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Chronology and distribution of Central and Eastern European Pleistocene rhinoceroses (Perissodactyla, Rhinocerotidae) – A review

Krzysztof Stefaniak [a], Oleksandr Kovalchuk [a,b,*], Urszula Ratajczak-Skrzatek [a], Aleksandra Kropczyk [a], Paweł Mackiewicz [c], Grzegorz Kłys [d], Magdalena Krajcarz [e], Maciej T. Krajcarz [f], Adam Nadachowski [g], Grzegorz Lipecki [g], Karol Karbowski [a], Bogdan Ridush [h], Martin Sabol [i], Tomasz Płonka [j]

[a] Department of Palaeozoology, Faculty of Biological Sciences, University of Wrocław, Wrocław, Poland
[b] Department of Palaeontology, National Museum of Natural History, National Academy of Sciences of Ukraine, Kyiv, Ukraine
[c] Department of Bioinformatics and Genomics, Faculty of Biotechnology, University of Wrocław, Wrocław, Poland
[d] Institute of Biology, Opole University, Opole, Poland
[e] Institute of Archaeology, Nicolaus Copernicus University in Toruń, Toruń, Poland
[f] Institute of Geological Sciences, Polish Academy of Sciences, Research Centre in Warsaw, Warszawa, Poland
[g] Institute of Systematics and Evolution of Animals, Polish Academy of Science, Kraków, Poland
[h] Department of Physical Geography, Geomorphology and Palaeogeography, Yuriy Fedkovych Chernivtsi National University, Chernivtsi, Ukraine
[i] Department of Geology and Paleontology, Faculty of Natural Sciences, Comenius University in Bratislava, Bratislava, Slovakia
[j] Department of Stone Age Archaeology, Institute of Archaeology, Faculty of Historical and Pedagogical Sciences, University of Wrocław, Wrocław, Poland

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ABSTRACT

The family Rhinocerotidae is a key component of the Cenozoic European fauna. It reached its peak diversity during Miocene and began to decline in the Pliocene; the last representatives became extinct in Europe during the Quaternary. The present state-of-the-art review takes stock of the knowledge accumulated on Central and Eastern European Pleistocene rhinos to date. Eight species were present in Central and Eastern Europe in the Quaternary; five belonged to the genus *Stephanorhinus* (*S. etruscus*, *S. jeanvireti*, S. *hundsheimensis*, *S. hemitoechus*, and *S. kirchbergensis*), one was the woolly rhino *Coelodonta antiquitatis*, and two species were members of the genus *Elasmotherium* (*E. peii* and *E. caucasicum*). This review also offered the opportunity to critically reconsider some aspects of the systematics and stratigraphic location of the finds. *Coelodonta antiquitatis* is shown to have still been present as late as the Interplenivistulian and the Last Glacial Maximum; radiocarbon dating of its latest remains provided the timing of the final disappearance of the woolly rhino from the studied region. The Late Pleistocene distribution of *Coelodonta antiquitatis* in Central and Eastern Europe was found to largely overlap that of the woolly mammoth.

1. Introduction

Rhinocerotidae is one of the most important families of large Cenozoic mammals. It evolved explosively during the Eocene and Oligocene peaking at the turn of the Miocene and Pliocene, with a Palearctic and Nearctic distribution. Like many other Perissodactyla, it started to decline from the Vallesian age. During the Quaternary, rhinos were still very widely distributed in the Old World (Guérin, 1980; Prothero et al., 1986; Antoine, 2002; Geraads, 2010; Pandolfi, 2018; Pandolfi et al., 2021a). Rhinocerotinae and Elasmotheriinae were the two subfamilies present in Europe during the Pleistocene: the former includes two genera, namely *Stephanorhinus* Kretzoi, 1938 and *Coelodonta* Bronn, 1831, and the latter only *Elasmotherium* J. Fischer, 1808. Despite the progress in research techniques, many issues of rhinocerotid taxonomy remain controversial. One prominent example is the genus *Stephanorhinus*. The genus first occurred in the fossil record of the European Pliocene (Guérin, 1980; Lacombat, 2007). By approximately mid-Pliocene times, *Stephanorhinus* extended across Europe, coming in successive migratory waves from Asia, although this hypothesis should be further tested since other authors suggested a local evolution of some

* Corresponding author. Department of Palaeozoology, Faculty of Biological Sciences, University of Wrocław, Wrocław, Poland.
E-mail address: biologiest@ukr.net (O. Kovalchuk).

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species (Fortelius et al., 1993; Cerdeño, 1998; Cappellini et al., 2019). During the latest Middle Pleistocene through early Late Pleistocene, some *Stephanorhinus* species coexisted with the woolly rhinoceros (Guérin, 1980).

For this work, because the status of the genus *Stephanorhinus* is still not clarified, we adopted the simplified approach assuming that the following species occurred in Europe (in chronological order): *Stephanorhinus etruscus* (Falconer, 1868) – Pliocene (3.5–3.0 Ma) to Early–Middle Pleistocene transition; *Stephanorhinus jeanvireti* (Guérin, 1980) – Late Pliocene to Early Pleistocene; *Stephanorhinus hundsheimensis* (Toula, 1902) – Early Pleistocene (1.4 (1.3) Ma to 0.6 Ma); *Stephanorhinus hemitoechus* (Falconer, 1859) – Middle Pleistocene (0.5 Ma) to late Late Pleistocene (35 ka); *Stephanorhinus kirchbergensis* (Jäger, 1839) – Middle Pleistocene (0.7–0.6 Ma) to late Late Pleistocene (ca. 40 ka) (Guérin, 1980; Lacombat, 2003, 2005, 2006, 2007; Pandolfi et al., 2013, 2016a, b; Kirillova et al., 2017; Pandolfi and Erten, 2017; Pandolfi and Rook, 2017; Pandolfi et al., 2017a, b, 2019, 2020, 2021a, b, 2022 and references therein).

The systematics and phylogenetic relationships within this group are unresolved and still debated. Some researchers suggest that the genus *Stephanorhinus* is paraphyletic. Most likely, there was a phyletic lineage *Stephanorhinus etruscus* – *S. hundsheimensis* – *S. hemitoechus* while *S. kirchbergensis* arose independently. The status, origin, and relationships of *Stephanorhinus jeanvireti* are still under discussion. Pandolfi et al. (2019) suggested retaining its species name, which is why we continue to use it herein (Azzaroli, 1962; Loose, 1975; Guérin, 1980; Cerdeño, 1990, 1992, 1993, 1995; Fortelius et al., 1993; Mazza et al., 1993; Kahlke, 1999; Reissig, 1999; Lacombat, 2003, 2005, 2006; Billia and Petronio, 2009; Made, 2010; Billia, 2011; Pandolfi and Petronio, 2011; Pandolfi, 2013; Billia and Zervanová, 2014; Pandolfi and Tagliacozzo, 2015; Ballatore and Breda, 2016, 2019; Pandolfi et al., 2016a, b, 2017a, b, 2019, 2020, 2021a, b, 2022; Kirillova et al., 2017; Pandolfi and Rook, 2017; Giaourtsakis, 2021).

Representatives of the genus *Stephanorhinus* were either medium-sized, gracile, warm forest-steppe dwellers (e.g., *S. etruscus*), or more robust representatives of cooler contexts (e.g., *S. hundsheimensis*). The steppe rhinoceros, *Stephanorhinus hemitoechus*, lived in temperate, cool, and dry steppes; its diet consisted mostly of grass. The largest of them all was *Stephanorhinus kirchbergensis*, a forest and forest-steppe dweller which fed on leaves, shoots, as well as low-growing plants (Guérin, 1980; Fortelius, 1982; Grübe, 2003; Kaiser and Kahlke, 2005; Made and Grübe, 2010; Kahlke and Kaiser, 2011; Van Asperen and Kahlke, 2015; Kirillova et al., 2017; Van Geel et al., 2019; Burkanova et al., 2020; Stefaniak et al., 2021b).

The genus *Coelodonta* first appeared in the Tibetan Plateau with *C. thibetana* Deng et al., 2011 at the beginning of the Late Pliocene (Deng et al., 2011). The woolly rhinoceros *Coelodonta antiquitatis* (Blumenbach, 1799) originated in China almost one million years ago. The species first appeared in Europe during the Middle Pleistocene, ca. 600–400 ka (the oldest fossil records are from Germany, France, and Greece), and it likely migrated back to Europe during cold periods, becoming a common associate of the woolly mammoth ca. 200 ka.

The oldest European woolly rhino remains are from the MIS (Marine Isotope Stage) 12 (ca. 450 ka) locality of Bad Frankenhausen, Germany (Kahlke and Lacombat, 2008; Kahlke, 2014; Uzunidis et al., 2022). It was a large rhinoceros, adapted to the cold and dry climate of the mammoth steppe. It had hypsodont teeth, a thick coat of long hair, like the woolly mammoth, and nasal septum that split the nasal cavity into two chambers for warming inhaled air (similarly to other members of the *Mammuthus-Coelodonta* assemblage). The woolly rhino distributed over a huge area from the Iberian Peninsula to Siberia and from Scotland as far south as Greece; however, its numbers and range began to decrease about 35 ka.

The species became extinct in Europe (starting from the western part of the continent) about 14 ka (Fortelius, 1983; Kahlke, 1999, 2014; Stuart and Lister, 2007, 2012; Kahlke and Lacombat, 2008; Boeskorov et al., 2009, 2011a, b; Kuzmin, 2010; Tiunov and Kirillova, 2010; Deng et al., 2011; Kahlke et al., 2011; Boeskorov, 2012; Lister and Stuart, 2013; Markova et al., 2013; Nadachowski et al., 2015b; Shvyreva, 2015; Stuart, 2015; Khubanova et al., 2016; Pandolfi, 2018; Kosintsev et al., 2019; Van Geel et al., 2019; Lord et al., 2020; Puzachenko et al., 2021a, b; Rey-Iglesia et al., 2021; Stefaniak et al., 2021b; Uzunidis et al., 2022).

Elasmotheriinae had a very long evolutionary history. The group bloomed in the Miocene and demised in the Plio-Pleistocene. Four species of the genus *Elasmotherium* occurred in Europe during the Quaternary: *E. caucasicum* Borissiak, 1914 (Early Pleistocene of southern Ukraine), *E. chaprovicum* Shvyreva, 2004 (Early Pleistocene of Moldova, northeastern Azov region), *E. peii* Chow, 1958 (Early Pleistocene of Moldova and southern Ukraine), and *E. sibiricum* Fischer, 1808 (Middle–Late Pleistocene of the lower Volga region). *Elasmotherium* became extinct at the end of the Late Pleistocene (Heissig, 1989; Antoine, 2002). The last representatives reached 2 m at the withers and 5 m head-to-tail length. These rhinos bore a huge, single horn on the forehead coupled with ever-growing hypsodont cheek teeth with typically wrinkled enamel. They were adapted to living in dry steppes and to feeding on tough, low-growing vegetation, which made them an ecological equivalent to the woolly rhinos. Elasmotheriinae appear to have become extinct around 39 ka, before the LGM (Shvyreva, 1995, 2015, 2016; Antoine, 2002; Zhegallo et al., 2005; Kosintsev et al., 2019).

Extinct rhinos have been the subject of a wealth of research, and yet those from the area of Central and Eastern Europe, including Poland, Czech Republic, Slovakia, and Ukraine, have received very little attention so far. Lister and Stuart (2013) provided only four dates for Polish rhino remains (Jasna Strzegowska and Perspektywiczna Caves), two dates are available for those from the Czech Republic (Předmostí), only a few for those from Ukraine (including that for the renown Starunia woolly rhino), while not even one from Slovakia has been dated up until now. The area of Central and Eastern Europe is a 'blank spot' also in synthetic publications (e.g., Puzachenko et al., 2021a; b, 2022). Nadachowski et al. (2015b) summarized the current state of knowledge about the occurrence and biochronology of large mammals, mainly those hunted by Palaeolithic people in Poland and Ukraine, clearly demonstrating the scantiness of the data.

The availability of new data prompted the publication of the present state of research on extinct rhinos from modern Poland, Czech Republic, Slovakia, and Ukraine, together with a comprehensive list of all known sites and rhino finds, their absolute datings, and their repositories. This synthesis will hopefully provide a new impetus to comprehensive studies on this important group of mammals, as well as a source of data for other researchers. Another aim of the present study is to assess the potential of rhinos for palaeoecological reconstructions and biochronological studies of Quaternary fauna in this region of Europe, which functioned either as an important migration corridor, or as a refugium (Sommer and Nadachowski, 2006).

2. Historical background

Extinct rhino finds were first reported from modern Poland by German (in Pomerania, Greater Poland and Silesia) and Polish authors (in central, eastern, and southern Poland and westernmost part of present-day Ukraine). A first summary paper was published in 1884 by A. Ślósarski. A woolly rhino skull and mandible were found in 1815 near Kamieńczyk (Ślósarski, 1884). Remains of *Stephanorhinus kirchbergensis* were first found in Szczęśliwice near Warsaw. German researchers focused on the areas of Silesia, Wielkopolska and Pomerania (Otto, 1837; Römer, 1867, 1873, 1879a, b, 1883, 1888; Kiesow, 1880; Schirmacher, 1882; Kunisch, 1883; Gürich, 1885, 1893, 1905, 1913; Wahnschaffe, 1914; Pax, 1921; Schroeder, 1930; Zeuner, 1932; Zotz, 1937) and published individual finds as well as lists of remains of *Coelodonta antiquitatis* and representatives of the genus *Stephanorhinus*. No monographs were published at the time.

The most significant and spectacular discovery after the dawn of the

20th century were remains of four woolly rhinos in Starunia (present-day Ukraine), with soft parts still preserved, including the complete carcass of a 3-year-old female (Bayger et al., 1914; Lubicz-Niezabitowski, 1911a, b; Lubicz-Niezabitowski et al., 1914; Nowak et al., 1930; Stach, 1930; Zeuner, 1934; Stefaniak et al., 2021b). The remains were found associated with those of the woolly mammoth. This discovery has sparked many studies until now, which have helped to gain many insights into the anatomical details of the woolly rhino, as well as information on the accompanying fauna and flora (Kubiak, 1971, 2003a, b, 2008; Borsuk-Białynicka, 1973; Granoszewski, 2002; Pawłowski, 2003; Alexandrowicz, 2004; Kubiak and Drygant, 2005; Kotarba, 2005, 2009; Kotarba and Stachowicz-Rybka, 2008; Kotarba et al., 2008). Lubicz--Niezabitowski (1926) described the remains of *Coelodonta antiquitatis* from Wielkopolska.

New specimens of rhinoceroses have been found during excavations conducted in caves and open-air localities from the mid-nineteenth century onwards. The first list of all finds and localities yielding rhino remains of the genera *Coelodonta* and *Stephanorhinus* (together with other Pleistocene mammals) from Poland was provided by Kowalski (1951, 1954, 1959).

New research, in particular in cave sites, provided remains of *Coelodonta antiquitatis* from the area of Kraków-Wieluń Jura, the foreland of the Tatra Mountains and the Holy Cross Mountains (e.g., Wojtal, 2007; Stefaniak et al., 2009a, b). Nadachowski et al. (2015a, b) provided detailed information on Palaeolithic sites with woolly rhino remains.

In 1970, a complete skull of *Stephanorhinus kirchbergensis* was found in the Vistula River near Siekierki (Warsaw) and described by Borsuk--Białynicka and Jakubowski (1972). A year later, Borsuk-Białynicka (1973) published a detailed morphometric study on Pleistocene woolly rhino remains, mainly from Poland. Then, rhinos eclipsed from the Polish research agenda. In 2016, K. Stefaniak and colleagues discovered an almost complete skeleton of *Stephanorhinus kirchbergensis* (including the skull, mandible, axial skeleton with forelimbs and right hind limb) in Gorzów Wielkopolski (Badura et al., 2017; Sobczyk et al., 2020; Alexandrowicz et al., 2021; Stefaniak et al., 2021b, c; Mirosław-Grabowska et al., 2022), which revived interest on extinct rhinos. The present study is a further contribution to this field.

Research on rhino fossils in the Czech Republic began at the end of the 19th century. Woldřich (1882, 1886, 1893) and Procházka (1890) made several publications on Czech woolly rhino remains. Želízko (1900) described a well-preserved skeleton of *Coelodonta antiquitatis* from Blato near Chrudim. Kafka (1903) published a paper on ungulates including rhinos from modern Czech Republic. Other authors who continued this topic were Zázvorka (1953), Fejfar (1957, 1961, 1964a, b) and Mostecký (1961, 1966). Musil (1955, 1957, 1958, 1959, 1960, 1962, 1965a, b, 1970, 1988, 1994, 1996, 1997, 2002, 2010) has authored numerous publications on Quaternary rhino fossil remains from several localities, mainly caves, in Moravia. Kahlke (1972) described rhino remains from the Middle Pleistocene of Stránská Skála. Picha (2013) prepared the first monograph based on the finds of rhino remains from the Czech Republic.

Schmidt (1969a, b) was the first to publish an overview of extinct species of rhinoceroses from Slovakia, although J. Skutil mentioned rhino remains from Palaeolithic sites in Slovakia and Ruthenia already in 1938. However, Schmidt's review was addressed to a wider scientific community and was published in two parts in the journal "Svet vedy" (The World of Science), with the first part devoted to thermophilic species and the second part – to cold-loving ones.

Zervanová (2014) prepared the first synopsis/synthesis of the fossil remains of rhinos from the Slovak territory in her dissertation. Individual finds were reported in special publications or in lists of finds (Zervanová, 2014 and references therein).

Palaeontological research in Ukraine has begun in the 18th century and continued in the 19th century (Pidoplichko, 1954). These studies were not systematic and were based mostly on accidental finds. Fossil remains of rhinos were historically found associated with mineral deposits associated with specimens of the most common species (especially woolly mammoth, woolly rhino and other representatives of the *Mammuthus–Coelodonta* faunal assemblage). Summary information about these finds was published in chronical form in local periodicals of the time. In the first half of the 20th century, especially in the 1920s–1950s, local museum collections were enriched with substantial numbers of fossils from Ukraine (Kovalchuk, 2012). Information on numerous localities yielding Quaternary rhino fossils were summarized by Pidoplichko (1938, 1956) in his book "Materials to the study of past faunas of the URSR".

A large amount of Pleistocene vertebrate fossils (including those of rhinos) was found during construction of hydroelectric power plants on the Dnieper River in the 1960–1970s. Svistun (1959, 1960, 1966), Svistun and Bachinsky (1962) and Svistun and Lomayev (1967) described finds of woolly rhino from these localities and discussed their age and taphonomy. Several publications focused on remains of Quaternary large mammals from archaeological sites of Ukraine (Tatarinov, 1959, 1961, 1977; Ivanova, 1969, 1982; Alekseeva, 1966, 1977, 1987; Vremir et al., 2000; Ridush, 2002, 2022; Stefaniak et al., 2022). Faunal lists include rhinos (e.g., *Stephanorhinus* and *Coelodonta*); a few papers provide brief descriptions of them.

Kovalchuk (2011) published a summary of what was known at the time of Quaternary mammal remains deposited in museums of the Sumy region (northeastern Ukraine); the lists include woolly rhino. Representatives of the genus *Elasmotherium* from the Pleistocene of Eurasia (including those from Ukraine) have been revised by Shvyreva (2016).

3. Material and methods

This review presents current state of knowledge of Quaternary rhinos from modern Czech Republic, Slovakia, Poland, and Ukraine. This article is supplemented with database representing each country and taxon for a clearer overview of the present situation (Appendix 1, 2). 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. This is especially the case of sites in Poland, formerly in Germany until the end of WWII (Silesia, Pomerania), and those in Ukraine. Stratigraphic ages and radiocarbon dates, with indication of the laboratory number of the analysed sample, are also given when available (Appendix 1).

Complete repository information is given for the existing specimens. The taxonomy of rhinos was not reviewed herein, except in the case of *Stephanorhinus etruscus* and *S. hemitoechus*. Middle Pleistocene specimens, which have erroneously been assigned from stratigraphic viewpoints to *Stephanorhinus etruscus*, were re-classified as *S. hemitoechus*. 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). Compiled $\delta^{18}O$ curves were used for four specific time slices: 0–9750 yrs. BP from North Greenland Ice Core Project 1 (NGRIP1) (Rasmussen et al., 2014; Seierstad et al., 2014), 9770–10,630 yrs. BP and 56,070–122,230 yrs. BP from North Greenland Ice Core Project2 (NGRIP2) (Rasmussen et al., 2014; Seierstad et al., 2014), 10,650–56,050 yrs. BP from Combined Cariaco and Greenland Ice Core Chronology 2005) (GICC05) (Cooper et al., 2015) and 123,000–5,320,000 yrs. BP from the benthic curve by Lisiecki and Raymo (2005). Radiocarbon dates were calibrated to years before present (BP) in OxCal v4.4 (Bronk Ramsey and Lee, 2013) using IntCal20

atmospheric curve (Reimer et al., 2020).

4. Results

4.1. Early Pleistocene

The fossil record of Central and Eastern European rhinos during the latest Pliocene–Early Pleistocene is represented by several species of two genera – *Elasmotherium* and *Stephanorhinus*.

The earliest Early Pleistocene species of the genus *Elasmotherium* in Ukraine is *E. peii*. Its presence was recorded in materials from four localities (Nikopol, Osypenko, Zhevakhova Gora, and Tokmak) located in the south of the country (Fig. 1) (Pidoplichko, 1956; Svistun, 1973; Shvyreva, 1995, 2015, 2016; Logvynenko, 2008). A well-preserved, 820 mm long skull was found in the gravel quarry near Tokmachka River, in Tokmak, Zaporizhia region (Fig. 1). The specimen is now in exhibition at the Palaeontological Museum of the National Museum of Natural History of the National Academy of Sciences of Ukraine. Remains of *Elasmotherium peii* from the other sites include a mandible, isolated tooth, a scapula, and a single rib.

