and demonstration of 58 new sites (Table 1). The general distributional pattern of the sites has not changed, but has densified due to the discovery of later findings by various authors (Table 1; Appendix 1).

A recent synthesis of fossil rhinos from Poland (Stefaniak et al., 2023) states that it "presents current state of knowledge of Quaternary rhinos from … Poland", but also comments that "The taxonomy of rhinos was not reviewed herein, except in the case of *Stephanorhinus etruscus* and *Stephanorhinus hemitoechus*." This means that Poland still lacks a published up-to-date detailed list of woolly rhinoceros sites. Assuming that sites that are stated in that article to contain woolly rhinoceros remains actually do so, and correcting some errors in the work (there are a few in Appendix 2), it seems that Stefaniak et al. (2023) listed 179 Polish sites, thus extending the list of Geraads et al. (2021), though without citing their work, with the addition of twenty two sites. Here we present a list of 215 sites from Poland where the remains of the woolly rhinoceros have been found. Thus, we are updating this list with another 36 archive sites.

Determining the origin of the specimens in line with the recently introduced contextual approach in palaeozoology (Pawłowska, 2022), is challenging, but will be possible after in-depth analysis. Data for Europe show that the woolly rhinoceros was widely distributed across northern Eurasia during the Pleistocene (among others: Álvarez-Lao & García, 2011; Boeskorov, 2001; Markova et al., 2013, Rey-Iglesia et al., 2021).

3.2. Demographic data

The number of identified specimens (NISP) of woolly rhinoceros from Poland is currently unknown for most sites (Table 1). Many of the assemblages have not been studied, and they particularly lack a consistent system of recording their state of preservation. One implication of this is that the number of individuals of woolly rhinoceros is also unknown. We thus still do not know how many woolly rhinoceros individuals there could have been in the Pleistocene in Poland. Individual papers have indicated the presence of single rhinoceroses (one to six: Table 1 and Appendix 1), although it is difficult to determine whether the methodological approach of these assessments was the same. The minimum number of individuals of woolly rhino from Zwoleń, given by Stefaniak et al. (2023) as 20, must be wrong, since Gautier (2005) established it to be four during studying this assemblage. For Europe, the data is also sporadic and the number is usually low, not exceeding ten (four for Whitemoor Haye in United K: Schreve et al., 2013; three for Jou Puerta in Spain: Álvarez-Lao, 2014).

Although several works have made reference to the age of death of woolly rhinoceroses, usually using unfused epiphysis with the shaft as the criterion, the most seminal work in this regard is the monograph by Borsuk-Białynicka (1973). The age of death for Polish woolly rhinoceros individuals (and also taking into account some material from Russia and the Czech Republic) was evaluated using the skulls of the woolly rhinoceros which were assigned into age groups (Borsuk-Białynicka, 1973).

Gender is rarely indicated in studies of Polish woolly rhinoceros (i.a. male: Góra Puławska; Kazimierz, Konin; Jóźwin, Konin; Łódź; Silesia and female: Pyskowice-Rzeczyce, River Vistula (near Warsaw), NN_4 (Borsuk-Białynicka, 1973). This may in part be due to the methodological difficulty of determining using traditional methods such as measurement.

Table 1. List of archive sites with remains of the woolly rhinoceros from Poland according to the order of authors' contributions, as of February 2024. NN: locality unknown; NISP: number of identified specimens; MNI: minimum number of individuals. No data means that the total data is not yet available.

No.	Site corrected WOOLRHINOPOLI PROJECT	NISP	MNI	Author 1	Author 2	Author 3	Author 4	Author 5	Others
1	Bełchatów	1	no data	Stefaniak et al., 2023 (and some references therein): for each citation here					
2	Bębłowska Dolna Cave, Bębło	no data	no data	Ossowski 1890	Kowalski 1951, 1959	Geraads et al. 2021	Stefaniak et al. 2023		
3	Bielkowo	2	no data	Kiesow 1880	Schirmacher 1882	Wolff 1903	Kowalski 1959	Geraads et al. 2021	Stefaniak et al. 2023
4	Bielkówko	1	no data	Hermann 1913	Sonntag 1919	Kowalski 1959	Geraads et al. 2021	Stefaniak et al. 2023	
5	Biśnik Cave	79	29	Madeyska 2002	Geraads et al. 2021	Stefaniak et al. 2021, 2023			
6	Bobrów	1	no data	Gürich 1885	Stefaniak et al. 2023				
7	Bogusław	1	no data	Kaczmarek 2004					
8	Bolimów	1	no data	Stefaniak et al. 2023					
9	Borsuka Cave	no data	no data	Wilczyński et al. 2016	Geraads et al. 2021				
10	Bramka Cave	no data	no data	Chmielewski 1975	Geraads et al. 2021				
11	Brodnica	2	no data	Hermann 1913	Sonntag 1919	Kowalski 1959	Geraads et al. 2021	Stefaniak et al. 2023	
12	Brzeziny	no data	no data	Kazanecka 2004	Marciszak et al. 2019	Geraads et al. 2021	Stefaniak et al. 2023		
13	Bychawa	1	no data	Wasilewski 1960	Geraads et al. 2021	Stefaniak et al. 2023			
14	Cave IV, Birów Mountain	no data	no data	Muzolf et al. 2009	Stefaniak et al. 2009	Leshchinskiy 2015	Geraads et al. 2021	Stefaniak et al. 2023	
15	Chmielnik	no data	no data	Król 1998	Geraads et al. 2021	Stefaniak et al. 2023			
16	Chorzów	no data	no data	Römer 1879b	Gürich 1885	Kowalski 1959	Geraads et al. 2021	Stefaniak et al. 2023	
17	Ciemna Cave, Ojców	2	1	Krukowski 1939	Kowalski 1951, 1959	Wojtal 2007	Gradziński et al. 2011	Geraads et al. 2021	Stefaniak et al. 2023
18	Czarkowy	no data	no data	Osmólski 1972	Borsuk-Białynicka 1973	Geraads et al. 2021	Stefaniak et al. 2023		
19	Czarniawka Stream	no data	no data	Stefaniak et al. 2023					
20	Czarnków	1	no data	Lubicz-Niezabitowski 1926	Kowalski 1959	Kaczmarek 2004	Pawłowska 2015b	Geraads et al. 2021	Stefaniak et al. 2023
21	Czechowice-Dziedzice	no data	no data	Konior 1936	Marciszak et al. 2019	Geraads et al. 2021	Stefaniak et al. 2023		
22	Czersk	no data	no data	Stefaniak et al. 2023					
23	Czerwonak near Poznań	2	no data	Lubicz-Niezabitowski 1926	Kowalski 1959	Kaczmarek 2004	Pawłowska 2015b	Geraads et al. 2021	Stefaniak et al. 2023
24	Czerwoniak	no data	no data	Kunisch 1883	Geraads et al. 2021	Stefaniak et al. 2023			
25	Czerwonka	1	no data	Conwentz 1901	Hermann 1913	Kowalski 1959	Geraads et al. 2021	Stefaniak et al. 2023	
26	Dąbrowa Górnicza	no data	no data	Stefaniak et al. 2023					
27	Dąbrówka Mała	no data	no data	Ryziewicz 1933	Stefaniak et al. 2023				