Remains of *Elasmotherium caucasicum* are known from three Early Pleistocene sites (Fig. 1), located along the Sea of Azov coast (Shvyreva, 1995, 2015, 2016; Logvynenko, 2008). The specimens include a juvenile left fragmental mandible from Berdiansk, a cervical vertebra from Mariupol, and a scapula fragment from Nogaisk (MIS 35–25, Calabrian: Appendix 1, 2).

Some other remains assigned to the genus *Elasmotherium* are described in open nomenclature. A radius and calcaneus of *Elasmotherium* sp. were found at Nogaisk, associated with other unidentifiable remains (Fig. 1). Other specimens were recovered from various other localities of unknown precise age, most probably of the Early Pleistocene (Derkach et al., 1999): Bilenke (humerus), Pishchana Balka near Melitopol, Khortytsia, and Balky (Fig. 1; Appendix).

The earliest rhino remains from Slovakia are dated back to the earliest Pleistocene (Mammalian Neogene Quaternary – MNQ – zone 17) and come from two sites (Fig. 1). The first is Nová Vieska with two species, *Stephanorhinus jeanvireti* and *S. etruscus* (Holec, 1996; Vlačiky et al., 2008, 2009, 2010, 2013b, 2015; Zervanová, 2014). The material from this locality is represented by three isolated mandibles and isolated teeth, all of *Stephanorhinus jeanvireti*, but it also includes isolated teeth of *S. etruscus*. A fragmental upper tooth, lower molars and mandible fragments of *Stephanorhinus jeanvireti* were found at Strekov (Holec, 1996, Appendix 1, 2), although some authors (e.g., Schmidt and Halouzka, 1970 or Zervanová, 2014) also reported the presence of '*Dihoplus*' *megarhinus* (or *D.* cf. *megarhinus*) at this site (Appendix 1).

The remains of *Stephanorhinus etruscus* are also recorded from five Early Pleistocene Ukrainian localities (Pidoplichko, 1956; Alekseeva, 1966, 1977; Logvynenko, 2008). Mandible fragments and isolated teeth (P3, P4, and two M1) were found in gravel sediments at Shutnivtsi. A fragmental mandible with p4-m3 teeth is described from a sand quarry near Reni, while two mandible fragments and femur come from the Mudrene locality. Bones assigned to this species were also collected in quarries near Velyka Komyshuvakha and Dolynske (MIS 49–36). This material is deposited in the Geological Institute of the Russian Academy of Sciences in Moscow; there is no further information in the literature about these remains (Appendix 1). Unidentifiable remains of *Stephanorhinus* are known from the Early Pleistocene site of Pishchane (Pidoplichko, 1956). Because of the lack of stratigraphic information and of the impossibility to access the material the specimens cannot be assigned a taxonomic designation beyond the genus level.

4.2. Middle Pleistocene

Remains of *Stephanorhinus hundsheimensis* occurred in two localities of early Middle Pleistocene age from Slovakia (Fig. 2). The earlier one is the Gombasek 'complex of sites' (MIS 19 or MIS 17) (Šuf, 1931; Tasnádi-Kubacska and Soós, 1935; Kretzoi, 1938; Skutil, 1938; Fejfar and Heinrich, 1985; Wagner and Gasparik, 2014), located in southern Slovakia, near Plešivec, district of Rozňava. Two mandible fragments, isolated teeth and other remains were found at Gombasek 3 or Gombasek – Quarry. These specimens were originally assigned to *Rhinoceros etruscus* (Šuf, 1931) or *Opsiceros etruscus* ssp. (Kretzoi, 1938), but they probably belong to *Stephanorhinus hundsheimensis*. Other rhino fossils from the Gombasek complex – 'Gombasek bei Plešivec – Fundstelle 1' (Fejfar, 1964a) – can probably also be attributed to this species.

The remains of *S. hundsheimensis* were also found in Srbsko – Chlum and Stránská skála in the Czech Republic (Fig. 2). The richest material (about 50 isolated molars of adults and juveniles) was collected from layer 4S of Srbsko – Chlum, near Prague (Fig. 2). These specimens were originally assigned to *Stephanorhinus etruscus*, although are likely to belong to *S. hundsheimensis* based on their stratigraphic positioning (Fejfar, 1961, 1964a, b; Wagner, 2004; Picha, 2013; Made, 2015; Pandolfi and Tagliacozzo, 2015; Horáček et al., 2016; Pandolfi et al., 2017a). Stránská skála, near Brno, yielded three isolated teeth and a calcaneus. These bones come from layers dated back to MIS 17–16 (Kahlke, 1972; Musil, 2002) (Appendix 1, 2).

Several bones from two Ukrainian sites are assigned to *Stephanorhinus kirchbergensis* (Fig. 2). The earlier ones (two mandible fragments) come from Biliayivka (MIS 17, Martonosha Interglacial) (Logvynenko, 2008), while the later specimens (with no anatomical indication) are

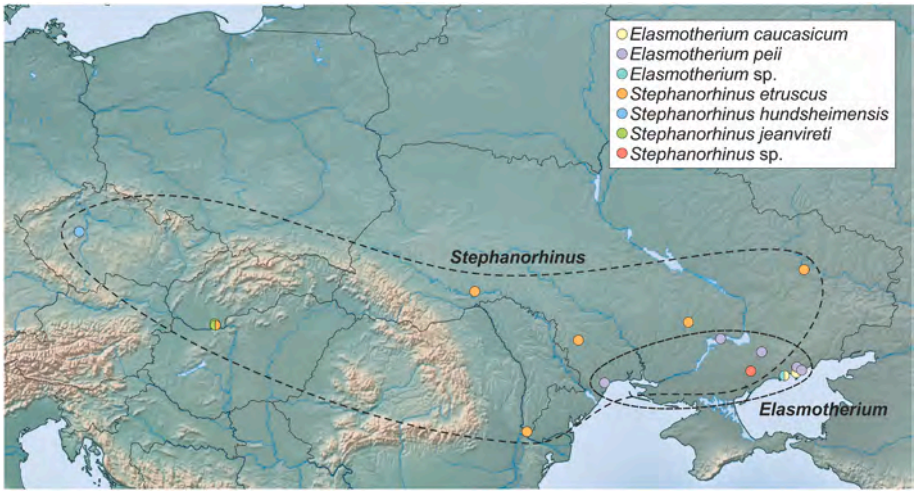

Fig. 1. Distribution of localities yielding rhino remains dated from the Late Pliocene to the Early Pleistocene (MN 16 – MIS 20) in Central and Eastern Europe.

Fig. 2. Distribution of localities yielding rhino remains dated from the late Early Pleistocene to the Middle Pleistocene (MIS 19 – MIS 9) in Central and Eastern Europe.

mentioned by Pidoplichko (1956) from Syniakove 1 (MIS 13–12) (Appendix 1). A very rich fauna complex, associated with traces of the presence of Lower Palaeolithic humans, was found in Medzhybizh 1 (MIS 11) in the west of Ukraine (Stefaniak et al., 2022). Rhino teeth from this site (Fig. 2) are dimensionally and morphologically consistent with either *Stephanorhinus kirchbergensis*, *S. hundsheimensis*, or *S. etruscus*. In the impossibility of a confident assignment of this material at the specific level, it is left here in open nomenclature (Stefaniak et al., 2022).

The only rhino fossil from the early Toringian period (probably Holsteinian Interglacial; MIS 11 or MIS 9?) of Slovakia are some isolated upper cheek teeth and a left toothed mandible, all of a single individual, originally described as *Dicerorhinus etruscus brychycephalus* (Holec, 1986). These fossils were assigned to *Stephanorhinus* cf. *hundsheimensis* (Zervanová, 2014). The specimens were found at the Levický Vápnik (Šiklóš) travertine site situated SE of Levice in the Ipeľská pahorkatina Upland (Fig. 2). Since the species *Stephanorhinus hundsheimensis* was no longer present in Europe in this period pending taxonomic revision, the remains are here referred to as *Stephanorhinus* sp. or *S. hemitoechus/kirchbergensis* (Appendix 1, 2).

The earliest remains of the woolly rhino *Coelodonta antiquitatis* are those found in the site of Tunel Wielki Cave in Poland, in layers dated to MIS 14–11 (Berto et al., 2021; Kot et al., 2022). This chronology corresponds to the earliest find of the species in Europe, the Bad Frankenhausen in Germany (Kahlke and Lacombat, 2008; Kahlke, 2014). Further finds come from the Biśnik Cave: the earliest ones from strata dated to MIS 8, while others from strata dated to MIS 7 or MIS 6 (Krajcarz et al., 2014b, b; Stefaniak, 2015; Krajcarz et al., 2022; Mazza et al., 2022). In addition, there are finds of this species from MIS 6 (Oder, Saalian glaciation) deposits in the Nietoperzowa Cave and the Eemian Interglacial of Biśnik Cave and Dziadowa Skała Cave.

The woolly rhinoceros is well represented in faunal assemblages from Ukrainian Pleistocene sites. There are at least 152 localities yielding remains of the species (Appendix 1, 2), eight of them are Middle Pleistocene sites, while the majority are dated back to the Late Pleistocene. Unfortunately, the stratigraphic information from many of these sites is unclear, and only four of them have been ^{14}C-dated so far (Appendix 1, 2). The results are nonetheless noteworthy and extend our knowledge as regards the Middle Pleistocene appearance and distribution of the woolly rhino. Like in Poland, the oldest Ukrainian finds of *Coelodonta antiquitatis* are reported from sites dated to MIS 13–12 – Syniakove 1 and Vasylivka (Pidoplichko, 1956; Derkach et al., 1999; Lindner et al., 2004, 2013; Krokhmal' et al., 2021; 2022). Their chronology spans the Lubny 2 Interglacial, Tiligul Glacial, which marks the earliest appearance of the species in Tunel Wielki Cave, Poland (Kahlke and Lacombat, 2008).

Four localities that yielded *Coelodonta antiquitatis* remains (Illinka, Zavadivka, Chygyryn, Pyvykha: Pidoplichko, 1956) are slightly younger (MIS 11–9, Mazovian Interglacial, Liwiecian Glacial, and Zbójnian Interglacial) (Appendix 1, 2). The woolly rhino is not reported from Poland and Slovakia at this time. The woolly rhino also occurred in Ukraine during the Krznanian Glaciation (MIS 8, Dnipro or Dnieper 1), as evidenced by the presence of its remains at Khalepia (Pidoplichko, 1956; this publication). The age of the material is the same as that from Polish sites, especially the one found in Biśnik Cave and Nietoperzowa Cave (Fig. 3).

The last three Middle Pleistocene sites with *Coelodonta antiquitatis* remains (Emine-Bair-Khosar, Molodova V, and Kaniv: Alekseeva, 1987; Lindner et al., 2004, 2013; Ridush et al., 2013, 2021) date back to the Tiasmyn (Odranian) glaciation, MIS 6 (Lindner et al., 2004, 2013). Biśnik Cave in Poland, and Gánovce-Hrádok (the lowermost layer) in Slovakia have similar age.

4.3. Late Pleistocene

Stephanorhinus kirchbergensis is reported from two Czech localities dated back to the Eemian Interglacial (MIS 5e) (Appendix 1, 2). Isolated upper and lower teeth, as well as bones of fore- and hindlimbs of both adults and juveniles were found in two layers ('Chlupáčova sluj' and 'Petrbokova sluj') of the site of Koněprusy, Zlatý kůň (Mostecký, 1961, 1966; Picha, 2013; Billia and Zervanová, 2014; 2015). Musil (2002, 2010) also reported the presence of woolly rhino remains among remains from the layer 9b of Kůlna Cave, Moravian Karst (Appendix 1, 2).

The remains of Merck's rhinoceros are known from 13 localities in Poland (Appendix 2). Three of them (Imbramowice, Konin, Gorzów Wielkopolski) were found embedded in sediments of the Eemian Interglacial (MIS 5e) and thus are the earliest confirmed occurrences of the species in Poland. However, the specimen found at the Wrocław-Hallera 1 site may be even earlier, based on recent geological investigations (Wiśniewski et al., 2009, 2013, 2022). The interglacial age may be supported by the results of δ^{13}C isotope studies of tooth enamel, which indicate that the Wrocław-Hallera 1 individual lived in a 'canopy forest' environment (Stefaniak et al., 2021b). Isotopic data obtained for a specimen from Siekierki in Warsaw indicate that the animal lived in a more open environment, closer to those typical of *Coelodonta antiquitatis* (Stefaniak et al., 2021b). Hence, the Siekierki rhino likely lived in a colder period (e.g., the end of the Eemian Interglacial or the beginning of the Last Glacial). This is the only information that allowed a possible stratigraphic attribution, in the absence of a precise dating for this

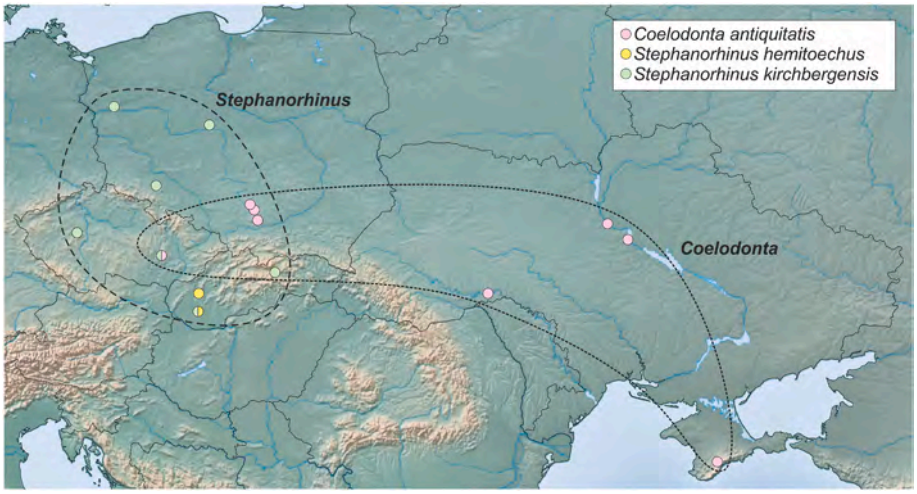

Fig. 3. Distribution of localities yielding rhino remains dated from the late Middle Pleistocene to the early Late Pleistocene (MIS 8 – MIS 5e) in Central and Eastern Europe.

specimen.

Based on the results of geological and palaeobotanical analyses, both the Konin and Gorzów Wielkopolski rhinos lived during the warmest stages of the Eemian Interglacial (E5) (Sobczyk et al., 2020; Stefaniak et al., 2021b, c). Polish remains of Merck's rhinoceros were found in Lower Silesia (2), Wielkopolska (3) and Pomerania (3), as well as in central and eastern Poland (4) (Appendix 1, 2). These are about half the occurrences reported by Kowalski (1959). The finds mostly come from lake deposits and fluvial sediments. Król (1998) reported finds (juvenile tibia and humerus fragment) from quarries, but their taxonomic attribution is still open.

Noteworthy is the recent find of an almost complete skeleton of Merck's rhinoceros female from Gorzów Wielkopolski (Fig. 8A and B), which, according to the results of osteometric studies, is one of the largest known individuals of the species (Stefaniak et al., 2021b). A complete skull of *Stephanorhinus kirchbergensis* was also described from Wisła near Siekierki.

Other Polish finds include skulls, mandibles and teeth (Ślósarski, 1884; Gürich, 1905, 1913; Hermann, 1911, 1913; Pax, 1921; Lubicz-Niezabitowski, 1926, 1929; Schroeder, 1930; Kowalski, 1959; Czyżewska, 1958, 1962; Borsuk-Białynicka and Jakubowski, 1972; Lorek, 1988; Wiśniewski et al., 2009, 2013; Badura et al., 2017; Marciszak et al., 2019; Sobczyk et al., 2020; Stefaniak et al., 2021b, c; Alexandrowicz et al., 2021; Wiśniewski et al., 2022).

The fluvial deposits of Váh River near Šaľa yielded Neanderthal skull fragments, associated with remains of *Stephanorhinus hemitoechus* and *S. kirchbergensis* (Schmidt, 1962, 1969b; Ďurišová, 1993, 1994; Zervanová, 2014) (Fig. 3). The faunal assemblage from the site is suggestive of the Eemian Interglacial. *Stephanorhinus hemitoechus* is represented by a fragment of right mandible with p2–m3 and *S. kirchbergensis* by a skull with left P4–M3 and a fragment of right maxilla with P2–M2 (Fig. 8C). Another important Neanderthal site with rhino remains is Gánovce–Hrádok, near Poprad, in northern Slovakia (Fig. 3). The hard, compact, and stratified gray travertine with occasional marl intercalations deposited during the Eemian Interglacial (ca. 105 ka BP; Jäger, 1989) and contained the fragment of a left maxilla with P2–M1, two cervical (?) vertebra and two ribs of *S. kirchbergensis* (Fejfar, 1958; Sabol et al., 2017). Another Eemian rhino remain, a damaged right mandible with p3–m3 (Fig. 8D), was also described from the lower sediments of Čertova pec Cave and assigned to *Stephanorhinus* cf. *hemitoechus*.

There are at least 219 localities the Czech Republic that yielded woolly rhino remains (Figs. 3–4). The list of the specimens in the Appendix 1 is not complete; it includes skulls, mandibles, isolated teeth, and postcranial bones and is mainly based on information given by Musil (2002, 2010) and Picha (2013). The stratigraphic positioning of the finds from caves is clearer than that of specimens found in open sites. The few dated woolly rhino remains span MIS 2 (Lister and Stuart,

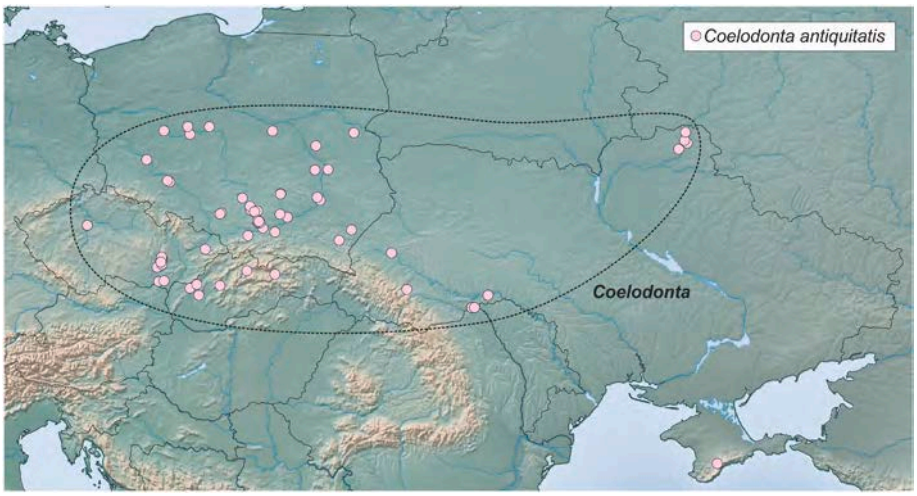

Fig. 4. Distribution of localities yielding rhino remains dated to the Late Pleistocene (MIS 5a-d – MIS 2) in Central and Eastern Europe.

2013). The earliest remains come from the Eemian Interglacial (MIS 5e) of Koněprusy, Kobyla, Chlupáčova sluj, Kůlna Cave and Želatovice. The bones well-dated stratigraphically span the Interplenivistulian, MIS 3 (Balcarova skála, Balcarka Cave, Barová Cave, Kůlna Cave, Pekárna Cave, Pod hradem, Šipka Cave, Švédův stůl, Stránská skála) as well as the LGM, MIS 2 (Kůlna Cave, Žitného Cave, Pavlov I), Velké Pavlovice, Předmostí) (Vaňura, 1942; Musil, 1958, 1959, 1960, 1962, 1965a, b, 1970, 1988, 1994, 1997, 2002, 2010; Rakovec, 1965; Sowa, 2007; Káňa and Roblíčková, 2013; Picha, 2013; Nerudová and Neruda, 2014).

At least 185 localities yielded woolly rhinoceros remains in Poland. Kowalski (1959) counted 100 sites. However, other authors (e.g., Borsuk-Białynicka, 1973) claim that many specimens are of unknown provenance. Nadachowski et al. (2015b) also mentioned over 100 localities with woolly rhino remains. Woolly rhino remains have been found a bit everywhere in Poland, although most of them come from from Pomerania, Wielkopolska, Silesia, central and south-eastern Poland (Fig. 4). They were mainly found in open-air localities (148), e.g., gravel pits, quarries, lignite mines, peat bogs, lake sediments, and, to a lesser extent, in cave sites (37). Most of the finds are of unclear stratigraphic provenance, although it is assumed that they may come from deposits of the Last Glacial (Appendix 1, 2).

Only some of the woolly rhino remains from Poland have been dated radiometrically. In total, 18 datings were obtained from 16 open-air localities and 15 datings – from seven cave sites (Fig. 9). The latest date, 13,444 ± 226 (16,460 ± 90 cal yrs. BP), was obtained from a scapula from Skarszyn. The earliest is the ulna of *Coelodonta antiquitatis* from Zawalowana Cave (49,000 ± 4000 BP). These dates indicate that Polish woolly rhinos became extinct before the great global warming at 14.7 ka, at the Greenland Stadial 2a (GS-2a)/Greenland Interstadial 1 (GI-1) transition, which is consistent with the results obtained by other authors (Stuart and Lister, 2012; Lister and Stuart, 2013; Markova et al., 2013; Puzachenko et al., 2021b).