No.	Site corrected WOOLRHINOPOLI PROJECT	NISP	MNI	Author 1	Author 2	Author 3	Author 4	Author 5	Others
28	Deszczowa Cave	21	4	Cyrek et al. 2000	Sudoł & Cyrek 2015	Wojtal 2007	Geraads et al. 2021	Stefaniak et al. 2023	
29	Dębiec, Poznań	12	no data	Lubicz-Niezabitowski 1926	Rakowski 1933	Wyrwicka 1946	Wasilewski 1960	Kowalski 1959	Kaczmarek 2004; Pawłowska 2015b; Geraads et al. 2021; Stefaniak et al. 2023
30	Długi Most	no data	no data	Hermann 1913	Sonntag 1919	Kowalski 1959	Geraads et al. 2021	Stefaniak et al. 2023	
31	Dobromierz	5	no data	Kaczmarek 2004					
32	Dobrzylin	no data	no data	Ślósarski 1884	Kowalski 1959	Karaszewski 1980	Geraads et al. 2021	Stefaniak et al. 2023	
33	Dzierżno	no data	no data	Heinevetter 1933, 1937	Geraads et al. 2021				
34	Garwolin	4	no data	Żarski et al. 2014	Geraads et al. 2021	Stefaniak et al. 2023			
35	Glinianki Szcześliwickie, Warsaw	no data	no data	Woroncowa-Marcinowska et al. 2013, 2017	Stefaniak et al. 2023				
36	Główna, Poznań	no data	no data	Lubicz-Niezabitowski 1926	Kowalski 1959	Pawłowska 2015b	Geraads et al. 2021	Stefaniak et al. 2023	
37	Gniew	1	no data	von Baer 1823	Hensche 1860	Müller 1863	Schirmacher 1882	Braun 1910	Hermann 1913; Sonntag, 1919; Kotański 1956; Kowalski 1959; Geraads et al. 2021; Stefaniak et al. 2023
38	Gniewięcin	1	no data	Król 1998	Geraads et al. 2021	Stefaniak et al. 2023			
39	Gołaszyn near Oborniki	1	no data	Lubicz-Niezabitowski 1926	Kowalski 1959	Kaczmarek 2004	Pawłowska 2015b	Geraads et al. 2021	Stefaniak et al. 2023
40	Gorzuchów-Święcko	3	no data	Kunisch 1883	Marciszak et al. 2019	Stefaniak et al. 2023			
41	Gostków	no data	no data	Kunisch 1883	Dathe 1899	Geraads et al. 2021			
42	Góra Kalwaria	2	no data	Stefaniak et al. 2023					
43	Góra Puławska	no data	no data	Krisztafowicz 1896	Czarnowski 1911b	Kozłowski 1922, 1924	Krukowski 1939	Kowalski 1959	Borsuk-Białynicka 1973; Woroncowa-Marcinowska et al. 2013, 2017; Geraads et al. 2021; Stefaniak et al. 2023
44	Góra Winnica near Kamień Mściowski	no data	no data	Kulczycki 1955	Karaszewski 1976	Woroncowa-Marcinowska et al. 2013, 2017	Geraads et al. 2021	Stefaniak et al. 2023	
45	Grupa	2	no data	Conwentz 1892, 1894	Nehring 1896	Jentzsch 1901	Hermann 1911, 1913	Sonntag 1919	Schroeder 1930; Kowalski 1959; Geraads et al. 2021; Stefaniak et al. 2023
46	Ibramowice	no data	no data	Gürich 1905	Geraads et al. 2021				

No.	Site corrected WOOLRHINOPOLI PROJECT	NISP	MNI	Author 1	Author 2	Author 3	Author 4	Author 5	Others
47	Izbica	1	no data	Karaszewski 1976	Geraads et al. 2021	Stefaniak et al. 2023			
48	Jankowo near Środa	1	no data	Lubicz-Niezabi-towski 1926	Kaczmarek 2004	Pawłowska 2015b	Kowalski 1959	Geraads et al. 2021	Stefaniak et al. 2023
49	Jasna Smoleńska Cave	no data	no data	Sudoł & Cyrek 2015	Sudoł et al. 2016	Geraads et al. 2021	Stefaniak et al. 2023		
50	Jasna Strzegowska Cave	no data	no data	Stuart & Lister 2012	Geraads et al. 2021	Stefaniak et al. 2023			
51	Jelenia Góra	1	no data	Gürich 1885	Kowalski 1959	Marciszak et al. 2019	Geraads et al. 2021	Stefaniak et al. 2023	
52	Jerzmanowice	no data	no data	Wojtal 2007					
53	Jóźwin	no data	no data	Borsuk-Białynicka 1973	Geraads et al. 2021				
54	Kadyny	1	no data	Conwentz 1909	Hermann 1913	Sonntag 1919	Kowalski 1959	Geraads et al. 2021	Stefaniak et al. 2023
55	Kadzielnia, Kielce	2	no data	Lubicz-Niezabi-towski 1926	Kowalski 1954, 1958a, 1959	Pawłowska 2015b	Woroncowa-Marci-nowska et al. 2013, 2017	Geraads et al. 2021	Stefaniak et al. 2023
56	Kalinowo	no data	no data	von Baer 1823	Kowalski 1959	Geraads et al. 2021	Stefaniak et al. 2023		
57	Kamieńczyk	2	no data	Staszic 1815	Stefaniak et al. 2023				
58	Karbowo	1	no data	Hermann 1913	Sonntag 1919	Kowalski 1959	Geraads et al. 2021	Stefaniak et al. 2023	
59	Karzec near Gostyń	2	no data	Lubicz-Niezabi-towski 1926	Kowalski 1959	Kaczmarek 2004	Pawłowska 2015b	Geraads et al. 2021	Stefaniak et al. 2023
60	Kazimierz, Konin	1	no data	Borsuk-Białynicka 1973					
61	Kłodzko	no data	no data	Otto 1837	Hensel 1852, 1853	Kunisch 1883	Gürich 1885	Kowalski 1959	
62	Kobylnica near Poznań	2	no data	Lubicz-Niezabi-towski 1926	Kowalski 1959	Kaczmarek 2004	Pawłowska 2015b	Geraads et al. 2021	Stefaniak et al. 2023
63	Komarowa Cave	43	4	Wojtal 2007	Nadachowski et al. 2009	Geraads et al. 2021	Stefaniak et al. 2023		
64	Komondzianka	no data	no data	Ślósarski 1884	Kowalski 1959	Geraads et al. 2021	Stefaniak et al. 2023		
65	Konin	no data	no data	Borsuk-Białynicka 1973		Stefaniak et al. 2023			
66	Kowanowo near Oborniki	1	no data	Lubicz-Niezabi-towski 1926	Kowalski 1959	Kaczmarek 2004	Pawłowska 2015b	Geraads et al. 2021	Stefaniak et al. 2023
67	Kowanówko near Oborniki	7	no data	Lubicz-Niezabi-towski 1926	Kowalski 1959	Pawłowska 2015b	Geraads et al. 2021	Stefaniak et al. 2023	
68	Koziarnia Cave, Sąspów	2	2	Römer 1883, 1884	Czarnowski 1911a	Kowalski 1951, 1959	Szulc 2005	Geraads et al. 2021	Stefaniak et al. 2023
69	Krosinko	in pro-gress	in pro-gress	Pawłowska 2009a, 2009b, 2010, 2015a, 2022	Pawłowska et al. 2022	Pawłowska 2015b	Stefaniak et al. 2023		
70	Kroszyce	no data	no data	Wojtal 2007					

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71	Krowodrza, Kraków	2	no data	Jura 1837	Kowalski 1959	Geraads et al. 2021	Stefaniak et al. 2023		
72	Lisia Góra	1	no data	Borsuk-Białynicka 1973	Geraads et al. 2021	Stefaniak et al. 2023			
73	Lubin	no data	no data	Anonymous 1908	Kowalski 1959	Marciszak et al. 2019	Geraads et al. 2021	Stefaniak et al. 2023	
74	Luboń near Poznań	1	no data	Lubicz-Niezabi-towski 1926	Kowalski 1959	Kaczmarek 2004	Pawłowska 2015b	Stefaniak et al. 2023	
75	Ludwinów, Kraków	1	no data	Kiernik 1911	Kowalski 1959	Geraads et al. 2021	Stefaniak et al. 2023		
76	Łabędy, Gliwice	no data	no data	Heinevetter 1937	Geraads et al. 2021				
77	Ławy near Siedlce	5	no data	Hrynowiecka et al. 2018	Stefaniak et al. 2023				
78	Łęcze	2	no data	Klien 1910	Hermann 1913	Kowalski 1959	Geraads et al. 2021	Stefaniak et al. 2023	
79	Łokietka Cave	no data	no data	Wojtal 2007	Geraads et al. 2021				
80	Łódź	1	no data	Borsuk-Białynicka 1973	Geraads et al. 2021	Stefaniak et al. 2023			
81	Maciejowice	1	no data	Stefaniak et al. 2023					
82	Malbork	1	no data	Stefaniak et al. 2023					
83	Malta, Poznań	4	no data	Maas 1899	Lubicz-Niezabi-towski 1926	Kaczmarek 2004	Kowalski 1959	Pawłowska 2015b	Geraads et al. 2021; Stefaniak et al. 2023
84	Mammutowa Cave, Wierzchowie	no data	1	Zawisza 1878, 1882a, 1882b	Kowalski 1951, 1959	Wojtal 2007	Wojtal et al. 2011	Geraads et al. 2021	Stefaniak et al. 2023
85	Maszycka Cave, Maszyce	no data	no data	Ossowski 1884, 1885	Kowalski 1951, 1959	Lasota-Moskalewska 1993	Geraads et al. 2021	Madeyska & Cyrek 2002	Stefaniak et al. 2023
86	Mechowo near Swarzędz	3	no data	Maas 1899	Lubicz-Niezabi-towski 1926	Kowalski 1959	Kaczmarek 2004	Pawłowska 2015b	Geraads et al. 2021; Stefaniak et al. 2023
87	Milowice, Sos-nowiec	48	6	Ryziewicz 1933	Kowalski 1959	Marciszak et al. 2019	Geraads et al. 2021	Stefaniak et al. 2023	
88	Minięta	3	no data	Conwentz 1895, 1897	Hermann 1911, 1913	Sonntag 1919	Schroeder 1930	Kowalski 1959	Stefaniak et al. 2023
89	Mroczna Cave	no data	no data	Geraads et al. 2021	Stefaniak et al. 2023				
90	Murek Cave, Czułów	no data	no data	Ossowski 1883	Kiernik 1912	Kowalski 1951, 1959	Geraads et al. 2021	Stefaniak et al. 2023	
91	Na Gaiku II Shelter, Mników	no data	no data	Ossowski 1883	Kowalski 1951, 1959	Geraads et al. 2021	Stefaniak et al. 2023		
92	Na Gołąbcu Cave, Piekary	41	3	Ossowski 1880	Kowalski 1951, 1959	Geraads et al. 2021	Stefaniak et al. 2023		
93	Na Wrzosach Północna Cave, Wrzosy	1	no data	Ossowski 1881	Kowalski 1951, 1959	Geraads et al. 2021	Stefaniak et al. 2023		
94	Nad Galoską Cave, Piekary	no data	no data	Ossowski 1881	Kowalski 1951, 1959	Geraads et al. 2021			