Remains of *Coelodonta antiquitatis* dated back to the beginning of the Last Glacial were found in the following caves: Obłazowa, Nietoperzowa, Biśnik, Deszczowa, and Ciemna (Appendix 1, 2). Most of the finds come from MIS 4 and MIS 3 periods. Sites with woolly rhino become rare for the LGM period (MIS 2); the species became extinct in Poland by 14.7 ka, most probably during the GS-2a period (Stuart and Lister, 2012; Lister and Stuart, 2013). Additional dating of the species will improve our understanding of how the occurrence of the woolly rhino changed through time during the MIS 3–2 transition in different districts, as it was in the case of woolly mammoth (Nadachowski et al., 2011, 2018; Baca et al., 2017). Woolly rhino finds from Polish cave sites include fragments of skulls, jaws, teeth, fragments of the axial skeleton, shoulder and pelvic girdles, and limb bones (Fig. 8E–G). Finds from open-air sites include complete skulls, elements of the axial skeleton, bones of girdles and limb bones (Appendix 1).

Woolly rhino remains were also found in 20 Slovakian sites. One of them is Gánovce-Hrádok, near Poprad (Appendix 1, 2). A right P3, right M2, and right p3-4 from this locality were found in the lowermost horizon, gray travertine sands, marls and clays affected by cryoturbation and supposedly dated to the late Saalian Glacial stage (MIS 6?). If the dating is correct, the find can be considered as one of the earliest occurrences of *Coelodonta* in Slovakia (Fejfar, 1958). Fossil remains of *Coelodonta antiquitatis* (upper molars, isolated lower teeth, two fragments of left mandible with teeth, two fragments of left mandible without teeth, a fragmental right mandible and 28 tooth fragments) were also found in a Last Glacial crumbling travertine to travertine breccia with soil strata (MIS 5d–3) and in loess-clayed sediments with travertine fragments (MIS 2) of the same site (Appendix 1, 2: Fejfar in Vlček, 1969; Sabol et al., 2017).

Woolly rhino remains from Čertova pec Cave were collected from Last Glacial deposits (Musil, 1985) spanning MIS 5a-d through MIS 2 (Putiška et al., 2017). AMS dating of charcoal and animal bones (GrN 2438, OxA–24106, OxA–24107, OxA–24108; Kaminská, 2014) provided an age of >50,000–38,320 yrs. BP, i.e., MIS 3 (Bárta, 1965; Jöris et al., 2006; Engelbrecht, 2012), although stone tools found are of Gravettian, Mousterian and Szeletian type.

Fluvial gravel deposits of the Morava River, near Malé Leváre, yielded fossils of large Pleistocene mammals. These include remains of elephantids, bovids and cervids, alongside Late Pleistocene remains of *Coelodonta antiquitatis* (Schmidt, 1969a; Holec, 1982; Ďurišová, 1984). Upper Pleistocene gravels of the Tisa River, in the East-Slovakian Basin, provided a damaged right mandible of woolly rhinoceros, which was described by Schmidt (1965) (Appendix 1, 2).

Coelodonta antiquitatis remains (mandible, teeth, atlas, vertebrae, scapulae, 10 humeri, 3 ulnae, 4 radii, 3 pelvis fragm., 4 femora, 6 tibiae, 2 calcanei, Mt III) are also known from the Last Glacial (MIS 3–2) travertines Bešeňová – Báňa, near Ružomberok (Sabol et al., 2022) and deciduous teeth, upper and lower cheek teeth, a fragment of the lower jaw, fragments of ribs, scapulae, pelvis and limb bones were collected from Prepoštská Cave, near Bojnice (Čeklovský, 2015; Čeklovský et al., 2016), and dated radiometrically to 37,749 ± 516 yrs. BP. However, the most complete woolly rhino remain is a cranium without the maxilla found at Hanušovce nad Topľou, in the Slovakian Western Carpathians (Ďurišová, 1996) (Appendix 1, 2).

Isolated woolly rhino teeth and mandible fragments (identified either as *Coelodonta antiquitatis* or *Coelodonta* sp.) are reported from other Slovakian Late Pleistocene sites, such as Dlhá nad Váhom, Hajnáčka, Hlohovec, Hodkovce, Krakovany – Strážov, Moravský Ján, Okoč, Santovka (Maďarovce), Silická Brezová, Slovenský Grob, Trakovice, and Trenčianske Bohuslavice – Pod Tureckom (Bárta, 1988; Verpoorte, 2002; Žaár, 2007; Vlačiky, 2009; Vlačiky et al., 2013a; Zervanová, 2014) (Appendix 1, 2). Radiocarbon dates span MIS 3 (Fig. 9).

Late Pleistocene finds of the woolly rhino from Ukraine are confined to different phases of the Last Glacial (MIS 5 and MIS 3). Emine-Bair-Khosar spans MIS 4-2 (so called Uday or Świecie stadial; Vitachiv interstadial; and Bug stadial or LGM), while others date to MIS 3 (Vitachiv interstadial, Grudziądz interstadial, Interplenivistulian) (Fig. 4). The sites listed in the Appendix 1 mostly have no age (Lebedinskyi, 1910; Polianskyi, 1929; Pidoplichko, 1940, 1947; Chernysh, 1947, 1954; Pasternak and Tatarinov, 1952; Svistun, 1959, 1960, 1966; Tatarinov, 1959, 1961, 1977, 2000; Svistun and Bachinsky, 1962; Shovkoplias, 1965; Svistun and Lomayev, 1967; Alekseeva, 1987; Kukharchuk, 1997; Derkach et al., 1999; Vremir et al., 2000; Ridush, 2002, 2012, 2022; Muzychenko, 2003; Kovalchuk, 2011; Chubur and Kovalchuk, 2013; Ridush et al., 2013, 2021; Westbury et al., 2020), although it is likely that most of them range at the time of the Last Glacial.

At Molodova V site, woolly rhino remains were found in layers 6, 7, 9, 10, and 11 (Alekseeva, 1987). Layers 6 and 7 can be stratigraphically dated to ca. 20.3–25.3 ka, which spans MIS 2, while layers 9 and 10 are bracketed in time between 28.7 and 30.4 ka, i.e., MIS 3 (Haesaerts et al., 2009, 2020). Layer 11 contains Mousterian artifacts and was previously dated to around 50 ka (Ivanova, 1982), but a recent, biostratigraphy-based revision antedated it to the end of the Saalian (Dnieper, MIS 6) (Ridush and Popiuk, 2020). A few woolly rhino bones, bearing evidence of cave hyena (*Crocuta crocuta spelaea*) gnawing and human use, were collected from the hyena den of Bukovynka Cave. Two ^{14}C dates were obtained for the remains of hyena and *Coelodonta antiquitatis* from this site (Vremir et al., 2000; Ridush, 2022).

The four woolly rhino corpses found in Starunia represent one of the greatest discoveries ever made, excluding the various carcasses recovered from Russian permafrost. All the Starunia specimens were found in ozokerite deposits, which allowed the soft parts to be preserved. The finds garnered wide appeal in the literature, and became the subject of extensive study, also extended to the accompanying fauna and flora (Stefaniak et al., 2021b and references therein).

Radiocarbon dating of the woolly rhino specimens from Ukraine was performed on samples collected from five sites and spanning 35,000 ± 900 through 41,300 + 1300/–1,100, i.e., MIS 3 (Fig. 9). A few dates

obtained from the Starunia specimens show very large age dispersion, from 14,140 ± 480, of earlier datings, to 47,000 ± 3000 of the ones recently achieved using different methodologies and tissues, even drawn from the same individual. Kuc et al. (2005) reanalysed the results and performed new ^{14}C AMS datings. The results range from 35.3 to 40.0 ka BP for specimen No. 2, 36.7 ± 0.6 ka BP for specimen No. 3, 45 ± 2 ka BP for specimen No. 1, and 40.3 ± 1.2 ka BP for specimen No. 4, which places all the individuals in MIS 3, consistently with many dates obtained for this species from Eastern Europe (Figs. 4 and 9).

4.4. Occurrence of central and Eastern European Quaternary rhino fossils

Figs. 5–7 show the Central and Eastern European localities that provided fossil remains of rhinoceros, each with its more or less precise stratigraphic age (finds with a broad chronology covering several MISs are not included). The full list of these sites is included in the Supplementary Material (Appendix 1, 2). Most Early Pleistocene rhinoceroses are known from Ukraine, and several more from Slovakia and Czech Republic (Fig. 5). They are assigned to either *Stephanorhinus* or *Elasmotherium*. The Middle Pleistocene remains of rhinoceroses were found in all four countries, but most come from Ukraine (Fig. 6). *Stephanorhinus* prevailed at the beginning of the Middle Pleistocene; *Coelodonta* appeared at MIS 14 and became dominant at the end of the Middle Pleistocene. It kept being the leading genus also in the Late Pleistocene in all four countries, whereas *Stephanorhinus* was exclusively present in MIS 5e, i.e., the Eemian Interglacial (Fig. 7). Most *Coelodonta* remains were found in MIS 3 and MIS 2 deposits.

Interestingly, sites with *Stephanorhinus* are mostly assigned to periods associated with a warmer climate. The number of the sites related to warmer and colder periods is 17 and 4, respectively, and the difference is statistically significant (G-test, p-value = 0.003). It can suggest a preference of a cooler climate by this genus. In fact, based on its morphoanatomical characteristics, on the results of isotopic and pollen studies conducted on its remains, and on the nature of the deposits in which it is generally found, *Stephanorhinus kirchbergensis* lived in various types of forests as well as in open landscapes. The diet of this rhino comprised leaves of deciduous trees and shrubs, as well as soft vegetation growing near flowing and standing waters (Stefaniak et al., 2021b). However, no significant bias in the distribution of *Coelodonta* sites was observed, i.e., 72 warm climate-sites vs. 62 cold climate-sites (G-test, p-value = 0.388).

4.5. Radiocarbon dating of Central and Eastern European woolly rhino remains

The largest number of radiocarbon-dated records of *Coelodonta antiquitatis* come from Poland (Fig. 9). The earliest datings, which are beyond the range of radiocarbon dating, come from Sąspowska Zachodnia Cave, Sochaczew, Zawalona Cave, Września and Krosinko. Conversely, the latest dated were obtained for a specimen found in Wilczyce, their median and 95.4%-confidence interval being 13,286 and 13,576–13,088 cal yrs. BP. The latter date was considered too young, probably due to contamination (Schild, 2014; Nadachowski et al., 2015b), whereby the next latest known samples become those from Skarszyn, 16,213 [16,949–15,601] cal. yrs. BP and the Nida River near Czarkowy, 16,765 [17,006–16,521] cal. yrs. BP. Radiocarbon records from other countries are restricted to MIS 3. Most dates range from 46,000 to 42,000 cal yrs. BP, with a relatively long gap between 25,000 and 22,000 cal yrs. BP (see Table 1).

The number of radiocarbon dates available for *Coelodonta antiquitatis* is still relatively small, and thereby drawing conclusions is challenging. At the present state of knowledge, dated records drop from MIS 3 to MIS 2, which may indicate a gradual extinction of the species.

This trend is also visible in the number of sites that provided its fossil remains (Fig. 7). The number of MIS 3 sites is 29 and those MIS 2 ones is

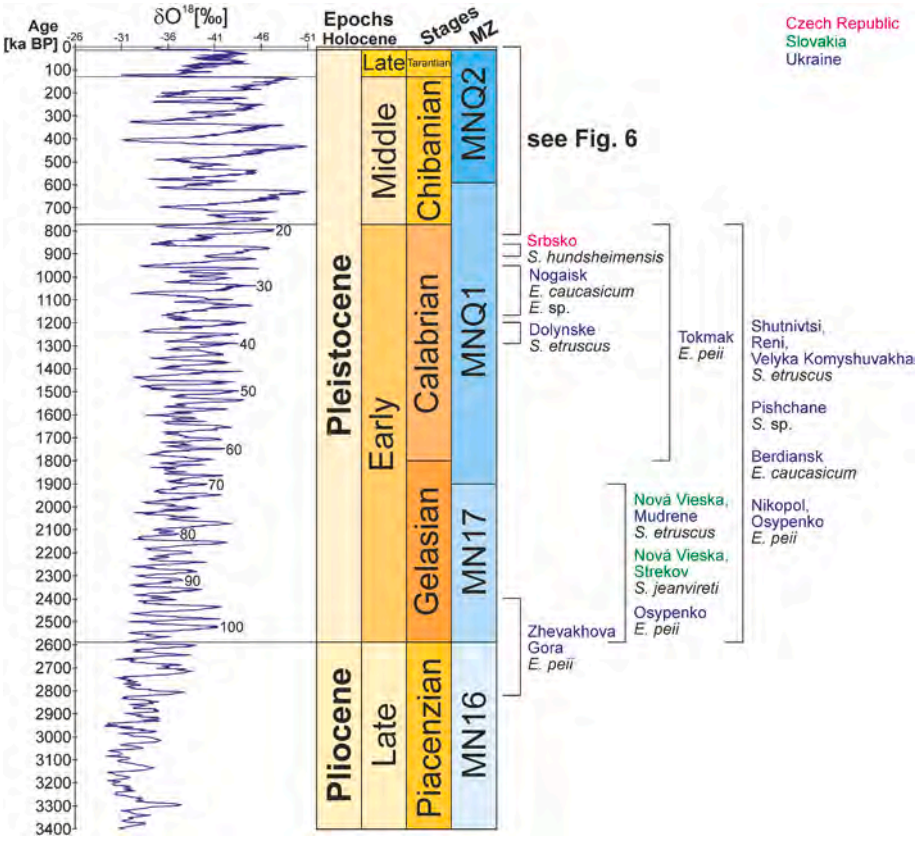

Fig. 5. Biostratigraphy and occurrence of fossil rhino remains in Central and Eastern Europe sites at the end of the Pliocene and in the Early Pleistocene. MZ, European Land Mammal Mega Zones; MIS, Marine isotope stages. Selected Marine isotope stages (MIS) were shown for the Early and Middle Pleistocene.

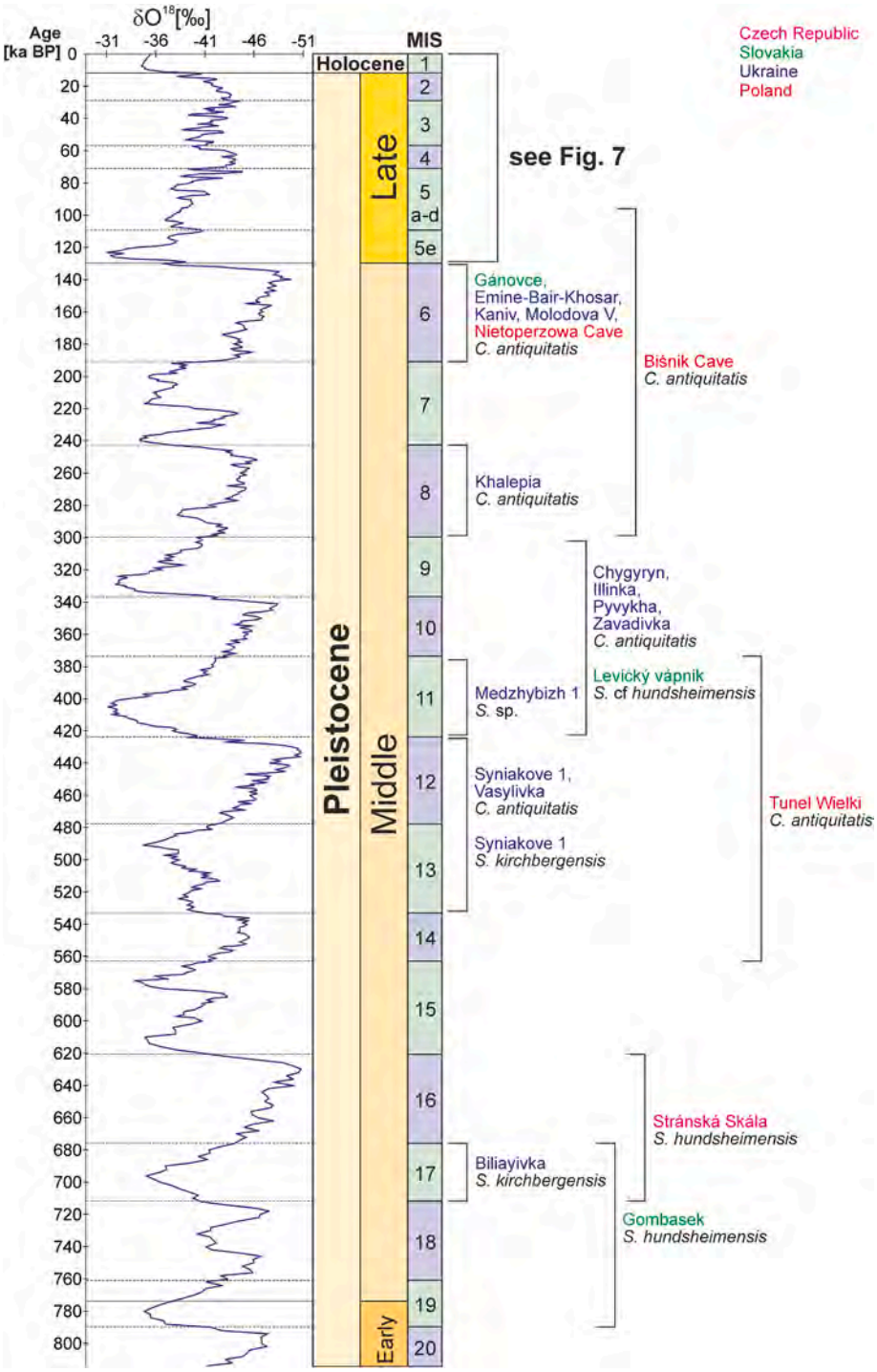

Fig. 6. Biostratigraphy and occurrence of fossil rhino remains in Central and Eastern Europe sites in the Middle Pleistocene. MIS, Marine isotope stages.

18. If this reflects actual modifications in the consistency of the species, the cold Last Glacial Maximum (LGM), which roughly corresponds to MIS 2, led to the disappearance of this rhinoceros. Similar scarcity of LGM records was also noticed in the case of *Mammuthus primigenius* and *Saiga tatarica* (Nadachowski et al., 2011, 2016, 2018; Baca et al., 2017), as well as in those of *Ursus spelaeus* and *U. ingressus* (Mackiewicz et al., 2017). However, individual species may have responded differently to similar climate changes: the number of *Ovibos moschatus* records, for instance, raised after ca. 32 ka BP and peaked at ca. 23 ka BP in the LGM (Stefaniak et al., 2021b).

5. Discussion

5.1. Regional patterns of taxonomic diversity of Central and Eastern European Pleistocene rhinos

The accumulated evidence reveals regional variations in the taxonomic diversity of Central and Eastern European Pleistocene rhinos. Species richness is the highest in Slovakia and Ukraine, while Poland was home to only two rhino species (Appendix 1, 2). Thirteen localities yielded remains of *Stephanorhinus kirchbergensis*, while over 180 sites gave remains of *Coelodonta antiquitatis*. The woolly rhino first appeared

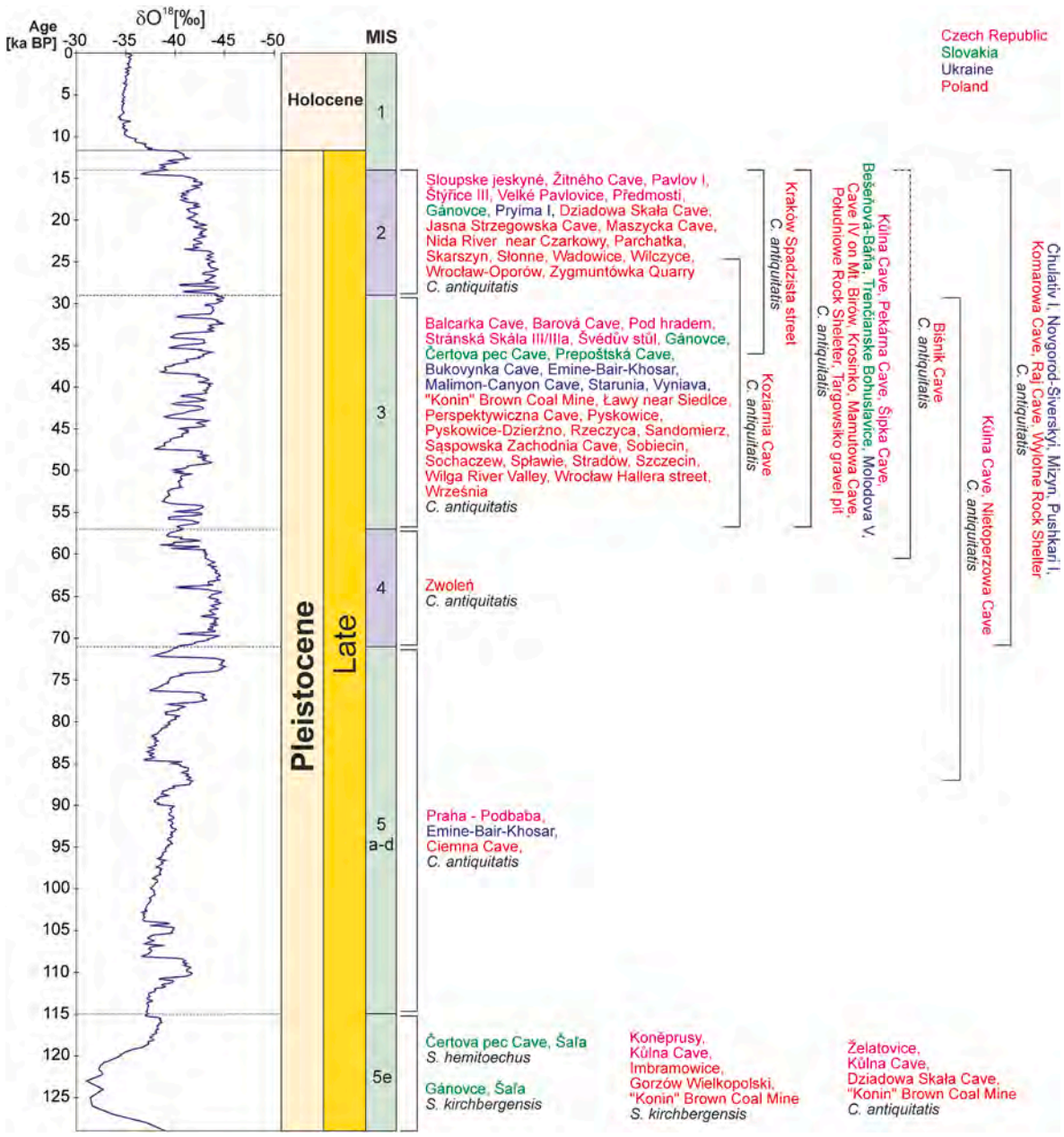

Fig. 7. Biostratigraphy and occurrence of fossil rhino remains in Central and Eastern Europe sites in the Late Pleistocene. MIS, Marine isotope stages.

in this part of Europe sometime during MIS 12. *Stephanorhinus kirchbergensis* appeared somewhat later, during the Eemian Interglacial (MIS 5e). No Rhinocerotidae remains are known from Early Pleistocene and from most Middle Pleistocene Polish localities (until about 480 ka). A possible explanation for this is the lack of fossil-bearing localities since almost the entire territory of Poland at the time was covered with ice. Remains of Merck's species are first known from the time spanning the San 2 Glacial (MIS 12? Lindner et al., 2004, 2013) when the South Polish ice sheet covered only the northern edge of the Kraków-Częstochowa Upland. Poland was home to the woolly rhino also during the latest Middle Pleistocene glaciations and the Vistulian Glacial (MIS 4-2). The Odranian (MIS 6) remains of the species as well as the most numerous one dated to the Last Glacial (Lindner et al., 2004, 2013; Stefaniak et al., 2009a, 2020) attest to an unusually late occurrence of the species.