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95	Nad Matką Boską Cave, Czułów	no data	no data	Ossowski 1883	Kowalski 1951, 1959	Geraads et al. 2021	Stefaniak et al. 2023		
96	Nad Potoczkiem Cave, Czułów	no data	no data	Ossowski 1883	Kowalski 1951, 1959	Geraads et al. 2021	Stefaniak et al. 2023		
97	Nietoperzowa Cave	8	6	Wojtal 2007	Geraads et al. 2021	Stefaniak et al. 2023			
98	NN_1	no data	no data	Lubicz-Niezabi-towski 1926	Pawłowska 2015b				
99	NN_2	no data	no data	Lubicz-Niezabi-towski 1926					
100	NN_3	no data	no data	Król 1998					
101	NN_4	1	no data	Borsuk-Białynicka 1973					
102	Nowa Dobra	no data	no data	Conwentz 1905	Hermann 1913	Sonntag 1919	Kowalski 1959	Geraads et al. 2021	Stefaniak et al. 2023
103	Nowawieś Chełmińska	2	no data	Hermann 1913	Stefaniak et al. 2023				
104	Nowe Pole	2	no data	Conwentz 1888	Hermann 1913	Sonntag 1919	Kowalski 1959	Geraads et al. 2021	Stefaniak et al. 2023
105	Obłazowa Cave	7	6	Valde-Nowak & Nadachowski 2014	Geraads et al. 2021	Stefaniak et al. 2023			
106	Oborniki	31	no data	Wahnschaffe 1900a, 1900b, 1914	Krause 1925	Lubicz-Niezabi-towski 1926	Schroeder 1930	Kowalski 1959	Kaczmarek 2004; Pawłowska 2015b; Stefaniak et al. 2023
107	Odrzywół	1	no data	Karaszewski 1976	Geraads et al. 2021	Stefaniak et al. 2023			
108	Ojrzanów near Mszczonów	2	no data	Stefaniak et al. 2023					
109	Okiennik Cave, Skarżyce	no data	no data	Lubicz-Niezabi-towski 1938	Krukowski 1939	Kowalski 1951, 1959	Pawłowska 2015b	Geraads et al. 2021	Stefaniak et al. 2023
110	Opatów	no data	no data	Król 1998					
111	Oporów, Wrocław	no data	no data	Wiszniowska et al. 2003	Marciszak et al. 2019	Geraads et al. 2021	Stefaniak et al. 2023		
112	Ostróda	no data	no data	Brandt 1877	Kowalski 1959	Geraads et al. 2021	Stefaniak et al. 2023		
113	Ostróg, Racibórz	no data	no data	Marciszak et al. 2019	Geraads et al. 2021	Stefaniak et al. 2023			
114	Ostrzeszów	1	no data	Lubicz-Niezabi-towski 1926	Kowalski 1959	Kaczmarek 2004	Pawłowska 2015b	Geraads et al. 2021	Stefaniak et al. 2023
115	Otmuchów	no data	no data	Römer 1870, 1873, 1879b	Gürich 1885	Kowalski 1959	Marciszak et al. 2019	Geraads et al. 2021	Stefaniak et al. 2023
116	Parchatka	1	no data	Karaszewski 1976	Pożaryski 1953	Geraads et al. 2021	Stefaniak et al. 2023		
117	Pawłowiczki	no data	no data	Römer 1879b	Gürich 1885	Pax 1921	Zeuner 1932	Kowalski 1959	Marciszak et al. 2019; Geraads et al. 2021; Stefaniak et al. 2023
118	Perspektywiczna Cave	12	no data	Stefaniak et al. 2023					

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119	Perzów	1	no data	Gürich 1885	Kowalski 1959	Marciszak et al. 2019	Geraads et al. 2021	Stefaniak et al. 2023	
120	Piaseczno	1	no data	Majewska 2015	Stefaniak et al. 2023				
121	Płock	no data	no data	Ślósarski 1884	Kowalski 1959	Karaszewski 1980	Geraads et al. 2021	Stefaniak et al. 2023	
122	Pod Kochanką Cave, Mników	no data	no data	Ossowski 1883	Kowalski 1951, 1959	Geraads et al. 2021	Stefaniak et al. 2023		
123	Połom Mountain Cave	no data	no data	Geraads et al. 2021					
124	Poznań	no data	no data	Hermann 1913	Sonntag 1919	Kowalski 1959	Stefaniak et al. 2023		
125	Przechówko	1	no data	Conwentz 1888	Hermann 1913	Sonntag 1919	Kowalski 1959	Geraads et al. 2021	Stefaniak et al. 2023
126	Przegińska Cave, Przeginia	no data	no data	Ossowski 1881	Kowalski 1951, 1959	Geraads et al. 2021	Stefaniak et al. 2023		
127	Przemyków	no data	no data	Zejszner 1856	Kowalski 1959	Geraads et al. 2021	Stefaniak et al. 2023		
128	Przemyśl-Jarosław	no data	no data	Zawadzki 1840	Temple 1869	Polanśkyj 1928a	Kowalski 1959	Geraads et al. 2021	Stefaniak et al. 2023
129	Pszczółki	1	no data	Hermann 1913	Sonntag 1919	Kotański 1956	Kowalski 1959	Geraads et al. 2021	Stefaniak et al. 2023
130	Pyskowice	no data	no data	Borsuk-Białynicka 1973	Woroncowa-Marci-nowska et al. 2013, 2017	Geraads et al. 2021	Stefaniak et al. 2023		
131	Pyskowice-Rzeczyce	no data	no data	Zieliński 1958	Stefaniak et al. 2023				
132	Pyzdry	no data	no data	Geraads et al. 2021					
133	Radłów	1	no data	Stefaniak et al. 2023					
134	Radochowska Cave	no data	no data	Kowalski 1954	Geraads et al. 2021				
135	Raj Cave	70	no data	Kowalski 1972	Majewska 2015	Geraads et al. 2021	Stefaniak et al. 2023		
136	Rataje, Poznań	no data	no data	Lubicz-Niezabi-towski 1926	Kowalski 1959	Stefaniak et al. 2023			
137	River Prosna	7	no data	Lubicz-Niezabi-towski 1926	Kowalski 1959	Kaczmarek 2004	Pawłowska 2015b	Geraads et al. 2021	Stefaniak et al. 2023
138	River Vistula (near Warsaw)	1	no data	Borsuk-Białynicka 1973	Stefaniak et al. 2023				
139	River Wisła	no data	no data	Jakubowski 1971	Borsuk-Białynicka 1973	Geraads et al. 2021			
140	River Wisznia	no data	no data	Polanśkyj 1928b	Kowalski 1959	Geraads et al. 2021	Stefaniak et al. 2023		
141	Rock Shelter in Strze-gowa; Zacisz-na Cave	no data	no data	Stefaniak et al. 2023					
142	Rozniszew	no data	no data	Stefaniak et al. 2023					
143	Rusko	no data	no data	Gürich 1913	Marciszak et al. 2019	Geraads et al. 2021	Stefaniak et al. 2023		
144	Rybaki-Czartoria	no data	no data	Ruprecht 1976	Geraads et al. 2021				
145	Rzeczyce near Pys-kowice	no data	no data	Kulczycki 1955	Kowalski 1959	Borsuk-Białynicka 1973	Marciszak et al. 2019	Geraads et al. 2021	Stefaniak et al. 2023
146	Sandomierz	1	no data	Stefaniak et al. 2023					