In Slovakia, the earliest rhino remains date back to the Early Pleistocene (MNQ 17) and belong to the genus *Stephanorhinus*. Two of them, i.e., the medium sized *Stephanorhinus jeanvireti* and the smaller *S. etruscus*, are brachiodont species. The remains of both these species were recovered from open-air localities (Guérin, 1980; Fortelius, 1982; Kahlke et al., 2011; Pandolfi and Petronio, 2011; Pandolfi et al., 2017a, 2019, 2021a, b, 2022; Pandolfi, 2018).

Stephanorhinus kirchbergensis occurred in the Czech Republic and Slovakia (as in Poland) during the Eemian Interglacial (MIS 5e). *Stephanorhinus hemitoechus* was also present in Slovakia at that time. It was well-suited for open steppe landscapes (Zeuner, 1934; Loose, 1975; Guérin, 1980; Fortelius, 1982; Grübe, 2003; Kaiser and Kahlke, 2005; Made and Grübe, 2010; Kahlke and Kaiser, 2011; Van Asperen and Kahlke, 2015; Kirillova et al., 2017; Van Geel et al., 2019; Burkanova et al., 2020; Stefaniak et al., 2021b). *Stephanorhinus hemitoechus* did not distribute in Poland, the Czech Republic and Ukraine. The woolly rhino is the most frequently found rhino in sites of the Czech Republic and Slovakia. The species first appeared in the Czech Republic in the Eemian Interglacial and in Slovakia in the MIS 6 period.

Pleistocene rhinos reached the highest diversity in Ukraine, which

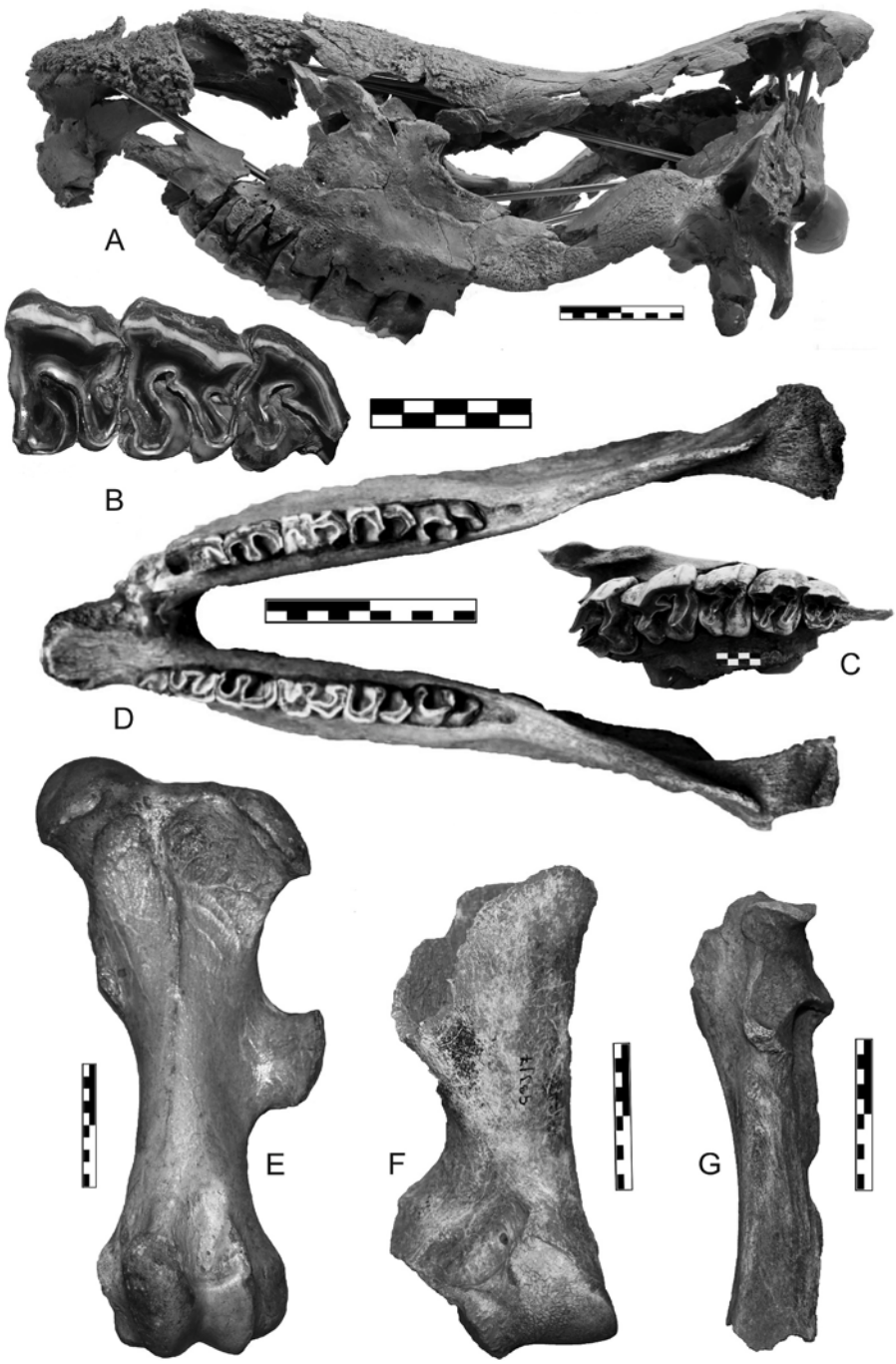

Fig. 8. Selected fossil remains of Pleistocene rhinoceroses from Central Europe: A – *Stephanorhinus kirchbergensis*, skull (ZPL/UWr/GI/80), lateral view, Gorzów Wielkopolski, Poland; B – *Stephanorhinus kirchbergensis*, upper molars (ZPL/UWr/GI/80), occlusal view, Gorzów Wielkopolski, Poland; C – *Stephanorhinus kirchbergensis*, fragment of maxilla with P2–M2 dext. (SNM-PM Z14170), occlusal view; D – *Stephanorhinus* cf. *hemitoechus*, mandible with p3–m3 dext. and p2–m3 sin., occlusal view, Čertova pec Cave, Slovakia (Zervanová, 2014); E – *Coelodonta antiquitatis*, left femur (ZPALUWr/B/1), dorsal view, Bełchatów Brown Coal Mine, Poland; F – *Coelodonta antiquitatis*, left humerus (ZPALUWr/GBJ/7) with cave hyena gnawing marks, dorsal view, Birów Cave, Poland; G – *Coelodonta antiquitatis*, left ulna (ZPALUWr/GBJ/35/9) with cave hyena gnawing marks, dorsal view, Birów Cave, Poland.

was not only home to *Stephanorhinus* and *Coelodonta*, but also to Elasmotheriinae. At the beginning of the Early Pleistocene, two species, *Elasmotherium peii* and *E. caucasicum*, occurred in southern Ukraine. *Elasmotherium sibiricum* was distributed to the eastern part of modern Ukraine, and yet it has never been recorded in the Middle and Late Pleistocene, when perhaps the palaeoenvironmental conditions were unsuitable for the species (Shvyreva, 2016).

5.2. Evolutionary history of rhinoceroses in Central and Eastern Europe

During the Miocene and Pliocene, European mammal diversity decreased, and several species became extinct, including elephants and rhinoceroses. The richness of rhino species declined during this time for several reasons, including progressive cooling, replacement, in the northern hemisphere, during the Pliocene and Early Pleistocene, of open habitats, suitable for the *Hipparion* fauna, with temperate forest environments suitable for new communities, then followed by tundra conditions that favoured the distribution of 'mammoth steppe' communities. New species fit to live in these environments appeared through time (Kahlke et al., 2011; Kahlke, 2014; Pandolfi, 2018; Pandolfi et al., 2021a, b).

Five rhino species were distributed in Europe during the Pliocene: *Pliorhinus megarhinus*, *P. miguelcrusafonti*, *Stephanorhinus jeanvireti*, *S. etruscus*, and *Elasmotherium peii* (Czyżewska, 1958; Fejfar, 1964a, b; Guérin, 1980; Fejfar and Heinrich, 1985; Cerdeño, 1992; Bajgusheva et al., 2001; Sabol, 2003; Ďurišová, 2004; Lacombat, 2007; Logvynenko, 2008; Bajgusheva and Titov, 2010; Shvyreva, 2016; Pandolfi et al., 2017a, b; Pandolfi, 2018).

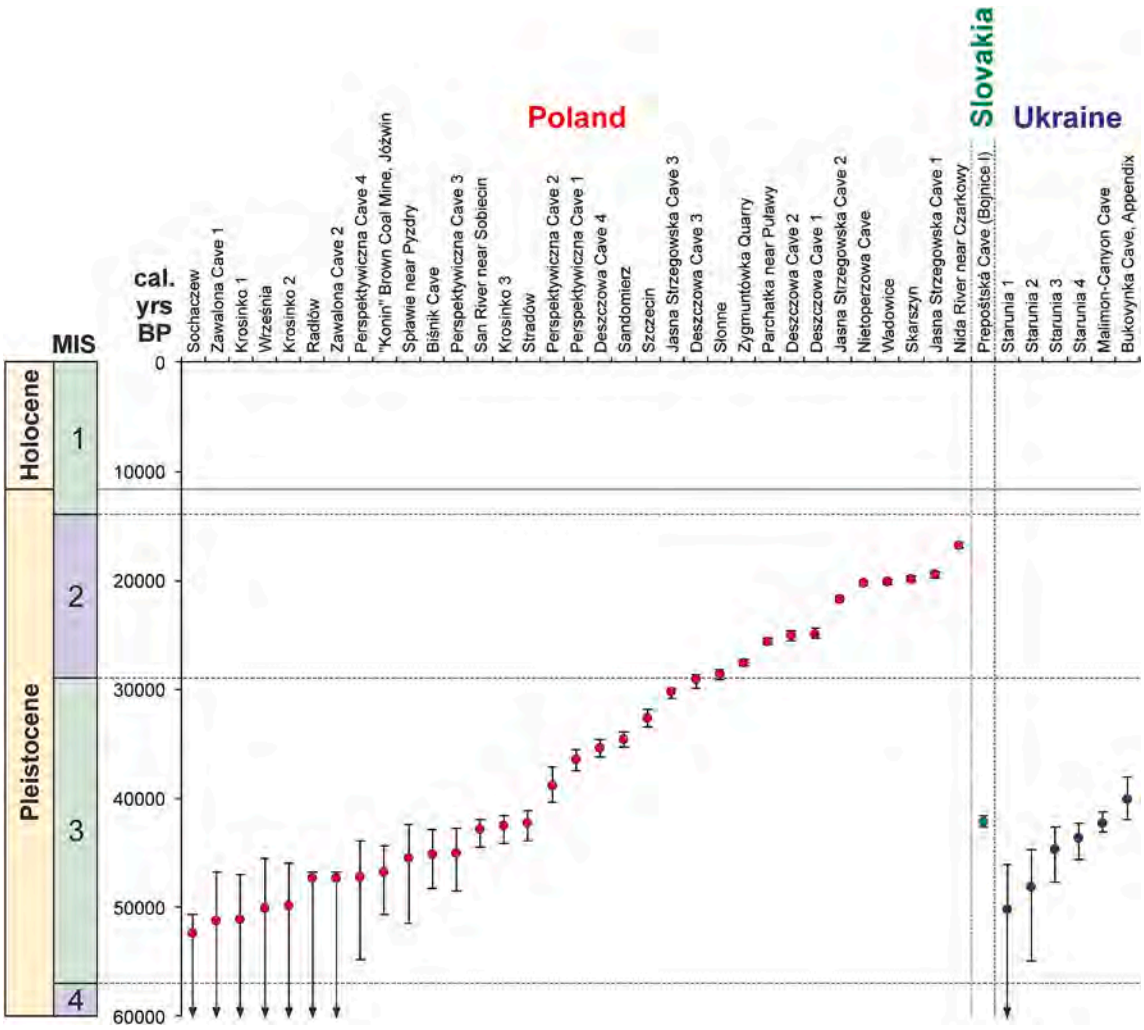

Fig. 9. Distribution of directly dated woolly rhinoceros remains in Central and Eastern Europe during Marine Oxygen Isotope Stage 2–4 (MIS 2–4).

Pliorhinus megarhinus was the most common species in Central and Eastern Europe (Pandolfi et al., 2021a). *Stephanorhinus jeanvireti* and *S.* sp. are reported from the southern part of modern Ukraine, which was the eastern extreme of the range of the genus. Except for *Pliorhinus miguelcrusafonti*, which was endemic to the Iberian Peninsula (Pandolfi et al., 2021a), Central and Eastern Europe shared the same rhinos as other parts of the continent.

The significant shift towards cooler climatic conditions drove faunal turnover at the Plio-Pleistocene boundary. It was the so-called *Elephas–Equus* event (Azzaroli et al., 1988). During this period, several species of thermophilic forested habitats disappeared, and were replaced by more temperate species. The beginning of the Pleistocene came as a rather abrupt ecosystem makeover—as evidenced especially in the spread of open-steppe conditions in Europe, meaning drier grasslands at the expense of the original wetter woodlands, and tundra in the north.

Rhinos apparently avoided Poland and the Czech Republic in the Gelasian. *Stephanorhinus jeanvireti* survived for a while in Slovakia, accompanied by *S. etruscus* which first appeared at this time, while *Elasmotherium peii* was confined to Ukraine. At the end of the Early Pleistocene, *Stephanorhinus jeanvireti* disappeared from Slovakia. *Stephanorhinus etruscus* appeared in Ukraine, and *Elasmotherium peii* in this region was replaced by *E. caucasicum*. The typical Middle Pleistocene rhino *Stephanorhinus hundsheimensis* appeared for the first time at the turn of the Early and Middle Pleistocene in the Czech Republic.

During the Gelasian, *Stephanorhinus etruscus* spread to the western and southern parts of Europe, while *S. jeanvireti* and *Elasmotherium chaprovicum* and *E. peii* were present in the territory of European Russia. During the Calabrian, *Stephanorhinus hundsheimensis* added to *S. etruscus* in Western and Southern Europe, while *Elasmotherium caucasicum* was confined to European Russia (Guérin, 1980; Mazza, 1988, 1993; Fortelius et al., 1993; Mazza et al., 1993; Rustioni et al., 1995; Made, 1999, 2001, 2010, 2015; Bajgusheva et al., 2001; Lacombat, 2003, 2007; Bajgusheva and Titov, 2010; Kahlke et al., 2011; Pandolfi and Petronio, 2011; Pandolfi and Tagliacozzo, 2015; Pandolfi and Erten, 2017; Pandolfi, 2013, 2018; Shvyreva, 2016; Made et al., 2017; Pandolfi et al., 2016b, 2017a, 2019, 2020, 2021a, b, 2022).

The beginning of the Middle Pleistocene was characterised by the expansion of ice sheets on the European continent driven by significant climatic changes as well as by the onset of larger-amplitude, 100 ka glacial-interglacial cycles. The more intense cooling brought several Villafranchian holdovers to extinction. They were replaced by new Eurasian incomers, which built up the so-called Cromerian fauna, more adapted to open landscapes under cold climatic conditions (Azzaroli

Table 1
Radiocarbon dates of *Coelodonta antiquitatis* remains from Central and Eastern Europe. Calibrated using OxCal (Reimer et al., 2020).

Site	Country	Lab code	^{14}C years BP	Cal. years BP			Remark	Material dated	%N:%C of whole specimen	Source
				95.4% range		Median				
Předmostí 1	Czech Republic		26870 ± 250	31420	30409	31040				this paper
Předmostí 2	Czech Republic		26320 ± 240	31030	30122	30583				this paper
"Konin" Brown Coal Mine, Jóźwin	Poland	Poz-34505	44000 ± 1400	50711	44344	46771	out of range	cranium	6.0 : 16.1	this paper
Biśnik Cave	Poland	Poz-90122	42200 ± 1400	48298	42882	45183		radius	1.2 : 5.0	this paper
Deszczowa Cave 1	Poland	Poz-111031	20720 ± 150	25344	24370	24966		rib	1.4 : 5.8	this paper
Deszczowa Cave 2	Poland	OxA-11060	20800 ± 150	25562	24636	25073		metapodial		Wojtal, 2007; Nadachowski et al., 2009
Deszczowa Cave 3	Poland	Poz-111032	24880 ± 250	29850	28675	29125		rib	0.8 : 4.7	this paper
Deszczowa Cave 4	Poland	Poz-23772	31000 ± 400	36174	34610	35391		phalanx	5.7 : 19.5	Lorenc, 2013
Jasna Strzegowska Cave 1	Poland	OxA-11159	16140 ± 90	19805	19180	19474		ulna		Stuart and Lister, 2012
Jasna Strzegowska Cave 2	Poland	OxA-11095	17880 ± 100	22027	21406	21729		upper molar		Stuart and Lister, 2012
Jasna Strzegowska Cave 3	Poland	Poz-79728	25950 ± 220	30820	29912	30237		ulna	3.0 : 9.5	Cyrek et al., 2016
Krosinko 1	Poland	OxA-26804	48400 ± 3200	–	46980	51158	out of range	femur		Pawłowska, 2022
Krosinko 2	Poland	OxA-26802	46500 ± 2600	–	46003	49847	out of range	radius		Pawłowska, 2022
Krosinko 3	Poland	Poz-53988	38500 ± 2000	48295	39768	43023	out of range	humerus		Pawłowska, 2022
Nida River near Czarkowy	Poland	Poz-30999	13810 ± 70	17006	16521	16765		cranium fr.	2.4 : 7.2	this paper
Nietoperzowa Cave	Poland	Poz-23626	16780 ± 80	20493	20065	20294		radius	5.7 : 19.2	this paper
Parchatka near Puławy	Poland	Poz-31000	21300 ± 130	25887	25292	25657		mandible fr.	1.4 : 4.9	this paper
Perspektywiczna Cave 1	Poland	Poz-83557	32100 ± 400	37465	35574	36489		pelvis	2.0 : 8.0	this paper
Perspektywiczna Cave 2	Poland	Poz-91891	33900 ± 600	40360	37158	38801		Mt II	3.4 : 9.5	this paper
Perspektywiczna Cave 3	Poland	Poz-99467	42000 ± 1500	48535	42715	45068		lower p/m fr.	2.6 : 7.8	this paper
Perspektywiczna Cave 4	Poland	Poz-91885	44000 ± 2000	54742	43925	47273	out of range	p3	3.8 : 11.4	this paper
Radłów	Poland	Poz-28772	>45000	47984	46795	47333		cranium	3.2 : 11.9	this paper
San River near Sobiecin	Poland	Poz-31458	39000 ± 1000	44444	41934	42863		cranium	2.3 : 5.7	this paper
Sandomierz	Poland	Poz-31001	30060 ± 360	35297	33931	34545		humerus	3.4 : 9.4	this paper
Sąspowska Zachodnia Cave	Poland	Poz-24205	49000 ± 400	–	50511	52378	out of range	ulna		this paper
Skarszyn	Poland	Poz-82384	13444 ± 226	16949	15601	16213		scapula		Marciszak et al., 2019a
Słonne	Poland	Poz-31457	24420 ± 170	29107	28149	28665		humerus	0.8 : 3.0	this paper
Sobiecin	Poland	Poz-31458	39000 ± 1000	44444	41934	42863		skull		this paper
Sochaczew	Poland	R-EVA 3410	>49000	–	50663	52351	out of range	cranium		this paper
Spławie near Pyzdry	Poland	Poz-34416	42000 ± 2000	51485	42427	45474	out of range	mandible	1.8 : 5.2	this paper
Starunia 1	Poland	Poz-11348	47000 ± 3000	–	46094	50240	out of range	soft tissue		Kuc et al., 2012
Starunia 2	Poland	Poz-11347	45000 ± 2000	54855	44668	48195	out of range	part of vertebra		Kuc et al., 2012
Stradów	Poland	Poz-30231	38000 ± 1000	43890	41114	42286		tooth	2.5 : 7.4	this paper
Szczecin	Poland	OxA-11059	28450 ± 250	33448	31828	32614		femur		Stuart and Lister, 2012
Wadowice	Poland	Poz-30232	16650 ± 100	20412	19867	20126		cranium	1.9 : 6.3	this paper
Wilczyce	Poland		11400 ± 135	13576	13088	13286		tooth		Schild, 2014

(*continued on next page*)

Table 1 (*continued*)

Site	Country	Lab code	^{14}C years BP	Cal. years BP			Remark	Material dated	%N:%C of whole specimen	Source
				95.4% range		Median				
		Ua-15720								
Września	Poland	Poz-38122	47000 ± 4000	–	45456	50103	out of range	skull		this paper
Zawalona Cave 1	Poland	Poz-24205	49000 ± 4000	–	46814	51252	out of range	ulna fr.	5.5 : 18.0	this paper
Zawalona Cave 2	Poland	Poz-24205	>45000	47984	46795	47333		humerus fr.	5.8 : 18.9	this paper
Zygmuntówka Quarry	Poland	Poz-25161	23380 ± 200	27844	27273	27566		femur	1.3 : 6.8	this paper
Prepoštská Cave (Bojnice I)	Slovakia	ETH-51815	37749 ± 516	42626	41557	42165		P/M		Čeklovský et al., 2016
Bukovynka Cave, Appendix	Ukraine	VERA-2529	35000 ± 900	41924	38015	40138		radius		this paper
Bukovynka Cave, Trapeznyi Chamber	Ukraine	VERA-2529	41300 ± 1300	46964	42562	44378				Ridush, 2009
Malimon-Canyon Cave	Ukraine	Poz-47727	38000 ± 800	43144	41275	42271		humerus	5.5 : 1.2	Ridush, 2022
Starunia 3	Ukraine	Poz-11349	41600 ± 1400	47714	42651	44667		part of a rib (collagen)		Kuc et al., 2012
Starunia 4	Ukraine	Poz-11350	40300 ± 1200	45660	42312	43714		part of a shoulder-blade (collagen)		Kuc et al., 2012
Vyniava	Ukraine		40770 ± 350	44429	43124	43785		canine		Westbury et al., 2020

et al., 1988; Bonifay, 1990, 1996; Lister, 1996; Palombo and Valli, 2003–2004; Rook and Martinez-Navarro, 2010; Kahlke et al., 2011; Stefaniak, 2015).