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147	Sąspowska Zachodnia Cave	no data	no data	Nadachowski 1988	Geraads et al. 2021	Stefaniak et al. 2023			
148	Shelter above Zegar Cave (Shelter No 388)	no data	no data	Stefaniak et al. 2023					
149	Shelter III (Wilcze I), Sokole Mountain	1	no data	Wojtal 2007	Stefaniak et al. 2009	Geraads et al. 2021	Stefaniak et al. 2023		
150	Shelter V, Złoty Potok	no data	no data	Waga 1853	Ślósarski 1884	Lubicz-Niezabitowski 1913, 1926	Kowalski 1951, 1959	Geraads et al. 2021	
151	Siedliszowice	no data	no data	Pawłowska 2012	Stefaniak et al. 2023				
152	Siemonia	no data	no data	Zieliński 1958	Marciszak et al. 2019	Geraads et al. 2021	Stefaniak et al. 2023		
153	Skarszyn	no data	no data	Römer 1881	Gürich 1885	Pax 1921	Kowalski 1959	Geraads et al. 2021	Stefaniak et al. 2021, 2023
154	Skowarcz	4	no data	Conwentz 1899, 1909	Kumm 1903	Wolff 1905	Staudinger 1908	Hermann 1911, 1913	Sonntag 1919; Schroeder 1930; Kotański 1956; Kowalski 1959; Geraads et al. 2021; Stefaniak et al. 2023
155	Słonne	1	no data	Stefaniak et al. 2023					
156	Sobiecin	1	no data	Stefaniak et al. 2023					
157	Sochaczew	no data	no data	Stefaniak et al. 2023					
158	Spławie	no data	no data	Pawłowska 2017b	Stefaniak et al. 2023				
159	Stajnia Cave	no data	no data	Geraads et al. 2021	Stefaniak et al. 2023				
160	Starogard Gdański	no data	no data	Kumm 1916	Kowalski 1959	Geraads et al. 2021	Stefaniak et al. 2023		
161	Starołęka, Poznań	no data	no data	Maas 1899	Lubicz-Niezabitowski 1926	Kowalski 1959	Pawłowska 2015b	Geraads et al. 2021	Stefaniak et al. 2023
162	Stęszew	2	no data	Kaczmarek 2004					
163	Stradów	1	no data	Stefaniak et al. 2023					
164	Strzegom	no data	no data	Volz 1897	Marciszak et al. 2019	Geraads et al. 2021			
165	Suchanino 1, Gdańsk	no data	no data	Kiesow 1880	Kowalski 1959	Geraads et al. 2021	Stefaniak et al. 2023		
166	Suchanino 2, Gdańsk	1	no data	Schirmacher 1882	Zeise 1903	Hermann 1913	Sonntag 1919	Kowalski 1959	Geraads et al. 2021; Stefaniak et al. 2023
167	Syrynia	1	no data	Wilke 2004	Marciszak et al. 2019	Geraads et al. 2021	Stefaniak et al. 2023		
168	Szczecin	no data	no data	Stuart & Lister 2012	Geraads et al. 2021	Stefaniak et al. 2023			
169	Śrem	1	no data	Lubicz-Niezabitowski 1926	Kowalski 1959	Pawłowska 2015b	Geraads et al. 2021	Stefaniak et al. 2023	
170	Święcko	no data	no data	Kunisch 1883	Gürich 1885	Kowalski 1959	Geraads et al. 2021	Stefaniak et al. 2023	
171	Świt	no data	no data	Maas 1905	Hermann 1913	Sonntag 1919	Geraads et al. 2021		

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172	Targowisko	no data	no data	Jach & Wojtal 2021	Stefaniak et al. 2023				
173	Tatarska Góra	2	no data	Krysiak 1938	Prószyński 1952	Kowalski 1959	Geraads et al. 2021	Stefaniak et al. 2023	
174	Terespol Pomorski	1	no data	Hermann 1913	Sonntag 1919	Kowalski 1959	Geraads et al. 2021	Stefaniak et al. 2023	
175	Tolkmicko	no data	no data	Conwentz 1899	Kowalski 1959	Geraads et al. 2021	Stefaniak et al. 2023		
176	Trzebnica	no data	no data	Römer 1888	Marciszak et al. 2019	Geraads et al. 2021	Stefaniak et al. 2023		
177	Tunel Wielki Cave	no data	no data	Nadachowski 1988	Geraads et al. 2021	Stefaniak et al. 2023			
178	Turek	1	no data	Geraads et al. 2021	Stefaniak et al. 2023				
179	ul. Hallera, Wrocław	2	no data	Wiszniowska et al. 2005	Badura & Wiśniewski 2008	Wiśniewski et al. 2009	Stefaniak et al. 2023		
180	ul. Michalska, Przasnysz	no data	no data	Karaszewski 1980	Stefaniak et al. 2023				
181	ul. Spadzista, Kraków	1	no data	Wojtal 2007	Geraads et al. 2021	Stefaniak et al. 2023			
182	ul. Szelągowska, Stare Miasto, Poznań	5	no data	Lubicz-Niezabitowski 1926, 1929	Kowalski 1959	Kaczmarek 2004	Pawłowska 2015b	Geraads et al. 2021	Stefaniak et al. 2023
183	vicinity of Chełm	no data	no data	Prószyński 1952	Kowalski 1959	Geraads et al. 2021	Stefaniak et al. 2023		
184	vicinity of Elbląg	no data	no data	Jentzsch 1878	Wahnschaffe 1909	Kumm 1913	Sonntag 1919	Geraads et al. 2021	
185	vicinity of Morąg	no data	no data	Jentzsch 1878	Schirmacher 1882	Kowalski 1959	Geraads et al. 2021	Stefaniak et al. 2023	
186	vicinity of Ojców	1	no data	Römer 1879a	Kowalski 1959	Wojtal et al. 2011	Geraads et al. 2021	Stefaniak et al. 2023	
187	vicinity of Poznań	1	no data	Maas 1900	Wahnschaffe 1909	Kowalski 1959	Kaczmarek 2004	Pawłowska 2015b	Geraads et al. 2021
188	W Dziadowej Skale Cave, Skarżyce	2 or more	2 or more	Kowalski 1958b	Chmielewski 1958	Kowalski 1959	Wojtal 2007	Geraads et al. 2021	Stefaniak et al. 2023
189	Wadowice	no data	no data	Stach 1956	Kowalski 1959	Borsuk-Białynicka 1973	Geraads et al. 2021	Stefaniak et al. 2023	
190	Walawa	1	no data	Dzieduszycki 1834	Bayger et al. 1914	Polanśkyj 1927	Kowalski 1959	Geraads et al. 2021	Stefaniak et al. 2023
191	Waplewo Wielkie	1	no data	Conwentz 1895,1899	Hermann 1911, 1913	Sonntag 1919	Kowalski 1959	Geraads et al. 2021	Stefaniak et al. 2023
192	Wielkopolska	no data	no data	Lubicz-Niezabitowski 1926	Pawłowska 2015b				
193	Wiercica Cave	1	no data	Woroncowa-Marcinowska et al. 2013, 2017	Geraads et al. 2021	Stefaniak et al. 2023			
194	Wierzchowska Górna Cave, Wierzchowie	no data	no data	Ossowski 1886, 1887a, 1887b	Kowalski 1951, 1959	Geraads et al. 2021			
195	Wierzenica near Mechowo	1	no data	Lubicz-Niezabitowski 1926	Kowalski 1959	Kaczmarek 2004	Pawłowska 2015b	Geraads et al. 2021	Stefaniak et al. 2023
196	Wilczy Młyn, Poznań	2	no data	Maas 1899	Lubicz-Niezabitowski 1926	Kowalski 1959	Kaczmarek 2004	Pawłowska 2015b	Geraads et al. 2021; Stefaniak et al. 2023

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197	Wilczyce	179	3	Bratlund 2002	Wiśniewski 2008	Nadachowski et al. 2014	Geraads et al. 2021	Stefaniak et al. 2023	
198	Wilda, Poznań	3	no data	Maas 1899	Lubicz-Niezabi-towski 1926	Rakowski 1934	Kowalski 1959	Wasilewski 1960	Kaczmarek 2004; Pawłowska 2015b; Geraads et al. 2021; Stefaniak et al. 2023
199	Wilkowice	no data	no data	Stefaniak et al. 2023					
200	Wola Przemykows-ka	1	no data	Borsuk-Białynicka 1973	Geraads et al. 2021	Stefaniak et al. 2023			
201	Września	no data	no data	Stefaniak et al. 2023					
202	Wylotne shelter	7	3	Nadachowski et al. 2015	Geraads et al. 2021	Stefaniak et al. 2023			
203	Zadębce	1	no data	Prószyński 1952	Kowalski 1959	Stefaniak et al. 2023			
204	Zalesie near Jarocin	3	no data	Behr & Tietze 1911	Hermann 1913	Sonntag 1919	Lubicz-Niezabi-towski 1926	Kowalski 1959	Pawłowska 2015b; Geraads et al. 2021; Stefaniak et al. 2023
205	Zawalona Cave	no data	no data	Aleksandrowicz et al. 1992	Geraads et al. 2021	Stefaniak et al. 2023			
206	Zegar Cave	no data	no data	Kowalski 1951 (1846)	Stefaniak et al. 2009	Geraads et al. 2021	Stefaniak et al. 2023		
207	Zegrze	no data	no data	Lubicz-Niezabi-towski 1926	Kowalski 1959	Karaszewski 1980	Geraads et al. 2021		
208	Zegrze, Poznań	2	no data	Kaczmarek 2004	Geraads et al. 2021				
209	Zgorzelec	no data	no data	Herr 1924	Heinke 1926	Marciszak et al. 2019	Geraads et al. 2021	Stefaniak et al. 2023	
210	Ziębice	2	no data	Gürich 1885, 1893	Kowalski 1959	Marciszak et al. 2019	Geraads et al. 2021	Stefaniak et al. 2023	
211	Zwoleń	190	4	Gautier 2005	Bratlund 2005	Wojtal 2007	Geraads et al. 2021	Stefaniak et al. 2023	
212	Zygmuntówka	no data	no data	Stefaniak et al. 2023					
213	Żabikowo	2	no data	Lubicz-Niezabi-towski 1926	Kowalski 1959	Kaczmarek 2004	Pawłowska 2015b	Geraads et al. 2021	Stefaniak et al. 2023
214	Żerków	1	no data	Kaczmarek 2004					
215	Żmigród	no data	no data	Römer 1873, 1879b	Gürich 1885	Kowalski 1959	Marciszak et al. 2019	Geraads et al. 2021	Stefaniak et al. 2023

3.3. Chronological evidence

Studying the chronology of megafauna is crucial to understanding the patterns of animal occupation of the area and the relationship of their presence with environmental change and the emergence of humans. However, in order to reconstruct these past events, it is necessary to cross-reference the results with the taphonomic events that affected the deposition of various assemblages. This is all the more important because the spatial and temporal distribution of fauna in the Pleistocene in Europe was not uniform, and some species, such as the woolly rhinoceros went extinction.

The remains of woolly rhinoceroses from Poland have not yet been studied with this approach. Dating of woolly rhinoceros remains has been performed by Stuart & Lister (2012) regarding the Szczecin site and Jasna Strzegowska Cave, while Wojtal (2007) has dated remains from Deszczowa Cave. The Krosinko open site is unique, and Pawłowska (2022, 2023) provided further radiocarbon dates for the woolly rhinoceros remains found there, which are embedded in the lithological and stratigraphic sequence. This is important in view of the unclear stratigraphic relations at other sites, including those from caves (or perhaps especially relating to those from caves). Moreover, the radiocarbon dates of the woolly rhinoceros from Krosinko are the oldest known from Poland (Table 2). Overall however, few radiocarbon dates are available at present — a total of n = 34 from 24 sites (Table 2). When dates are excluded due to being out of range and errors (Table 2), this is reduced to 24 radiocarbon dates from 17 sites. This results in the fact that there is for the time being no basis on which to infer the chronology of the woolly rhinoceros in Poland. The published dates as they are now would suggest that the remains of the woolly rhinoceros come from the range 47.3–19.5 cal. ka BP, though this does not allow use to assess the nature of the colonization of Poland by the woolly rhinoceros in the Pleistocene (Table 2). According to Marciszak et al. (2024), the youngest woolly rhinos from Poland comes from Skarszyn site, dated ca. 16.5 ka BP.

A detailed chronology of *C. antiquitatis* in Europe was reconstructed by Stuart & Lister (2012), with the conclusion that this species was widespread across the continent, though its range apparently contracted from ca 35 cal. ka BP. These authors' stratigraphic gap for 40–38 ka BP has recently been verified (Pawłowska, 2022, 2023) by revealing the presence of woolly rhinoceros at this time (38 ka BP) in Poland, east of Krosinko, as indicated by the taphonomic data of the assemblage from this site (Pawłowska, 2023).

3.4. Genetic and pathology evidences

The maintenance of a healthy population depends on the preservation of as much genetic diversity as possible, as this affects the survival of the young, general resistance to disease, and the ability to adapt to altered conditions (Dąbrowski, 2006).

The usefulness of ancient DNA in inferring megafauna population sizes and diversity has been shown by many authors, such as Shapiro et al. (2004) and Campos et al. (2010), who drew conclusions regarding steppe bison and muskoxen.

Palaeopopulation results for woolly rhinoceroses in Poland are lacking for sufficiently large samples to allow estimation of population size and condition. Neither have pathological studies of woolly rhinoceros remains been carried out in a systematic or screening manner, which prevents inferences from being drawn concerning the condition of individuals in the Polish palaeopopulation.