Stephanorhinus etruscus was replaced by *S. hundsheimensis*, and *Elasmotherium caucasicum* by *E. sibiricum*. Two new representatives of the genus *Stephanorhinus*, namely *S. hemitoechus* and *S. kirchbergensis*, appeared at the end of the Middle Pleistocene. *Stephanorhinus hundsheimensis* reached the Czech Republic and Slovakia, while *S. kirchbergensis* is reported for the first time from Biliayivka (MIS 17), in Ukraine, marking one of the earliest occurrences of this species in Europe. *Elasmotherium sibiricum* has been recorded in the Middle Pleistocene of European Russia (Shvyreva, 2016).

The *Mammuthus–Coelodonta* faunal assemblage appeared in Europe about 480,000 years ago, at the beginning of MIS 12 (Guthrie, 1982, 1995; Vereshchagin and Baryshnikov, 1982; Kahlke, 1999, 2014; Kahlke et al., 2011). *Coelodonta antiquitatis* made its first appearance and rapidly spread throughout the studied area. The species appeared at the same time in Poland, Ukraine, and in other European localities (Kahlke, 1999, 2014; Kahlke and Lacombat, 2008; Deng et al., 2011; Kahlke et al., 2011; Pandolfi, 2018; Rey-Iglesia et al., 2021; Uzunidis et al., 2022). The only exception is the Czech Republic, which was not reached by rhinoceroses during MIS 12–6. At that time, *Stephanorhinus* cf. *hundsheimensis* or *Stephanorhinus* sp. was present in Slovakia, *S. kirchbergensis*, *Stephanorhinus* sp. and *Coelodonta antiquitatis* in Ukraine, and *C. antiquitatis*, *S. kirchbergensis* and *Elasmotherium sibiricum* in the European part of Russia. During MIS 12–6, *Coelodonta antiquitatis*, *Stephanorhinus hemitoechus*, and *S. kirchbergensis* were distributed in the south and west of Europe (Guérin, 1980; Made, 1999, 2001, 2010, 2010, 2015, 2010; Lacombat, 2003, 2005, 2006; Kahlke and Lacombat, 2008; Billia and Petronio, 2009; Billia, 2011; Kahlke et al., 2011; Pandolfi and Tagliacozzo, 2015; Pandolfi and Erten, 2017; Pandolfi, 2018; Shvyreva, 2016; Made et al., 2017; Pandolfi et al., 2021a).

The last significant spread and the final extinction of rhinos in Europe took place in the Late Pleistocene. During the Eemian Interglacial (MIS 5e), *Stephanorhinus kirchbergensis* appeared in Poland, in addition to the resident *Coelodonta antiquitatis*. Both species were also present in the Czech Republic at the time. *Stephanorhinus kirchbergensis* and *S. hemitoechus* characterised the Eemian Interglacial of Slovakia, while none of these species was present in Ukraine. *Coelodonta antiquitatis* and *Elasmotherium sibiricum* occurred in the European part of Russia. *Coelodonta antiquitatis*, *Stephanorhinus kirchbergensis* and *S. hemitoechus* were also distributed throughout Southern and Western Europe (Guérin, 1980; Kahlke, 1999; Made, 2010; Musil, 2010; Billia, 2011; Markova et al., 2013; Billia and Zervanová, 2014; Badura et al., 2017; Kirillova et al., 2017, 2021; Shpansky and Boeskorov, 2018; Puzachenko et al., 2022).

The timing and causes of extinction and final palaeogeographic distribution of *Stephanorhinus kirchbergensis*, *S. hemitoechus*, *Coelodonta antiquitatis* and *Elasmotherium sibiricum* remain unclear. *Elasmotherium sibiricum* and *Coelodonta antiquitatis* have been the subject of numerous studies. The last representatives of the genus *Elasmotherium* are dated to about 39 ka from Central Siberia. *Stephanorhinus hemitoechus* survived in Europe until the Last Glacial and probably became extinct by MIS 3. The species is last reported from Italy at ca. 35 ka. The fate of *Stephanorhinus kirchbergensis* is unclear in the youngest phases of the Vistulian Glacial (MIS 4 and MIS 3). The species likely disappeared from Europe at the onset of the cold phases of the Last Glacial (MIS 4). It was widely distributed throughout Asia and all the way north to northern Siberia at ca. 40 ka; the latest dated remains of Merck's rhino span MIS 2 and come from China, which may have been the last refugium for the species.

The woolly rhino and woolly mammoth became extinct in Europe at about 14 ka. During the Last Glaciation, *Coelodonta antiquitatis* was distributed throughout Europe. The areal distribution of radiocarbon-dated finds of the species indicate that its decline was gradual. It first disappeared from the British Isles and probably also from the whole Western European territory. In Poland, this species became extinct at 14.7 ka, in the GS-2a. It survived in the Middle Urals and Western Siberia up to 10.7 ka (Orlova et al., 2008; Boeskorov et al., 2009, 2011a, b; Kuzmin, 2010; Boeskorov, 2012; Markova et al., 2013; Khubanova et al., 2016; Shpansky, 2017; Kosintsev et al., 2019; Puzachenko et al., 2021a, b).

The woolly rhinoceros was rarely represented in Magdalenian art of Central Europe (Bosinski, 1982; Serangeli, 2006; Płonka, 2012). Twenty-two representations of this animal are known from four Magdalenian sites in Central Europe. Most of the figures were found at Gönnersdorf, in Rhineland (Bosinski, 1996, 2008); two pictures were identified at Děravá Cave (Klíma, 1971, 1985) and one from both Kniegrotte (Feustel, 1974; Höck, 2000) and Teufelsbrücke (Feustel, 1980; Housley et al., 1997), in Thüringen. The ones from Gönnersdorf and Děravá Cave were incised on stone slabs, whereas the figures from

Kniegrotte and Teufelsbrücke were incised on an antler grip (?) and on a hammer/retoucher, respectively. The rhinos were usually depicted in full size, with massive trunk and large distal nasal horn (Fig. 10). The latter was often figured exaggeratedly large, whereas nostrils, eyes and ears were completely omitted. The incised figures from Gönnersdorf and Děravá Cave are depicted with a set of lines issuing from the trunks, which could be interpreted as spears. The reproductions are so detailed to suggest that the woolly rhino were made as they appeared in nature, or perhaps, but less likely, copied from older representations. Most of the Gönnersdorf woolly rhino pictures were found, associated with most of the representations of the woolly mammoth, in the site's Concentration (hut) I. The rest of the pictures of the woolly rhino come from Concentration IIa, but they are rather sketchy. Raw material analysis showed that the settlers from the Concentration I used Baltic flint and had travelled about 80–100 km to the north to collect it (Bosinski, 1989). Settlers from the Concentration IIa made extensive use of Maas flint, which could be collected north-west from the site, where rhinos and mammoths were very rare. The Gönnersdorf, Kniegrotte and Teufelsbrücke are radiocarbon-dated to the end of the Oldest Dryas and Bølling Interstadial.

Changes in the Central and Eastern European Pleistocene megamammals have received little attention so far, surely not as much as an area that was a very important crossroad of faunal migration and/or a potential refugium would deserve (Sommer and Nadachowski, 2006; Doan et al., 2018, 2021; Stefaniak et al., 2021a; Rabiniak et al., 2023). The literature dedicated to this part of Europe is sparse (e.g., Stuart and Lister, 2012; Markova et al., 2013); no article aimed at providing a summary of current knowledge on the Pleistocene fauna of the area. As far as rhinos are concerned, Stefaniak et al. (2009a, b) and Nadachowski et al. (2015a, b, 2016) have contributed some information, but to date no comprehensive study has focused on the Central and Eastern European Quaternary members of these pachyderms. The results of this study are an addition to our knowledge on the diversity and distribution of Pleistocene rhinos of this region.

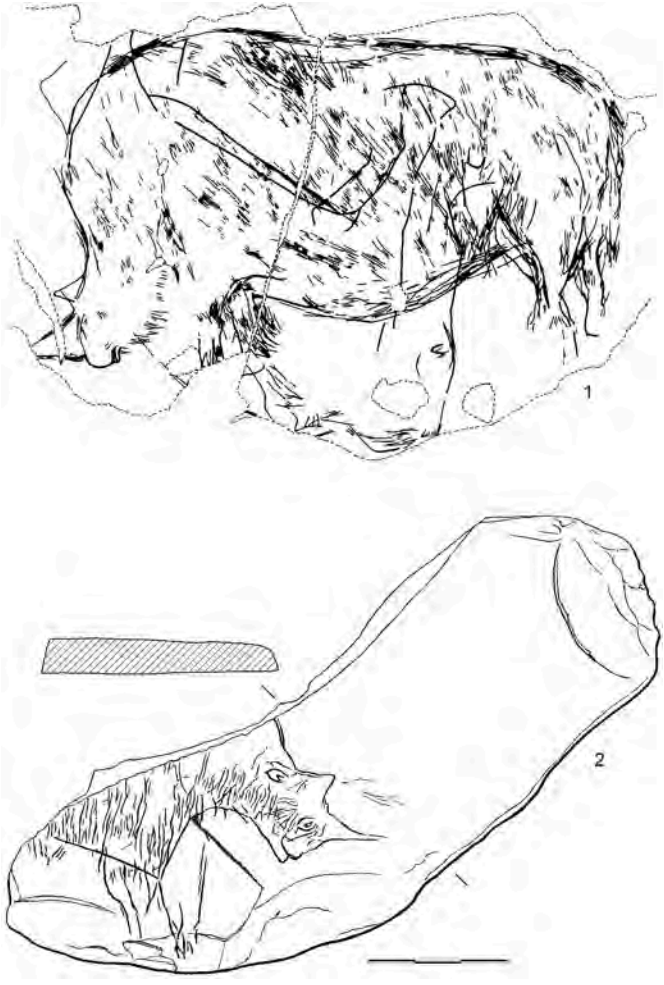

Fig. 10. Incised representations of the woolly rhino: 1 – Gönnersdorf, slab no. 88 + 89, 2 – Děravá Cave (after Bosinski, 2008).

6. Conclusions

Stephanorhinus kirchbergensis and *Coelodonta antiquitatis* roamed throughout Poland in the Quaternary. Based on the fossil remains from eight localities (included those from Wrocław-Hallera 1 which, however, were probably older), the former was present during the Eemian Interglacial (MIS 5e). The woolly rhino appeared during the Saalian 2 glaciation (Elsterian, MIS 12), marking the earliest occurrence of this species in Europe. The at least 186 localities that provided its remains, most of which dated to the Last Glacial, indicate that the woolly rhino survived the MIS 8 through MIS 6 glacials and interglacials.

The radiocarbon dates available so far for *Coelodonta antiquitatis* span MIS 3 and MIS 2. Most dates range from 46,000 through 42,000 cal yrs. BP. Based on these data, the woolly rhino became extinct in Poland in the GS-2a, by 14.7 ka. The fossil record of the species is punctuated with gaps in Poland, but further information is available. The record of the woolly rhino is especially defective at the end of MIS 3, in the LGM, between 25,000 and 22,000 cal yrs. BP.

Stephanorhinus hemitoechus is the first to appear in the Czech Republic, as attested to by the Early to Middle Pleistocene finds (MIS 23–22/21) from Koněprusy and the Middle Pleistocene ones (MIS 17–16) of Stránská Skála. *Stephanorhinus kirchbergensis* arrived in the Eemian Interglacial, but its presence is witnessed by remains from only two localities. *Coelodonta antiquitatis* also appeared in the Czech Republic during the Eemian Interglacial, but it distributed far more widely throughout the country and survived until the end of the last glaciation, as revealed by its fossil record from a total of 219 localities.

Slovakia was inhabited by a higher number of rhinos during the Quaternary, compared to Poland and the Czech Republic. *Stephanorhinus jeanvireti* and *S. etruscus* are recorded from the very beginning of the Pleistocene (late Villanyian, MNQ 17). *Stephanorhinus hundsheimensis*, a typical late Early Pleistocene to early Middle Pleistocene representative, was reported only from Slovakia in MIS 19 or MIS 17. On the other hand, *Stephanorhinus kirchbergensis* and *S. hemitoechus* distributed widely in Slovakia during the Eemian Interglacial (MIS 5e), preceded by the woolly rhino which appeared in the Saalian (MIS 6) and lasted until MIS 3, as indicated by evidence, some of which radiocarbon-dated, from 20 Late Pleistocene Slovakian localities. *Stephanorhinus etruscus* first appeared in Ukraine during the Early Pleistocene. *Stephanorhinus kirchbergensis* during a temperate cycle, either MIS 17 (Martonosha Interglacial) or MIS 11 (Zavadivka Interglacial). The earliest woolly rhino appeared in Ukraine in MIS 13–12, approximately at the same time as in Poland and the whole of Europe. It is also reported from deposits dated to MIS 11–9, MIS 8, the Saalian (MIS 6), various phases of the last glaciation, and a few dates indicate that it apparently survived until MIS 3.

In the Early Pleistocene, Ukraine was home to the earlier *Elasmotherium peii* and the later *E. caucasicum,* as well as to the still uncertainly identified *Elasmotherium* sp.

At the end of the Pliocene and in the Early Pleistocene, the Carpathians represented an insuperable barrier for *Stephanorhinus jeanvireti* and *S. etruscus* which never made it to Poland. Ukraine and Moldova were the furthest west *Elasmotherium* could get: probably these giant rhinos could not find environments suitable for them beyond these territories.

Author contributions

KS, OK, PM, AN, BR and MS conceptualized the study. URS, PM and TP prepared the figures. All authors wrote the original draft of the manuscript and participated in its editing.

Declaration of competing interest

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

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.quaint.2023.02.004.

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Chronology and distribution of Central and Eastern European Pleistocene rhinoceroses (Perissodactyla, Rhinocerotidae) – A review

Krzysztof Stefaniak[a], Oleksandr Kovalchuk[a,b,*], Urszula Ratajczak-Skrzatek[a], Aleksandra Kropczyk[a], Paweł Mackiewicz[c], Grzegorz Kłys[d], Magdalena Krajcarz[e], Maciej T. Krajcarz[f], Adam Nadachowski[g], Grzegorz Lipecki[g], Karol Karbowski[a], Bogdan Ridush[h], Martin Sabol[i], Tomasz Płonka[j]

[a]*Department of Palaeozoology, Faculty of Biological Sciences, University of Wrocław, Wrocław, Poland*

[b]*Department of Palaeontology, National Museum of Natural History, National Academy of Sciences of Ukraine, Kyiv, Ukraine*

[c]*Department of Bioinformatics and Genomics, Faculty of Biotechnology, University of Wrocław, Wrocław, Poland*

[d]*Institute of Biology, Opole University, Opole, Poland*

[e]*Institute of Archaeology, Nicolaus Copernicus University in Toruń, Toruń, Poland*

[f]*Institute of Geological Sciences, Polish Academy of Sciences, Research Centre in Warsaw, Warszawa, Poland*

[g]*Institute of Systematics and Evolution of Animals, Polish Academy of Science, Kraków, Poland*

[h]*Department of Physical Geography, Geomorphology and Palaeogeography, Yuriy Fedkovych Chernivtsi National University, Chernivtsi, Ukraine*

[i]*Department of Geology and Paleontology, Faculty of Natural Sciences, Comenius University in Bratislava, Bratislava, Slovakia*

[j]*Department of Stone Age Archaeology, Institute of Archaeology, Faculty of Historical and Pedagogical Sciences, University of Wrocław, Wrocław, Poland*

* Corresponding author. E-mail address: biologiest@ukr.net (O. Kovalchuk).

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Chronology and distribution of Central and Eastern European Pleistocene rhinoceroses (Perissodactyla, Rhinocerotidae) – A review

Krzysztof Stefaniak[a], Oleksandr Kovalchuk[a,b,*], Urszula Ratajczak-Skrzatek[a], Aleksandra Kropczyk[a], Paweł Mackiewicz[c], Grzegorz Kłys[d], Magdalena Krajcarz[e], Maciej T. Krajcarz[f], Adam Nadachowski[g], Grzegorz Lipecki[g], Karol Karbowski[a], Bogdan Ridush[h], Martin Sabol[i], Tomasz Płonka[j]

[a]*Department of Palaeozoology, Faculty of Biological Sciences, University of Wrocław, Wrocław, Poland*

[b]*Department of Palaeontology, National Museum of Natural History, National Academy of Sciences of Ukraine, Kyiv, Ukraine*

[c]*Department of Bioinformatics and Genomics, Faculty of Biotechnology, University of Wrocław, Wrocław, Poland*

[d]*Institute of Biology, Opole University, Opole, Poland*

[e]*Institute of Archaeology, Nicolaus Copernicus University in Toruń, Toruń, Poland*

[f]*Institute of Geological Sciences, Polish Academy of Sciences, Research Centre in Warsaw, Warszawa, Poland*

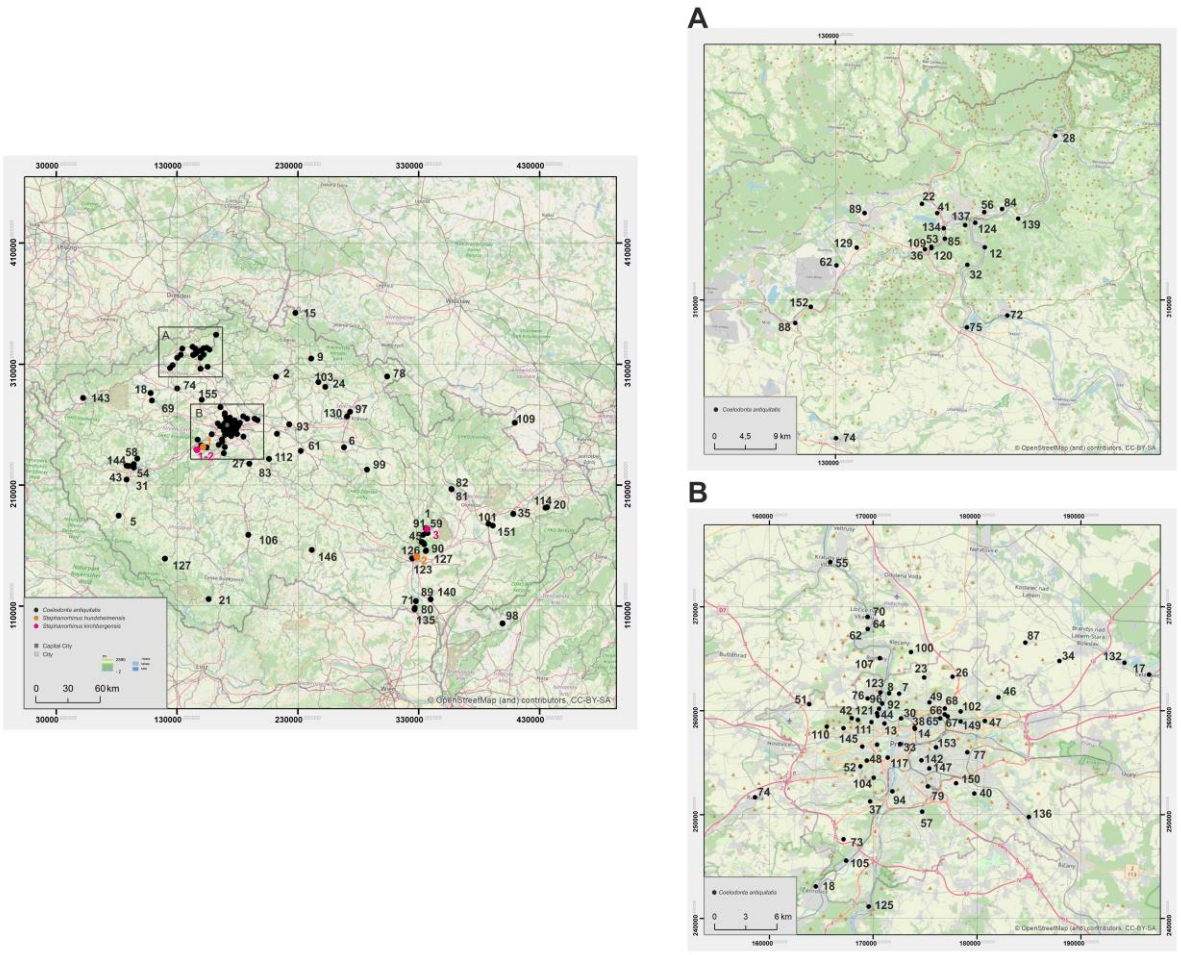
[g]*Institute of Systematics and Evolution of Animals, Polish Academy of Science, Kraków, Poland*

[h]*Department of Physical Geography, Geomorphology and Palaeogeography, Yuriy Fedkovych Chernivtsi National University, Chernivtsi, Ukraine*

[i]*Department of Geology and Paleontology, Faculty of Natural Sciences, Comenius University in Bratislava, Bratislava, Slovakia*

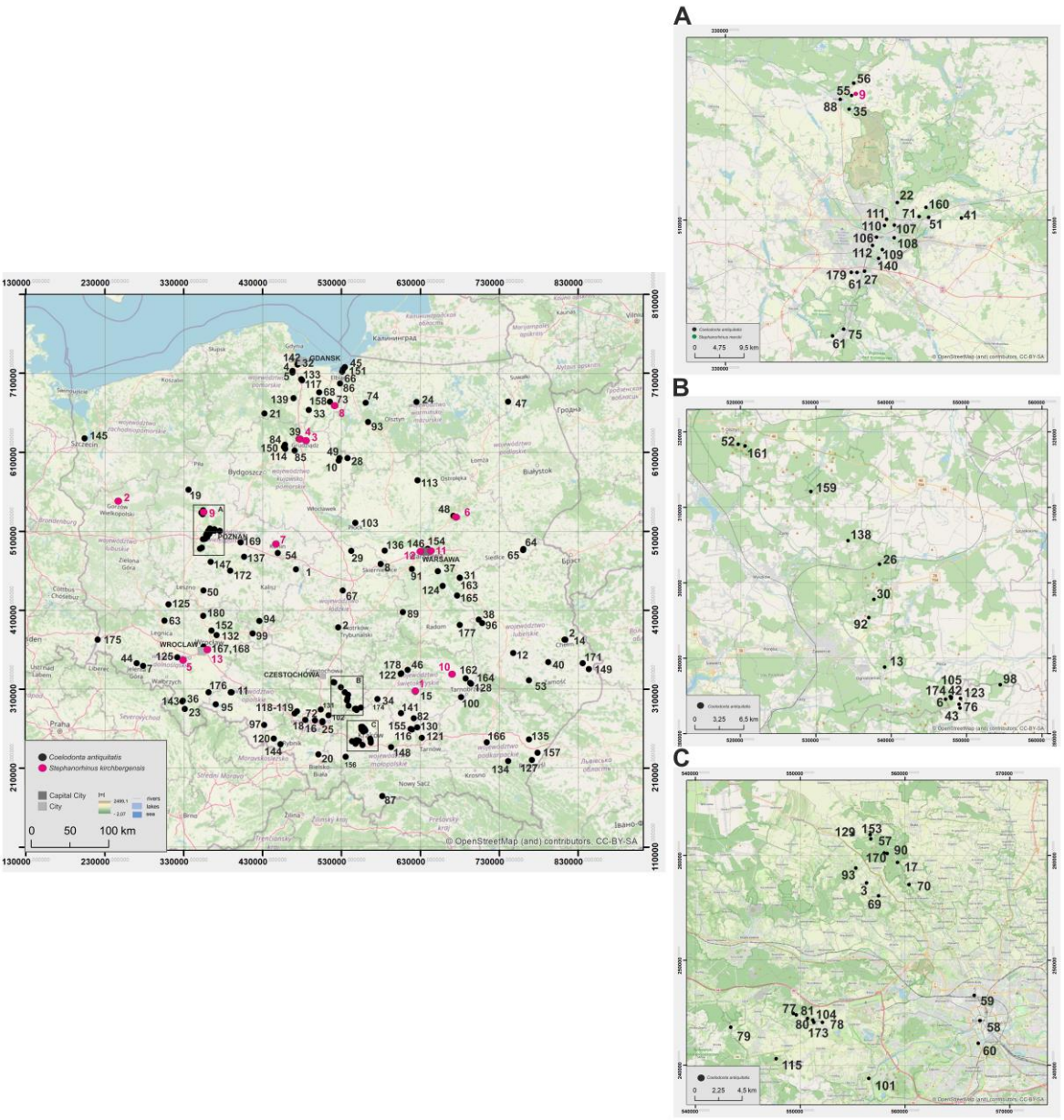
[j]*Department of Stone Age Archaeology, Institute of Archaeology, Faculty of Historical and Pedagogical Sciences, University of Wrocław, Wrocław, Poland*

* Corresponding author: biologiest@ukr.net (O. Kovalchuk).



Distribution of Pleistocene localities yielding rhino remains in the Czech Republic. ***Coelodonta antiquitatis:*** 0 – Balcarova skála, Balcarka Cave, 1 – Balov, 2 – Barová Cave, 3 – Beroun - Eternitka / Hýskov, 4 – Bezděkov, 5 – Blato, 6 – Bohnice, 7 – Bohnice,Podhoří, 8 – Božkov, 9 – Břevnov, Panenská, 10 – Březno, Langova cihelna, 11 – Brná, 12 – Bubeneč, 13 – Bubny, 14 – Bulovka, 15 – Býčí skála, 16 – Čelákovice, 17 – Čeradice, 18 – Černošice, 19 – Čertova díra, 20 – Český Krumlov, dobrkovická, 21 – Chabařovice, důl Petří, 22 – Chabry, 23 – Chotěč, 24 – Chotutice, 25 – Ďáblice, 26 – Davle, 27 – Děčín, 28 – Dejvice, 29 – Dejvice, Stromovka, 30 – Dobřany, 31 – Dolní Chabry, 32 – Dolní Zálezly, 33 – Dřevčice,cihelna, 34 – Hlavicova Cave, 35 – Hliňany, 36 – Hlubočepy, 37 – Holešovice, 38 – Holešovice, jatka, 39 –Hostím, jeskyně nad Kačákem, 40 – Hostivař, 41 – Hrbovice, 42 – Jenerálka, 43 – Jikalka, 44 – Juliska, 45 – Katařinská Cave, 46 – Kbely, 47 – Kbely, cihelna, 48 – Klanovka, 49 – Kobylisy, 50 –

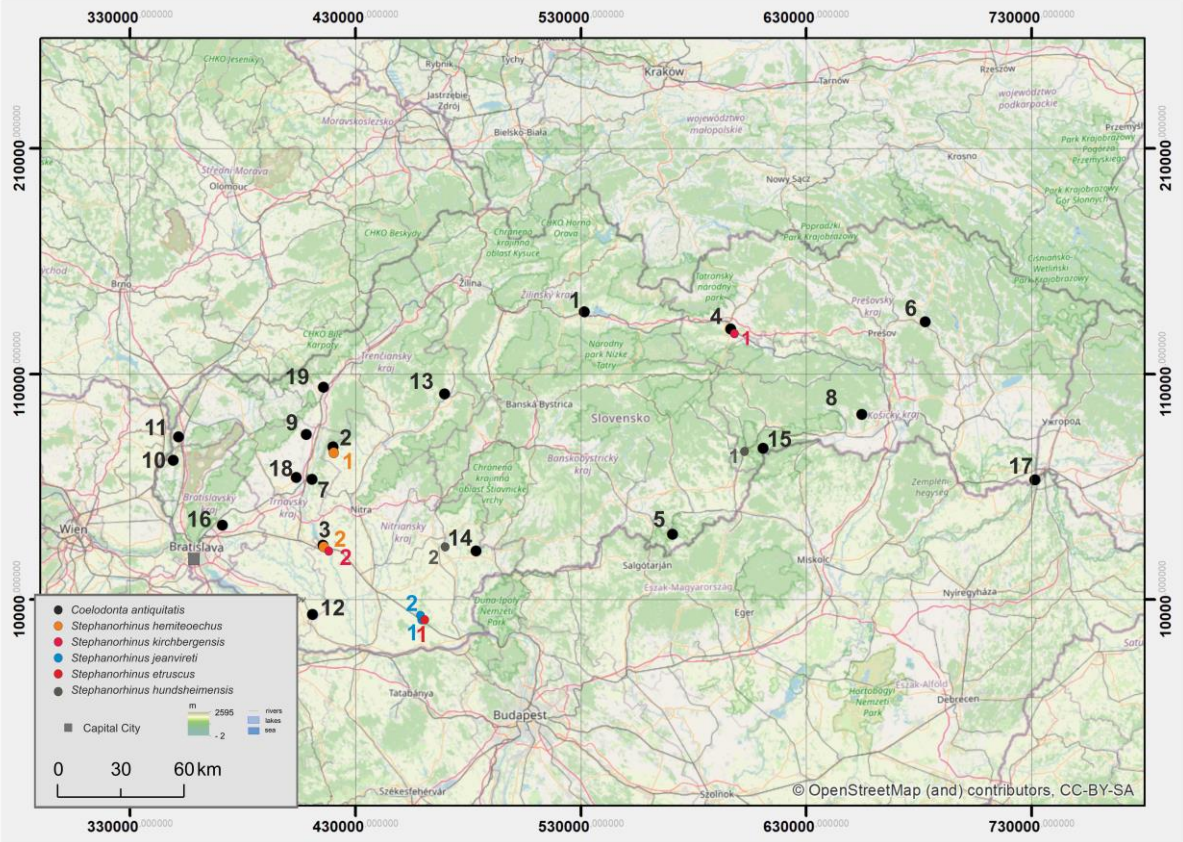
Koněprusy, 51 – Košíře, 52 – Koštov, 53 – Košutka, 54 – Kralupy, 55 – Krásné Březno, 56 – Krč, 57 – Křimice, 58 – Křimice-Košutka, 59 – Kůlna Cave, 60 – Kutná hora, 61 – Ledvice, 62 – Letky, 63 – Libčice, 64 – Libeň, 65 – Libeň, Báně, 66 – Libeň, Kundrátka, 67 – Libeň, Střížkovská ulice, 68 – Libořice, 69 – Libřice nad Vltavou, 70 – Liščí díra, 71 – Litoměřice, 72 – Lochkov, 73 – Louny, 74 – Lovosice, 75 – Lysolaje, 76 – Malešice, 77 – Manžusko, 78 – Michle, 79 – Mikulov, 80 – Mladeč, 81 – Mladečské jeskyně (I-II), 82 – Mráč, 83 – Neštěmice, 84 – Nové Stadice, 85 – Novosedlice, 86 – Nový Brázdim, 87 – Obrnice, 88 – Pavlov I (Southeast), 89 – Pekárna Cave, 90 – Pod hradem, 91 – Podbaba, 92 – Poděbrady, 93 – Podolí, Dvorce, 94 – Praha, 95 – Praha - Podbaba, 96 – Předměřice, 97 – Předmostí, 98 – Předradí, 99 – Přemyšlany, 100 – Přerov, 101 – Prosek, 102 – Radim, 103 – Radlice, 104 – Radotín, 105 – Roudná, 106 – Roztoky, 107 – Rudná-Hořelce, 108 – Rusko, 109 – Šárka, 110 – Šárka ,Dubový mlýn, 111 – Sázava, Bílí kámen, 112 – Sedlec u Prahy, 113 – Šipka Cave, 114 – Sklep, 115 – Sloupské jeskyně, 116 – Smíchov, 117 – Šošůvská Cave, 118 – Srbsko, Chlum, Poslední dóm, 119 – Stadice, 120 – Šťáhlavka, 121 – Strahov, 122 – Stránská Skála III and IIIa, 123 – Střekov, 124 – Strnady, cihelna, 125 – Štýřice III, 126 – Sudslavice II, 127 – Švédův stůl, 128 – Světec u Bíliny, 129 – Svobodné dvory, 130 – Tetín, Turská maštal, poslední síň, 131 – Toušeň,cihelna, 132 – Třemošná, 133 – Trmice, 134 – Turold, 135 – Uhříněves,Středočeské cihelny, 136 – Ústí nad Labem, 137 – V Hložku, 138 – Velké březno, 139 – Velké Pavlovice, 140 – Vinckova Cave, 141 – Vinohrady, 142 – Vintířov, 143 – Vochov, 144 – Vokovice, 145 – Volevčice, 146 – Vršovice, 147 – Výpustek, 148 – Vysočany, 149 – Záběhlice, 150 – Želatovice, 151 – Želenice, 152 – Žižkov, 153 – Zkamenělý zámek, 154 – Zlonice. ***Stephanorhinus hundsheimensis:*** 1 – Srbsko, Chlum, IV layer, 2 – Stránská Skála. ***Stephanorhinus kirchbergensis:*** 1 – Koněprusy, Kobyla, Chlupáčova sluj, 2 – Koněprusy, Zlatý kůň, Petrbokova sloj, 3 – Kůlna Cave.



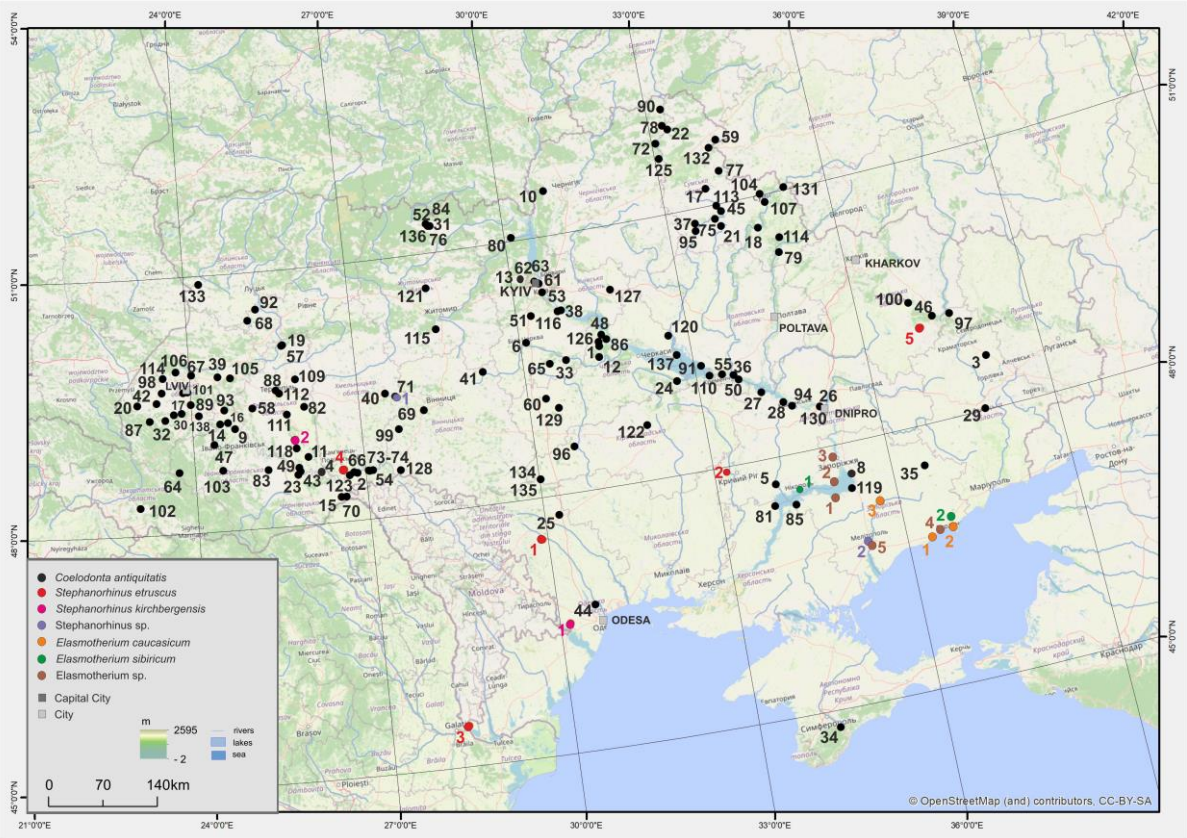
Distribution of Pleistocene localities yielding rhino remains in Poland. ***Coelodonta antiquitatis:*** 1 – "Adamów" Turek Brown Coal Mine, 2 – Belchatów Brown Coal Mine, 3 – Bębłowskie Dolne Rock Shelter, 4 – Bielkowo, county Gdańsk, 5 – Bielkówko, county Gdańsk, 6 – Biśnik Cave, 7 – Bobrów, 8 – Bolimów, 9 – Borsucza Cave, 10 – Brodnica, 11 – Brzeziny, 12 – Bychawa, 13 – Cave IV on Mt. Birów, 14 – Chełm, 15 – Chmielnik quarry, 16 – Chorzów, 17 – Ciemna Cave, 18 – Czarnawka stream near Zabrze, 19 – Czarnków, 20 – Czechowice-Dziedzice, 21 – Czersk, 22 – Czerwonak (Poznań, Czerwonak), 23 – Czerwoniak, county Kłodzko, 24 –

Czerwonka, county Reszel, 25 – Dąbrówka Mała, 26 – Deszczowa Cave, 27 – Dębiec near Poznań, 28 – Długi Most, county Brodnica, 29 – Dobrzylin, county Kutno, 30 – Dziadowa Skała Cave, 31 – Garwolin, 32 – Gdańsk, Cyganki, 33 – Gniew, 34 – Gniewięcin near Sędziszów, 35 – Gołaszyn, county Oborniki, 36 – Gorzóchów, 37 – Góra Kalwaria, 38 – Góra Puławska, 39 – Grupa, county Świecie, 40 – Izbica near Krasnystaw, 41 – Jankowo, county Środa, 42 – Jasna Smoleńska Cave, 43 – Jasna Strzegowska Cave, 44 – Jelenia Góra, 45 – Kadyny, county Elbląg, 46 – Kadzielnia, 47 – Kalinowo, county Ełk, 48 – Kamieńczyk, 49 – Karbowo, county Brodnica, 50 – Karzec, county Gostyń, 51 – Kobylnica, county Poznań, 52 – Komarowa Cave, 53 – Komodzianka, county Zamość, 54 – "Konin" Brown Coal Mine, 55 – Kowanowo, county Oborniki, 56 – Kowanówko, county Oborniki, 57 – Koziarnia Cave, 58 – Kraków Spadzista Street, 59 – Kraków, Krowodrza, 60 – Kraków, Ludwinów, 61 – Krosinko, 62 – Lubań, county Poznań, 63 – Lubin, 64 – Ławy near Łosice, 65 – Ławy near Siedlce, 66 – Łęcze, county Elbląg, 67 – Łódź, 68 – Malbork, 69 – Mamutowa Cave, 70 – Maszycka Cave, 71 – Mechowo near Swarzędz, 72 – Milowice, Sosnowiec, 73 – Minięta, county Sztum, 74 – Morąg, 75 – Mosina, 76 – Mroczna in Pośrednica Cave, 77 – Murek Cave, 78 – Na Gaiku II Rock Shelter, 79 – Na Wrzosach Południowa Cave, 80 – Nad Matką Boską Cave, 81 – Nad Potoczkiem Rock Shelter, 82 – Nida River near Czarkowy, 83 – Nietoperzowa Cave, 84 – Nowa Dęba, county Świecie, 85 – Nowawieś Chełmińska, 86 – Nowe Pole, county Elbląg, 87 – Obłazowa Cave, 88 – Oborniki, 89 – Odrzywół near Nowe Miasto n. Pilicą, 90 – Ojców, undefined cave, 91 – Ojrzanów near Mszczonów, 92 – Okkiennik Cave (Okiennik Rock Sheleter), 93 – Ostróda, 94 – Ostrzeszów, 95 – Otmuchów, county Grodków, 96 – Parchatka near Puławy, 97 – Pawłowiczki, county Koźle, 98 – Perspektywiczna Cave, 99 – Perzów, county Kępno, 100 – Piaseczno, 101 – Piekary, Na Gołąbcu Cave, 102 – Pillar sand mine" Kuźnica Warężyńska S.A." in Dąbrowa Górnicza, 103 – Płock, 104 – Pod Kochanką Cave, 105 – Południowe Rock Shelter; Shelter above Zegar Cave, 106 – Poznań, 107 – Poznań, Główna, 108 – Poznań, Malta, 109 – Poznań, Rataje, 110 – Poznań, Szeląg, 111 – Poznań, Wilczy Młyn, 112 – Poznań, Wilda, 113 – Przasnysz, 114 –