Genetic results to date from Eastern Europe and Asia suggest that the woolly rhinoceros' population there can be considered to have been healthy, based on the lack of evidence of any decline in genetic diversity in the fossil material that has been studied from 81 sites in Germany (n = 2), the North Sea (n = 6), Russia (n = 69), and China (n = 4) (Lorenzen et al., 2011).

3.5. Taphonomic evidence

Taphonomy deals with the transition of animal remains from the biosphere to the lithosphere (Efremov, 1940) and involves all processes that act on organic remains, from the death of the organism through fossilization (Behrensmeyer & Hill, 1980). These processes affect the degree and quality of preservation of animal remains. The use of taphonomic analysis in studies of Pleistocene faunal material provides an opportunity to assess the factors (including cultural factors) responsible for the modifications, reworking, and accumulation of material at a given site (Pawłowska, 2010, 2023).

Although the general suitability of taphonomic analysis for palaeozoological research of Polish assemblages has already been shown (Pawłowska, 2010), it is relatively rarely employed in these studies. There are several reasons for this: (1) the poor preservation of the material may make it difficult to carry out taphonomic studies or to recognize

Table 2. List of previous results of radiocarbon dating of woolly rhinoceros remains. Data from: Wojtal (2007), Pawłowska (2012, 2022), Stuart & Lister (2012), Schild (2014), Marciszak et al. (2019), and modified data from Stefaniak et al. (2023). The symbols … and – mean that the date may extend out of range; n/a = not applicable.

	Site name	BP	Calibrated from	Calibrated to	Calibrated median	References	Comments
5	Krosinko	46500 ± 2600	…	46003	-	Pawłowska 2022	excluded; date may extend out of range
6	Nida River near Czarkowy	n/a	n/a	n/a	n/a	Stefaniak et al. 2023	excluded; authors given various data for one dating (13810 ± 70; 13810 ± 700BP) (16750 [18741–14844] cal BP; 16765 [17006–16521] cal BP)
20	Radłów	>45000	n/a	n/a	n/a	Stefaniak et al. 2023	excluded; authors given various data for one dating (n/a for cal BP) (47333 [47984–46795] cal BP)
22	Sochaczew	>49000	…	50663	-	Stefaniak et al. 2023	excluded; date may extend out of range
21	Sąspowska Zachodnia Cave	49000 ± 400	…	50511	-	Stefaniak et al. 2023	excluded; date may extend out of range
17	Wadowice	n/a	n/a	n/a	n/a	Stefaniak et al. 2023	excluded; authors given various data for one dating (16500 ± 100 BP; 16650 ± 100 BP) (19923 [20200–19595] cal BP; 20126 [20412–19867] cal BP)
23	Września	47000 ± 4000	…	45456	-	Stefaniak et al. 2023	excluded; date may extend out of range
24	Zawalona Cave	49000 ± 4000	…	46814	-	Stefaniak et al. 2023	excluded; date may extend out of range
1	Konin	n/a	n/a	n/a	n/a	Stefaniak et al. 2023	excluded; authors given various data for one dating (44000 ± 1400 BP; 44000 ± 140 BP) (46771 [50711–44344] cal BP; 46269 [46835–45838] cal BP)
19	Wilczyce	11400 ± 135	13576	13088	13332	Schild 2014	excluded according to the Stefaniak et al. 2023
11	Skarszyn	13444 ± 226	16949	15601	16275	Marciszak et al. 2019	excluded; the author changed the date to 16,460 ± 90 BP, 20,126-19,583 cal. BP, Poz-82384) in his latest work (Marciszak et al., 2024).
4	Jasna Strzegowska Cave	16140 ± 90	19805	19180	19493	Stuart & Lister 2012	
7	Nietoperzowa Cave	16780 ± 80	20493	20065	20279	Stefaniak et al. 2023	
4	Jasna Strzegowska Cave	17880 ± 100	22027	21406	21717	Stuart & Lister 2012	
3	Deszczowa Cave	20720 ± 150	25344	24370	24857	Stefaniak et al. 2023	
3	Deszczowa Cave	20800 ± 150	25562	24636	25099	Wojtal 2007	
8	Parchatka near Puławy	21300 ± 130	25887	25292	25590	Stefaniak et al. 2023	
18	Zygmuntówka Quarry near Chęciny	23380 ± 200	27844	27273	27559	Stefaniak et al. 2023	
12	Słonne	24420 ± 170	29107	28149	28628	Stefaniak et al. 2023	
3	Deszczowa Cave	24880 ± 250	29850	28675	29263	Stefaniak et al. 2023	
16	Szczecin	28450 ± 250	33448	31828	32638	Stuart & Lister 2012	
10	Sandomierz	30060 ± 360	35297	33931	34614	Stefaniak et al. 2023	
4	Jasna Strzegowska Cave	29950 ± 220	34849	33996	34849	Cyrek et al. 2016	
3	Deszczowa Cave	31000 ± 400	36174	34610	35392	Lorenc 2013	

	Site name	BP	Calibrated from	Calibrated to	Calibrated median	References	Comments
3	Deszczowa Cave	31400 ± 400	36550	34840	35695	Wojtal 2007	
9	Perspektywiczna Cave	32100 ± 400	37465	35574	36520	Stefaniak et al. 2023	
9	Perspektywiczna Cave	33900 ± 600	40360	37158	38759	Stefaniak et al. 2023	
15	Stradów	38000 ± 1000	43890	41114	42502	Stefaniak et al. 2023	
5	Krosinko	38500 ± 2000	44074	41621	42848	Pawłowska 2022	
13	Sobiecin	39000 ± 1000	44444	41934	43189	Stefaniak et al. 2023	
2	Biśnik Cave	42200 ± 1400	48298	42882	45590	Stefaniak et al. 2023	
9	Perspektywiczna Cave	42000 ± 1500	48535	42715	45625	Stefaniak et al. 2023	
14	Spławie near Pyzdry	42000 ± 2000	51485	42427	46956	Stefaniak et al. 2023	date may extend out of range
21	Sąspowska Zachodnia Cave	>45000	47984	46795	47390	Stefaniak et al. 2023	
24	Zawalona Cave	>45000	47984	46795	47390	Stefaniak et al. 2023	
9	Perspektywiczna Cave	44000 ± 2000	54742	43925	49334	Stefaniak et al. 2023	date may extend out of range
5	Krosinko	48400 ± 32	54759	50055	52407	Pawłowska 2022	date may extend out of range

marks; (2) taphonomy requires knowledge of the scope of the marks and an ability to recognise them; and (3) taphonomy requires high-resolution methods. Moreover, the limitations seen to date on the use of taphonomic analysis in the study of Polish Pleistocene faunal material from caves shows that it is necessary to undertake such studies on materials from a fluvial context — which are the most numerous materials represented in Polish Pleistocene faunal assemblages — and from eolian contexts.