Przechówko, county Świecie, 115 – Przegińska Cave, 116 – Przemyków county Proszowice, 117 – Pszczółki, county Gdańsk, 118 – Pyskowice, 119 – Pyskowice-Dzierżno, 120 – Racibórz-Ostróg, 121 – Radłów near Tarnów, 122 – Raj Cave, 123 – Rock-Shelter in Strzegowa, Zaciszna Cave, 124 – Rozniszew, Pilica River, 125 – Rusko, 126 – Rzeczyca near Pyskowice, 127 – San River near Przemyśl, 128 – Sandomierz, 129 – Sąspowska Zachodnia Cave, 130 – Siedliszowice, Dunajec River, 131 – Siemonia, 132 – Skarszyn, 133 – Skowarcz, county Gdańsk, 134 – Słonne, county Dubiecko, 135 – Sobiecin, county Jarosław, 136 – Sochaczew, 137 – Spławie neat Pyzdry, 138 – Stajnia Cave, 139 – Starogard Gdański, 140 – Starołęka, county Poznań, 141 – Stradów, county Czarnocin, 142 – Suchanino, county Gdańsk, 143 – Swięcko, county Kłodzko, 144 – Syrynia, 145 – Szczecin, 146 – Szczęśliwickie Lake, 147 – Śrem, 148 – Targowsiko gravel pit, 149 – Tatarska Góra, county Hrubieszów, 150 – Terespol Pomorski, county Świecie, 151 – Tolkmicko, county Elbląg, 152 – Trzebnica, 153 – Tunel Wielki, 154 – Vistula River near Warsaw, 155 – Vistula River, Wola Przemkowska, 156 – Wadowice, 157 – Walawa, county Radymno, 158 – Waplewo Wielkie, county Sztum, 159 – Wiercica Cave, 160 – Wierzenica, county Poznań, 161 – Wilcze I Rock Shelter; Schronisko w Górach Sokolich III, 162 – Wilczyce, 163 – Wilga River Valley county Garwolin, 164 – Winnica Mountain near Kamień Mściowski, 165 – Wisła River, Maciejowice, 166 – Wisłok River, Rzeszów, Lisia Góra, 167 – Wrocław Hallera Street 1, 168 – Wrocław-Oporów, 169 – Września, 170 – Wylotne Rock Shelter, 171 – Zadębce, county Hrubieszów, 172 – Zalesie, county Jarocin, 173 – Zawalona cave, 174 – Zegar Cave, 175 – Zgorzelec, 176 – Ziębice, 177 – Zwoleń, 178 – Zygmuntówka Quarry near Chęciny, 179 – Żabikowo, Luboń, 180 – Żmigród. ***Stephanorhinus kirchbergensis:*** 1 – Chmeilnik quarry, 2 – Gorzów Wielkopolski, 3 – Grudziądz, Wisła River, 4 – Grupa, county Świecie, 5 – Imbramowice, 6 – Kamieńczyk, 7 – "Konin" Brown Coal Mine, 8 – Minięta, county Sztum, 9 – Oborniki, 10 – Opatów, 11 – Siekierki, Wisła River, 12 – Szczęśliwice, 13 – Wrocław Hallera Street 1.



Distribution of Pleistocene localities yielding rhino remains in Slovakia. ***Coelodonta antiquitatis:*** 1 – Bešeňová-Báňa, 2 – Čertova pec Cave, 3 – Dlhá n/Váhom, 4 – Gánovce, 5 – Hajnáčka, 6 – Hanušovce nad Topľou, 7 – Hlohovec, 8 – Hodkovce, 9 – Krakovany - Strážov, 10 – Malé Leváre, 11 – Moravský Ján, 12 – Okoč, 13 – Prepoštská jaskyňa Cave, 14 – Santovka, 15 – Silická Brezová, 16 – Slovenský Grob, 17 – Tisa River, 18 – Trakovice, 19 – Trenčianske Bohuslavice – Pod Tureckom. ***Stephanorhinus hemitoechus:*** 1 – Čertova pec Cave, 2 – Šaľa. ***Stephanorhinus kirchbergensis:*** 1 – Gánovce, 2 – Šaľa. ***Stephanorhinus jeanvireti:*** 1 – Nová Vieska, 2 – Strekov. ***Stephanorhinus etruscus:*** 1 – Nová Vieska. ***Stephanorhinus hundsheimensis:*** 1 – Gombasek, 2 – Levický vápnik.



Distribution of Pleistocene localities yielding rhino remains in Ukraine. ***Coelodonta antiquitatis:*** 1 – Babychi, 2 – Babyn I, 3 – Bakhmut (Artemivsk), 4 – Balamutivka Kostatiiv Yar, 5 – Bazavluk (Sholokhove), 6 – Bila Tserkva, 7 – Bilche, 8 – Bilenke, 9 – Bilshivtsi, 10 – Birky, 11 – Borshchiv, 12 – Brovakhy, 13 – Bucha, 14 – Bukachivtsi, 15 – Bukovynka Cave, 16 – Burshtyn, 17 – Buryn, 18 – Byshkin, 19 – Bear Cave, 20 – Chapli, 21 – Chervona Sloboda, 22 – Chulativ I, 23 – Chunkiv, 24 – Chygyryn, 25 – Demydivka, 26 – Dnipro, 27 – Dniprovo-Kamianka, 28 – Dniprovske, 29 – Donetsk, 30 – Dovge, 31 – Dovgynychi, 32 – Drohobych, 33 – Dybyntsi, 34 – Emine-Bair-Khosar, 35 – Fedorivka, 36 – Gorishni Plavni, 37 – Haii, 38 – Halepia, 39 – Hlyniany, 40 – Holovchyntsi, 41 – Hopchytsia, 42 – Hordynia, 43 – Horodok, 44 – Illinka, 45 – Ivanytsia, 46 – Izium, 47 – Kalush, 48 – Kaniv, 49 – Kasperivtsi, 50 – Keleberda, 51 – Kodak, 52 – Koptivshchyna, 53 – Korchuvate, 54 – Korman IV, 55 – Kremenchuk, 56 – Malo-Kokhnovsky Quarry, 57 – Kremenets, 58 – Kryve, 59 – Kucherivka, 60 – Kuty, 61 – Kyiv, Hlybochytsia, 62 – Kyiv, Kurenivka, 63 – Kyiv, Kyrylivska, 64 – Liskovets, 65 – Lisovychi, 66 – Luka Vrublivetska, 67 – Lviv, 68 – Lypa, Polishchukiv Riv, 69 – Lysianka, 70 – Malimon-

Canyon Cave, 71 – Medzhybizh, 72 – Mizyn, 73 – Molodova I, 74 – Molodova V, 75 – Nedryhailiv, 76 – Norynsk, 77 – Nova Sloboda, 78 – Novgorod-Siverskyi, 79 – Okhtyrka, 80 – Orane, 81 – Osokorivka, 82 – Ostapove, 83 – Ostrivets, 84 – Ovruch, 85 – Pavlokichkas, 86 – Pekari, 87 – Pidbuzh, 88 – Proniatyn, 89 – Pryima I, 90 – Pushkari I, 91 – Pyvykha, 92 – Radomyshl, 93 – Rohatyn, 94 – Romankove, 95 – Romny, 96 – Rozsohuvatets, 97 – Rubtsi, 98 – Rudky, 99 – Semenky, 100 – Shchurivka, 101 – Shchyrets, 102 – Sobatyn, 103 – Starunia, 104 – Stetskivka, 105 – Stinka, 106 – Stradch, Pishchana Gora, 107 – Sumy, 108 – Syniakove, 109 – Syniava, 110 – Taburyshche, 111 – Terebovlia, 112 – Ternopil, 113 – Terny, 114 – Trostianets, 115 – Troyaniv, 116 – Trypillia, 117 – Tuchapy, 118 – Ulashkivtsi, 119 – Vasylivka, 120 – Velyka Burimka, 121 – Horoshiv, 122 – Volodymyrivka, 123 – Voronovytsia, 124 – Vyniava, 125 – Vyshenky, 126 – Yabluniv, 127 – Yagotyn, 128 – Yaryshiv, 129 – Yurpil, 130 – Zaporizhia, 131 – Zapsillia, 132 – Zarutske, 133 – Zaslavok, 134 – Zavadivka, 135 – Zavallia, 136 – Zbranky, 137 – Zhovnyne, 138 – Zhydachiv. ***Stephanorhinus etruscus:*** 1 – Dolynske, 2 – Mudrene, 3 – Reni, 4 – Shutnivtsi, 5 – Velyka Komyshuvakha. ***Stephanorhinus kirchbergensis:*** 1 – Biliayivka, 2 – Syniakove 1. ***Stephanorhinus* sp.:** 1 – Medzhybizh, 2 – Pishchane. ***Elasmotherium caucasicum:*** 1 – Berdiansk, 2 – Nogaisk, 3 – Tokmak. ***Elasmotherium sibiricum:*** 1 – Nikopol, 2 – Osypenko. ***Elasmotherium* sp.:** 1 – Balky, 2 – Bilenke, 3 – Khortytsia, 4 – Nogaisk, 5 – Pishchana Balka.

Chronology and distribution of Central and Eastern European Pleistocene rhinoceroses (Perissodactyla, Rhinocerotidae) – A review

Krzysztof Stefaniak[a], Oleksandr Kovalchuk[a,b,*], Urszula Ratajczak-Skrzatek[a], Aleksandra Kropczyk[a], Paweł Mackiewicz[c], Grzegorz Kłys[d], Magdalena Krajcarz[e], Maciej T. Krajcarz[f], Adam Nadachowski[g], Grzegorz Lipecki[g], Karol Karbowski[a], Bogdan Ridush[h], Martin Sabol[i], Tomasz Płonka[j]

[a]*Department of Palaeozoology, Faculty of Biological Sciences, University of Wrocław, Wrocław, Poland*

[b]*Department of Palaeontology, National Museum of Natural History, National Academy of Sciences of Ukraine, Kyiv, Ukraine*

[c]*Department of Bioinformatics and Genomics, Faculty of Biotechnology, University of Wrocław, Wrocław, Poland*

[d]*Institute of Biology, Opole University, Opole, Poland*

[e]*Institute of Archaeology, Nicolaus Copernicus University in Toruń, Toruń, Poland*

[f]*Institute of Geological Sciences, Polish Academy of Sciences, Research Centre in Warsaw, Warszawa, Poland*

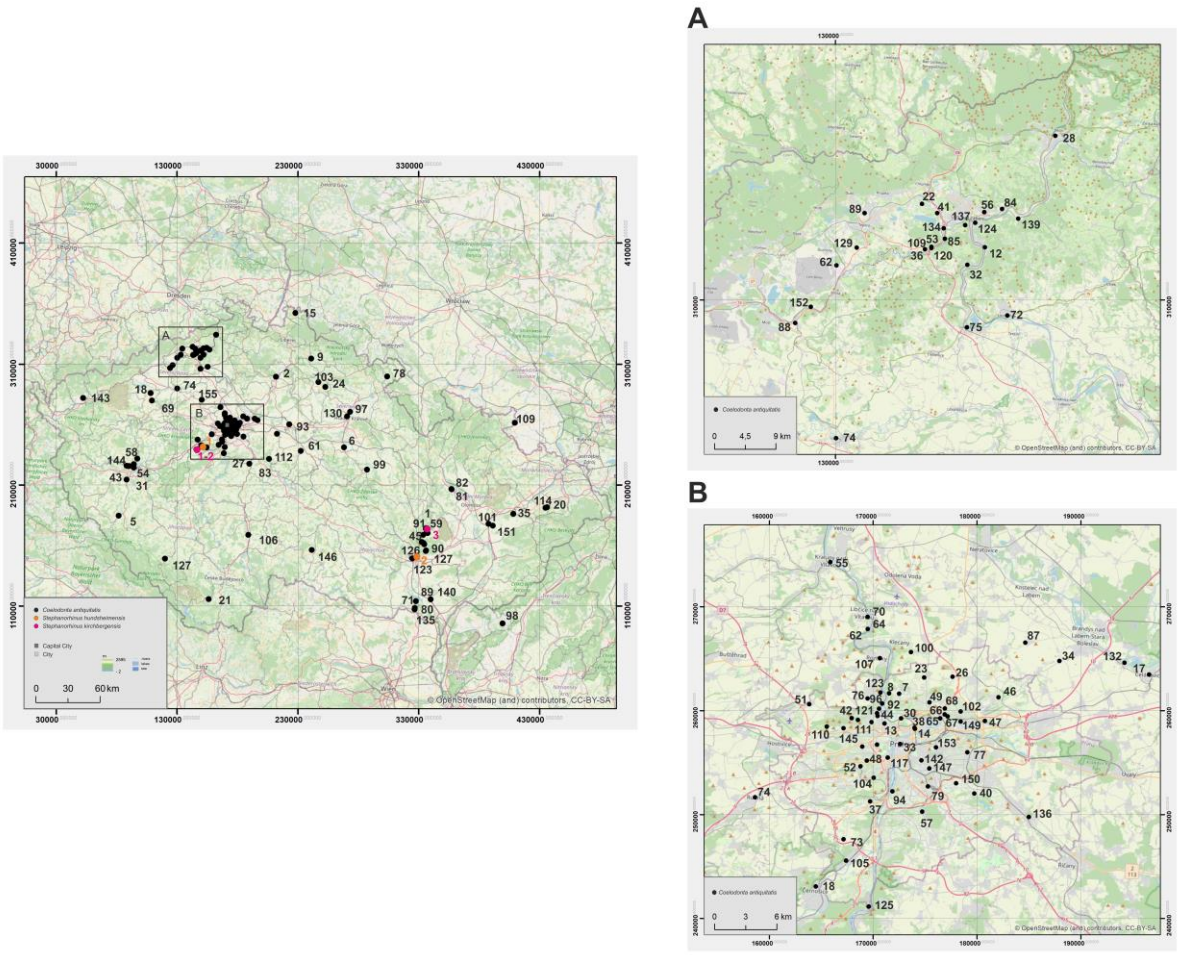
[g]*Institute of Systematics and Evolution of Animals, Polish Academy of Science, Kraków, Poland*

[h]*Department of Physical Geography, Geomorphology and Palaeogeography, Yuriy Fedkovych Chernivtsi National University, Chernivtsi, Ukraine*

[i]*Department of Geology and Paleontology, Faculty of Natural Sciences, Comenius University in Bratislava, Bratislava, Slovakia*

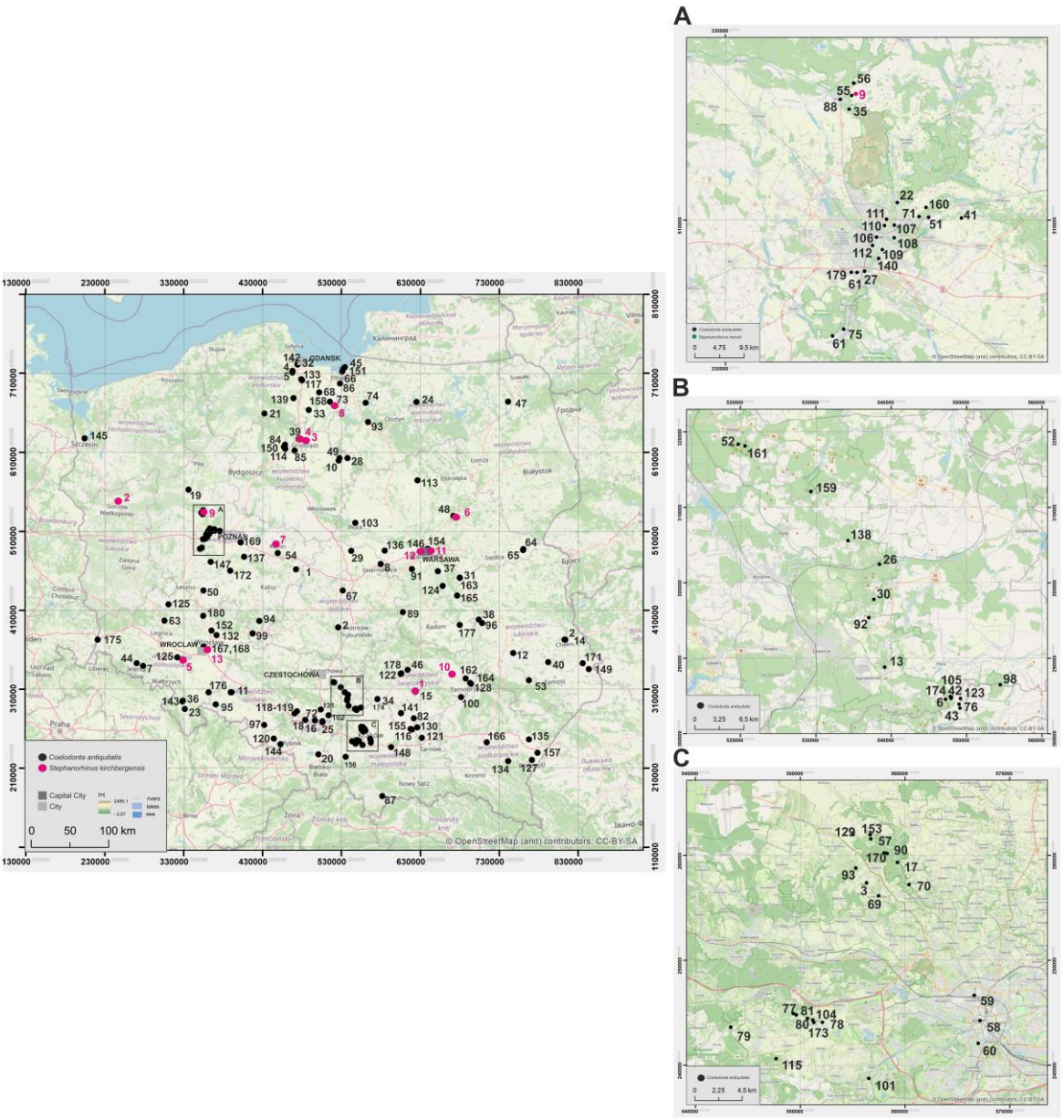
[j]*Department of Stone Age Archaeology, Institute of Archaeology, Faculty of Historical and Pedagogical Sciences, University of Wrocław, Wrocław, Poland*

* Corresponding author: biologiest@ukr.net (O. Kovalchuk).