To date, in studies of Polish collections, taphonomic studies of fossil rhinoceroses have been carried out in the fluvial context for both the forest rhino (*Stephanorhinus kirchbergensis*; known from 14 sites in Poland) (Geraads et al., 2021; Pawłowska, 2017 unpublished results;) and the woolly rhino (*Coelodonta antiquitatis*) (Pawłowska, 2023). In the case of the forest rhino (*Stephanorhinus kirchbergensis*) from Gorzów Wielkopolski, the taphonomic study did not reveal marks resulting from hominid activity. Instead, these studies made it possible to discover and study by Kamilla Pawłowska pathological changes, which were located mainly in the joints (Pawłowska, 2017 unpublished results). In the case of the woolly rhinoceros, taphonomic analysis revealed a secondary context for its remains, in the form of the effects of a braided river as depositional factor, and showed, for the first time in a Polish study, the effect of temperature on rhino bones, in the form of burn marks (Pawłowska, 2023).

For other assemblages from Poland, evidence of processing in the form of potential cultural marks needs to be verified using modern techniques. Cut marks on a woolly rhinoceros mandible were described by Bratlund (2005) as evidence of defleshing of the head in order to extract the muscle. Other marks identified as cut marks on animal bones from this site were however deemed not to be evidence of human activity, and are instead regarded as resulting from natural causes, such as trampling. They are thus not cultural marks (Gautier, 2005).

Knowledge of cultural marks from the Pleistocene is very relevant to identifying the activity associated with the type of marks, and thus in understanding whether access to carcasses was early or late, the stages of the processing of carcasses, and the manufacturing process. These topics have been treated by various authors, who have formulated a palaeogeography of butchering for Pleistocene (Pawłowska, 2017a) and subsistence strategy (Bunn, 1986; Alhaique et al., 2004; Rivals et al., 2006; Domínguez-Rodrigo et al., 2015; Van Kolfschoten et al., 2015; Espigares et al., 2019).

Social environment can also be studied by other marks induced by hominids (Pawłowska, 2020), such as worked pieces. However, there is a little data in this respect from Poland (Pawłowska, 2022).

Our summary of studies of Polish woolly rhinoceroses has also shown that none of the studies conducted to date have included taphonomic analysis on a countrywide scale in order to identify factors of faunal material deposition. Individual works have drawn attention to marks of biting by predators, the influence of water, and other effects (Appendix 1).

3.6. Art

There is no evidence of Palaeolithic art or worked objects involving the woolly rhinoceros from Poland.

3.7. Summary of state of art and perspectives

The woolly rhinoceros (*Coelodonta antiquitatis* Blumenbach 1799) and the woolly mammoth are the main representatives of the Pleistocene megafauna. To date, however, the majority of scholarly attention has been paid to the woolly mammoth, the remains of which have received morphometric, radiocarbon dating, DNA, and isotope analysis. There is a surprising dearth of research on the woolly rhinoceros given the relative abundance of its remains in Poland (Kowalski, 1959; Geraads et al., 2021). We thus have no knowledge of general demographic data, phylogenetic relationships, or other details of the presence of woolly rhinoceroses in Poland. For example, we do not know if the woolly rhinoceros' presence was permanent, temporary, or periodic. We also lack knowledge in relation to other aspects — such as, for example, the condition of the animals, which would assist in reconstructing the life and death of individuals. The archive data remains scattered, but research and metadata collection should make it possible to create a comprehensive database and to draw useful conclusions.

To address this gap, a multifaceted study, the WOOLRHINOPOLI Project, was proposed in 2020, and since 2022 has been implemented step by step in line with the issues to be examined and the work schedules. The WOOLRHINOPOLI Project brings together eleven researchers from Europe with the aim of unravelling the chronological, geographical, and taphonomic complexities of the occurrence of the woolly rhinoceros in the Pleistocene contexts of Poland (WOOLRHINOPOLI) and Europe. Since reliable conclusions can only be drawn on the basis of the metadata, and not from studies that deal with individual samples, reaching these milestones on the European scale will involve examining the remains of woolly rhinoceroses from Poland, the North Sea, and selected European countries (Germany, the Czech Republic, the Netherlands, the United Kingdom, France, Spain, Italy, Romania, Beringia, and Moldova).

4. Conclusions

The woolly rhinoceros, an extinct representative of the megafauna, has been the subject of Polish research since the nineteenth century. Our focus has been on its remains found in various archive locations in Poland, summarizing our knowledge of this taxon as a starting point for further multifaceted research that will be implemented. The conclusions of previous research are as follows:

The lack of verification of the taxonomic and anatomical designations of woolly rhinoceros remains since the 1960s, as well as the lack of large-scale field research, means that the quantity of woolly rhinoceros remains, the number of individuals, and consequently our state of knowledge of sites with woolly rhinoceros remains in Poland are unknown.

As a consequence of the first point, details of the distribution of the woolly rhinoceros in Poland, as well as in Central and Western Europe, are currently unknown.

The limited number of currently available published radiocarbon dates for the remains of the woolly rhinoceros does not allow for the reconstruction of its chronology in Poland during the Pleistocene and Holocene. Also, in light of the development of research methods, the radiocarbon dates alone are insufficient to provide a scenario of events of the occupation of Poland by the woolly rhinoceros.

The analysis of taphonomical characteristics from the biostratinomical and diagenetic stages is a necessary approach to studies of Pleistocene mammals, and such studies should be deepened and more widely applied to woolly rhinoceros remains.

Several issues regarding hominid–rhinoceros relationships have been addressed for individual sites in Polish studies (Pawłowska, 2022, 2023); this also sets the direction for further in-depth and synthetic analyses.

There is no known figural depictions or paintings showing depictions of the woolly rhinoceros from Poland.

The state of research on woolly rhinoceros remains is, unfortunately, unsatisfactory, but this allows us to set the direction for the further research currently being carried out under the auspices of the WOOLRHINOPOLI Project.

The main conclusion is thus that the woolly rhinoceros, as an extinct species of rhino and the main representative of the *Mammuthus–Coelodonta* Faunal Complex (Kahlke, 2014), deserves more attention and systematic research in Polish research that aims to reveal its Quaternary history.

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Appendices

Appendix 1 and 2 are available on http://www.geologos.com.pl/

Appendix 1. List of publications on the study of fossil rhinoceros remains from Poland discusses here, as of February 2024.

Appendix 2. A list of changes made to the scope of the recent synthesis (Stefaniak et al., 2023) of fossil rhinoceros remains, including woolly rhinoceros, which were necessary for the compilation presented here.

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