Distribution of Pleistocene localities yielding rhino remains in the Czech Republic. ***Coelodonta antiquitatis:*** 0 – Balcarova skála, Balcarka Cave, 1 – Balov, 2 – Barová Cave, 3 – Beroun - Eternitka / Hýskov, 4 – Bezděkov, 5 – Blato, 6 – Bohnice, 7 – Bohnice,Podhoří, 8 – Božkov, 9 – Břevnov, Panenská, 10 – Březno, Langova cihelna, 11 – Brná, 12 – Bubeneč, 13 – Bubny, 14 – Bulovka, 15 – Býčí skála, 16 – Čelákovice, 17 – Čeradice, 18 – Černošice, 19 – Čertova díra, 20 – Český Krumlov, dobrkovická, 21 – Chabařovice, důl Petří, 22 – Chabry, 23 – Chotěč, 24 – Chotutice, 25 – Ďáblice, 26 – Davle, 27 – Děčín, 28 – Dejvice, 29 – Dejvice, Stromovka, 30 – Dobřany, 31 – Dolní Chabry, 32 – Dolní Zálezly, 33 – Dřevčice,cihelna, 34 – Hlavicova Cave, 35 – Hliňany, 36 – Hlubočepy, 37 – Holešovice, 38 – Holešovice, jatka, 39 –Hostím, jeskyně nad Kačákem, 40 – Hostivař, 41 – Hrbovice, 42 – Jenerálka, 43 – Jikalka, 44 – Juliska, 45 – Katařinská Cave, 46 – Kbely, 47 – Kbely, cihelna, 48 – Klanovka, 49 – Kobylisy, 50 –

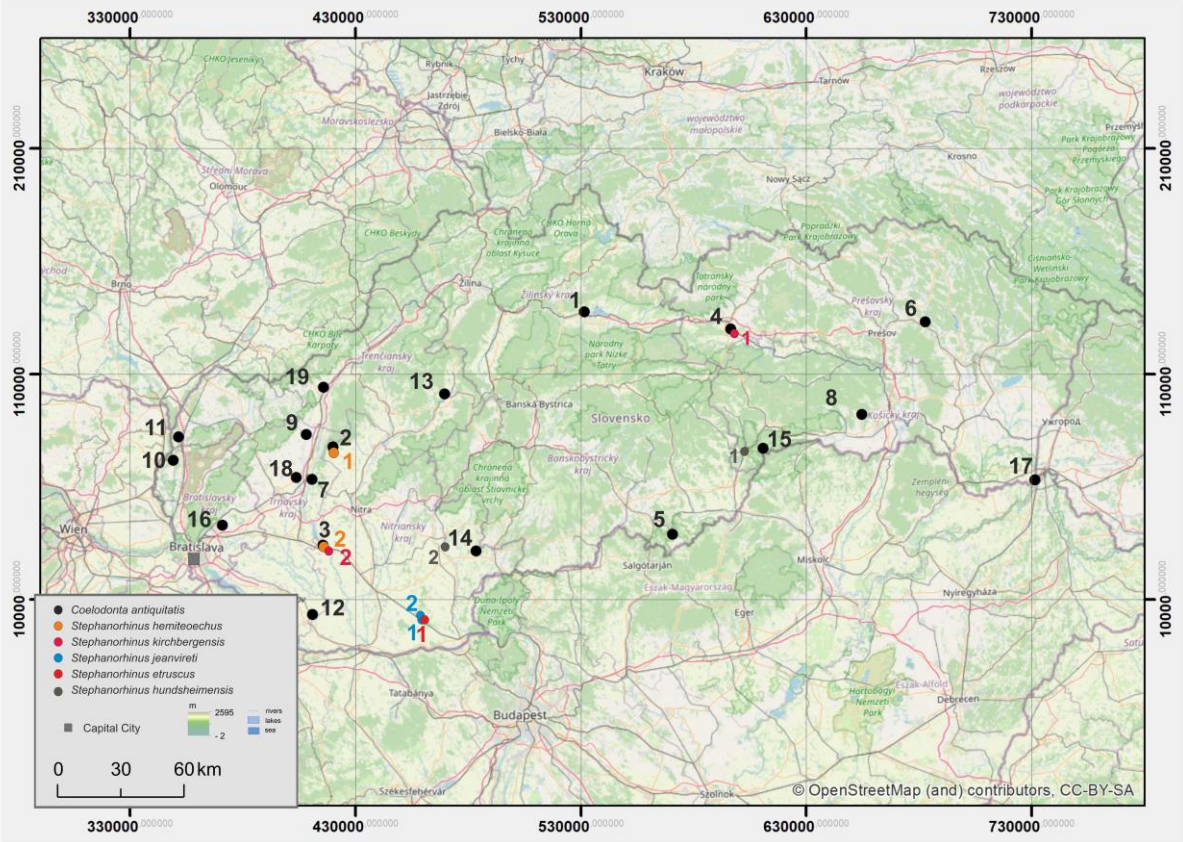
Koněprusy, 51 – Košíře, 52 – Koštov, 53 – Košutka, 54 – Kralupy, 55 – Krásné Březno, 56 – Krč, 57 – Křimice, 58 – Křimice-Košutka, 59 – Kůlna Cave, 60 – Kutná hora, 61 – Ledvice, 62 – Letky, 63 – Libčice, 64 – Libeň, 65 – Libeň, Báně, 66 – Libeň, Kundrátka, 67 – Libeň, Střížkovská ulice, 68 – Libořice, 69 – Libřice nad Vltavou, 70 – Liščí díra, 71 – Litoměřice, 72 – Lochkov, 73 – Louny, 74 – Lovosice, 75 – Lysolaje, 76 – Malešice, 77 – Manžusko, 78 – Michle, 79 – Mikulov, 80 – Mladeč, 81 – Mladečské jeskyně (I-II), 82 – Mráč, 83 – Neštěmice, 84 – Nové Stadice, 85 – Novosedlice, 86 – Nový Brázdim, 87 – Obrnice, 88 – Pavlov I (Southeast), 89 – Pekárna Cave, 90 – Pod hradem, 91 – Podbaba, 92 – Poděbrady, 93 – Podolí, Dvorce, 94 – Praha, 95 – Praha - Podbaba, 96 – Předměřice, 97 – Předmostí, 98 – Předradí, 99 – Přemyšlany, 100 – Přerov, 101 – Prosek, 102 – Radim, 103 – Radlice, 104 – Radotín, 105 – Roudná, 106 – Roztoky, 107 – Rudná-Hořelce, 108 – Rusko, 109 – Šárka, 110 – Šárka ,Dubový mlýn, 111 – Sázava, Bílí kámen, 112 – Sedlec u Prahy, 113 – Šipka Cave, 114 – Sklep, 115 – Sloupské jeskyně, 116 – Smíchov, 117 – Šošůvská Cave, 118 – Srbsko, Chlum, Poslední dóm, 119 – Stadice, 120 – Šťáhlavka, 121 – Strahov, 122 – Stránská Skála III and IIIa, 123 – Střekov, 124 – Strnady, cihelna, 125 – Štýřice III, 126 – Sudslavice II, 127 – Švédův stůl, 128 – Světec u Bíliny, 129 – Svobodné dvory, 130 – Tetín, Turská maštal, poslední síň, 131 – Toušeň,cihelna, 132 – Třemošná, 133 – Trmice, 134 – Turold, 135 – Uhříněves,Středočeské cihelny, 136 – Ústí nad Labem, 137 – V Hložku, 138 – Velké březno, 139 – Velké Pavlovice, 140 – Vinckova Cave, 141 – Vinohrady, 142 – Vintířov, 143 – Vochov, 144 – Vokovice, 145 – Volevčice, 146 – Vršovice, 147 – Výpustek, 148 – Vysočany, 149 – Záběhlice, 150 – Želatovice, 151 – Želenice, 152 – Žižkov, 153 – Zkamenělý zámek, 154 – Zlonice. ***Stephanorhinus hundsheimensis:*** 1 – Srbsko, Chlum, IV layer, 2 – Stránská Skála. ***Stephanorhinus kirchbergensis:*** 1 – Koněprusy, Kobyla, Chlupáčova sluj, 2 – Koněprusy, Zlatý kůň, Petrbokova sloj, 3 – Kůlna Cave.



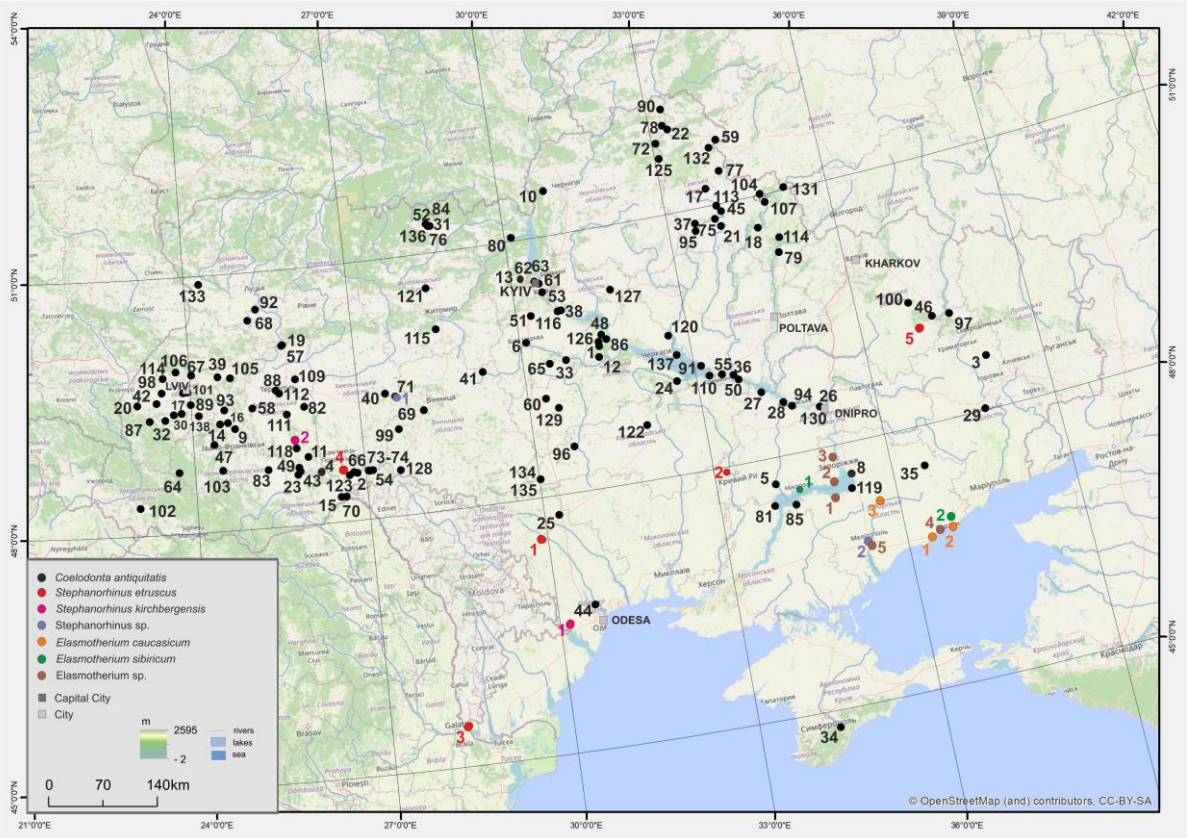
Distribution of Pleistocene localities yielding rhino remains in Poland. ***Coelodonta antiquitatis:*** 1 – "Adamów" Turek Brown Coal Mine, 2 – Belchatów Brown Coal Mine, 3 – Bębłowskie Dolne Rock Shelter, 4 – Bielkowo, county Gdańsk, 5 – Bielkówko, county Gdańsk, 6 – Biśnik Cave, 7 – Bobrów, 8 – Bolimów, 9 – Borsucza Cave, 10 – Brodnica, 11 – Brzeziny, 12 – Bychawa, 13 – Cave IV on Mt. Birów, 14 – Chełm, 15 – Chmielnik quarry, 16 – Chorzów, 17 – Ciemna Cave, 18 – Czarnawka stream near Zabrze, 19 – Czarnków, 20 – Czechowice-Dziedzice, 21 – Czersk, 22 – Czerwonak (Poznań, Czerwonak), 23 – Czerwoniak, county Kłodzko, 24 –

Czerwonka, county Reszel, 25 – Dąbrówka Mała, 26 – Deszczowa Cave, 27 – Dębiec near Poznań, 28 – Długi Most, county Brodnica, 29 – Dobrzylin, county Kutno, 30 – Dziadowa Skała Cave, 31 – Garwolin, 32 – Gdańsk, Cyganki, 33 – Gniew, 34 – Gniewięcin near Sędziszów, 35 – Gołaszyn, county Oborniki, 36 – Gorzóchów, 37 – Góra Kalwaria, 38 – Góra Puławska, 39 – Grupa, county Świecie, 40 – Izbica near Krasnystaw, 41 – Jankowo, county Środa, 42 – Jasna Smoleńska Cave, 43 – Jasna Strzegowska Cave, 44 – Jelenia Góra, 45 – Kadyny, county Elbląg, 46 – Kadzielnia, 47 – Kalinowo, county Ełk, 48 – Kamieńczyk, 49 – Karbowo, county Brodnica, 50 – Karzec, county Gostyń, 51 – Kobylnica, county Poznań, 52 – Komarowa Cave, 53 – Komodzianka, county Zamość, 54 – "Konin" Brown Coal Mine, 55 – Kowanowo, county Oborniki, 56 – Kowanówko, county Oborniki, 57 – Koziarnia Cave, 58 – Kraków Spadzista Street, 59 – Kraków, Krowodrza, 60 – Kraków, Ludwinów, 61 – Krosinko, 62 – Lubań, county Poznań, 63 – Lubin, 64 – Ławy near Łosice, 65 – Ławy near Siedlce, 66 – Łęcze, county Elbląg, 67 – Łódź, 68 – Malbork, 69 – Mamutowa Cave, 70 – Maszycka Cave, 71 – Mechowo near Swarzędz, 72 – Milowice, Sosnowiec, 73 – Minięta, county Sztum, 74 – Morąg, 75 – Mosina, 76 – Mroczna in Pośrednica Cave, 77 – Murek Cave, 78 – Na Gaiku II Rock Shelter, 79 – Na Wrzosach Południowa Cave, 80 – Nad Matką Boską Cave, 81 – Nad Potoczkiem Rock Shelter, 82 – Nida River near Czarkowy, 83 – Nietoperzowa Cave, 84 – Nowa Dęba, county Świecie, 85 – Nowawieś Chełmińska, 86 – Nowe Pole, county Elbląg, 87 – Obłazowa Cave, 88 – Oborniki, 89 – Odrzywół near Nowe Miasto n. Pilicą, 90 – Ojców, undefined cave, 91 – Ojrzanów near Mszczonów, 92 – Okkiennik Cave (Okiennik Rock Sheleter), 93 – Ostróda, 94 – Ostrzeszów, 95 – Otmuchów, county Grodków, 96 – Parchatka near Puławy, 97 – Pawłowiczki, county Koźle, 98 – Perspektywiczna Cave, 99 – Perzów, county Kępno, 100 – Piaseczno, 101 – Piekary, Na Gołąbcu Cave, 102 – Pillar sand mine" Kuźnica Warężyńska S.A." in Dąbrowa Górnicza, 103 – Płock, 104 – Pod Kochanką Cave, 105 – Południowe Rock Shelter; Shelter above Zegar Cave, 106 – Poznań, 107 – Poznań, Główna, 108 – Poznań, Malta, 109 – Poznań, Rataje, 110 – Poznań, Szeląg, 111 – Poznań, Wilczy Młyn, 112 – Poznań, Wilda, 113 – Przasnysz, 114 –

Przechówko, county Świecie, 115 – Przegińska Cave, 116 – Przemyków county Proszowice, 117 – Pszczółki, county Gdańsk, 118 – Pyskowice, 119 – Pyskowice-Dzierżno, 120 – Racibórz-Ostróg, 121 – Radłów near Tarnów, 122 – Raj Cave, 123 – Rock-Shelter in Strzegowa, Zaciszna Cave, 124 – Rozniszew, Pilica River, 125 – Rusko, 126 – Rzeczyca near Pyskowice, 127 – San River near Przemyśl, 128 – Sandomierz, 129 – Sąspowska Zachodnia Cave, 130 – Siedliszowice, Dunajec River, 131 – Siemonia, 132 – Skarszyn, 133 – Skowarcz, county Gdańsk, 134 – Słonne, county Dubiecko, 135 – Sobiecin, county Jarosław, 136 – Sochaczew, 137 – Spławie neat Pyzdry, 138 – Stajnia Cave, 139 – Starogard Gdański, 140 – Starołęka, county Poznań, 141 – Stradów, county Czarnocin, 142 – Suchanino, county Gdańsk, 143 – Swięcko, county Kłodzko, 144 – Syrynia, 145 – Szczecin, 146 – Szczęśliwickie Lake, 147 – Śrem, 148 – Targowsiko gravel pit, 149 – Tatarska Góra, county Hrubieszów, 150 – Terespol Pomorski, county Świecie, 151 – Tolkmicko, county Elbląg, 152 – Trzebnica, 153 – Tunel Wielki, 154 – Vistula River near Warsaw, 155 – Vistula River, Wola Przemkowska, 156 – Wadowice, 157 – Walawa, county Radymno, 158 – Waplewo Wielkie, county Sztum, 159 – Wiercica Cave, 160 – Wierzenica, county Poznań, 161 – Wilcze I Rock Shelter; Schronisko w Górach Sokolich III, 162 – Wilczyce, 163 – Wilga River Valley county Garwolin, 164 – Winnica Mountain near Kamień Mściowski, 165 – Wisła River, Maciejowice, 166 – Wisłok River, Rzeszów, Lisia Góra, 167 – Wrocław Hallera Street 1, 168 – Wrocław-Oporów, 169 – Września, 170 – Wylotne Rock Shelter, 171 – Zadębce, county Hrubieszów, 172 – Zalesie, county Jarocin, 173 – Zawalona cave, 174 – Zegar Cave, 175 – Zgorzelec, 176 – Ziębice, 177 – Zwoleń, 178 – Zygmuntówka Quarry near Chęciny, 179 – Żabikowo, Luboń, 180 – Żmigród. ***Stephanorhinus kirchbergensis:*** 1 – Chmeilnik quarry, 2 – Gorzów Wielkopolski, 3 – Grudziądz, Wisła River, 4 – Grupa, county Świecie, 5 – Imbramowice, 6 – Kamieńczyk, 7 – "Konin" Brown Coal Mine, 8 – Minięta, county Sztum, 9 – Oborniki, 10 – Opatów, 11 – Siekierki, Wisła River, 12 – Szczęśliwice, 13 – Wrocław Hallera Street 1.



Distribution of Pleistocene localities yielding rhino remains in Slovakia. ***Coelodonta antiquitatis:*** 1 – Bešeňová-Báňa, 2 – Čertova pec Cave, 3 – Dlhá n/Váhom, 4 – Gánovce, 5 – Hajnáčka, 6 – Hanušovce nad Topľou, 7 – Hlohovec, 8 – Hodkovce, 9 – Krakovany - Strážov, 10 – Malé Leváre, 11 – Moravský Ján, 12 – Okoč, 13 – Prepoštská jaskyňa Cave, 14 – Santovka, 15 – Silická Brezová, 16 – Slovenský Grob, 17 – Tisa River, 18 – Trakovice, 19 – Trenčianske Bohuslavice – Pod Tureckom. ***Stephanorhinus hemitoechus:*** 1 – Čertova pec Cave, 2 – Šaľa. ***Stephanorhinus kirchbergensis:*** 1 – Gánovce, 2 – Šaľa. ***Stephanorhinus jeanvireti:*** 1 – Nová Vieska, 2 – Strekov. ***Stephanorhinus etruscus:*** 1 – Nová Vieska. ***Stephanorhinus hundsheimensis:*** 1 – Gombasek, 2 – Levický vápnik.



Distribution of Pleistocene localities yielding rhino remains in Ukraine. ***Coelodonta antiquitatis:*** 1 – Babychi, 2 – Babyn I, 3 – Bakhmut (Artemivsk), 4 – Balamutivka Kostatiiv Yar, 5 – Bazavluk (Sholokhove), 6 – Bila Tserkva, 7 – Bilche, 8 – Bilenke, 9 – Bilshivtsi, 10 – Birky, 11 – Borshchiv, 12 – Brovakhy, 13 – Bucha, 14 – Bukachivtsi, 15 – Bukovynka Cave, 16 – Burshtyn, 17 – Buryn, 18 – Byshkin, 19 – Bear Cave, 20 – Chapli, 21 – Chervona Sloboda, 22 – Chulativ I, 23 – Chunkiv, 24 – Chygyryn, 25 – Demydivka, 26 – Dnipro, 27 – Dniprovo-Kamianka, 28 – Dniprovske, 29 – Donetsk, 30 – Dovge, 31 – Dovgynychi, 32 – Drohobych, 33 – Dybyntsi, 34 – Emine-Bair-Khosar, 35 – Fedorivka, 36 – Gorishni Plavni, 37 – Haii, 38 – Halepia, 39 – Hlyniany, 40 – Holovchyntsi, 41 – Hopchytsia, 42 – Hordynia, 43 – Horodok, 44 – Illinka, 45 – Ivanytsia, 46 – Izium, 47 – Kalush, 48 – Kaniv, 49 – Kasperivtsi, 50 – Keleberda, 51 – Kodak, 52 – Koptivshchyna, 53 – Korchuvate, 54 – Korman IV, 55 – Kremenchuk, 56 – Malo-Kokhnovsky Quarry, 57 – Kremenets, 58 – Kryve, 59 – Kucherivka, 60 – Kuty, 61 – Kyiv, Hlybochytsia, 62 – Kyiv, Kurenivka, 63 – Kyiv, Kyrylivska, 64 – Liskovets, 65 – Lisovychi, 66 – Luka Vrublivetska, 67 – Lviv, 68 – Lypa, Polishchukiv Riv, 69 – Lysianka, 70 – Malimon-

Canyon Cave, 71 – Medzhybizh, 72 – Mizyn, 73 – Molodova I, 74 – Molodova V, 75 – Nedryhailiv, 76 – Norynsk, 77 – Nova Sloboda, 78 – Novgorod-Siverskyi, 79 – Okhtyrka, 80 – Orane, 81 – Osokorivka, 82 – Ostapove, 83 – Ostrivets, 84 – Ovruch, 85 – Pavlokichkas, 86 – Pekari, 87 – Pidbuzh, 88 – Proniatyn, 89 – Pryima I, 90 – Pushkari I, 91 – Pyvykha, 92 – Radomyshl, 93 – Rohatyn, 94 – Romankove, 95 – Romny, 96 – Rozsohuvatets, 97 – Rubtsi, 98 – Rudky, 99 – Semenky, 100 – Shchurivka, 101 – Shchyrets, 102 – Sobatyn, 103 – Starunia, 104 – Stetskivka, 105 – Stinka, 106 – Stradch, Pishchana Gora, 107 – Sumy, 108 – Syniakove, 109 – Syniava, 110 – Taburyshche, 111 – Terebovlia, 112 – Ternopil, 113 – Terny, 114 – Trostianets, 115 – Troyaniv, 116 – Trypillia, 117 – Tuchapy, 118 – Ulashkivtsi, 119 – Vasylivka, 120 – Velyka Burimka, 121 – Horoshiv, 122 – Volodymyrivka, 123 – Voronovytsia, 124 – Vyniava, 125 – Vyshenky, 126 – Yabluniv, 127 – Yagotyn, 128 – Yaryshiv, 129 – Yurpil, 130 – Zaporizhia, 131 – Zapsillia, 132 – Zarutske, 133 – Zaslavok, 134 – Zavadivka, 135 – Zavallia, 136 – Zbranky, 137 – Zhovnyne, 138 – Zhydachiv. ***Stephanorhinus etruscus:*** 1 – Dolynske, 2 – Mudrene, 3 – Reni, 4 – Shutnivtsi, 5 – Velyka Komyshuvakha. ***Stephanorhinus kirchbergensis:*** 1 – Biliayivka, 2 – Syniakove 1. ***Stephanorhinus* sp.:** 1 – Medzhybizh, 2 – Pishchane. ***Elasmotherium caucasicum:*** 1 – Berdiansk, 2 – Nogaisk, 3 – Tokmak. ***Elasmotherium sibiricum:*** 1 – Nikopol, 2 – Osypenko. ***Elasmotherium* sp.:** 1 – Balky, 2 – Bilenke, 3 – Khortytsia, 4 – Nogaisk, 5 – Pishchana Balka.