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Environmental conditions across Poland during the Eemian Interglacial reconstructed from vertebrate remains

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ABSTRACT:

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Knowledge on the Eemian (MIS 5e) fauna of Poland is based on vertebrate remains from 16 open-air localities and 8 cave sites. Considering the short period of time covered by MIS 5e, the amount of data is surprisingly large. There is still an ongoing debate on whether the age of some assemblages is Eemian, latest Saalian or even earliest Weichselian. There are faunal assemblages or stratigraphically isolated finds with some disputable evidence. The full picture of the evolution of the Eemian vertebrate fauna in the present-day territory of Poland is still far from being complete. The finds of various groups of vertebrates (fishes, amphibians, reptiles, birds and mammals) from the Eemian Interglacial of Poland are analysed in terms of their environmental preferences. A number of thermophilic species or forms which preferred temperate climate conditions are known from this period. Among them, *Clethrionomys glareolus*, *Glis glis*, *Meles meles*, *Martes martes*, *Lynx lynx*, *Felis silvestris*, *Sus scrofa*, *Palaeoloxodon antiquus*, and *Stephanorhinus kirchbergensis* indicate a forest environment. The presence of species that preferred more open environments (*Cricetus cricetus*, *Mammuthus primigenius*, *Coelodonta antiquitatis*, and *Equus ferus*) is also recorded for the Eemian Interglacial of Poland. Characteristic was the presence of the large broad-toothed and flat-headed *Ursus arctos taubachensis*, which additionally often outnumbered remains of *Ursus spelaeus* sensu lato in the contemporary layers. The Eemian vertebrate fauna of Poland consisted of about 150 species (representing 61 genera and 26 families), most of which were recorded earlier from other localities of this age in central and eastern Europe.

Key words: Vertebrates; MIS 5e; Eemian; Faunal assemblage; Palaeoenvironment; Poland.

INTRODUCTION

The stratigraphy of Pleistocene deposits in Poland, including those accumulated during the Eemian Interglacial, has been discussed in a number of publications (e.g., Lindner 1988, 1991, 1992; Lindner and Marks 1994, 2008; Lindner *et al.* 1995, 2004, 2013; Ber 2005; Bruj and Roman 2007; Marks *et al.* 2016; Ber *et al.* 2007a, b). The knowledge on the Eemian faunas of Poland is relatively scarce since vertebrate remains of this age have never been the subject of a thorough revision. Previous researchers have tried to discuss it within a broader, usually Late Pleistocene, context. Therefore, the Polish bibliography lacks a synthetic work that would summarize the current state of knowledge on vertebrate fauna of the Eemian Interglacial. It is especially noteworthy that a large number of localities yielding vertebrate remains of Eemian age is documented from the territory of adjacent countries, e.g. Germany and the Czech Republic (Soergel 1920; Toepfer 1958; Mostecký 1961, 1963, 1969; Sickenberg 1969; Musil 1970, 2002, 2010, 2018; Valoch *et al.* 1970; Mania 1973; Philips 1974; Kahlke 1978; Valoch 1988; Kowalski 1989; Eissmann 1990; Benecke *et al.* 1990; Böhme 1991; Fischer 1991; Hartung 1991; Heinrich 1991; Koenigswald 1991; Schweigert 1991; Lindner 1992; Mania 1992; Kahlke 1994; Wenzel 1996; Pfeiffer 1998; Bratlund 1999; Koenigswald and Heinrich 1999; Kolfschoten 2000; Turner 2000; Pushkina 2007; Holm and Svenning 2014; Felde *et al.* 2020; Kindler *et al.* 2020; Marciszak *et al.* 2023 and others).

In Poland, about 300 localities with riverine and lacustrine sediments of the Eemian Interglacial have been reported so far (Noryśkiewicz 1978, 1979; Kuszel 1997, 1998; Jastrzębska-Mamełka 1985; Mamakowa 1989; Kupryjanowicz and Drzymulska 2002; Malkiewicz 2002, 2018; Granoszewski 2003; Urbański and Winter 2005; Bruj and Roman 2007; Kupryjanowicz 2008; Mirosław-Grabowska *et al.* 2009, 2018, 2022; Mirosław-Grabowska and Gąsiorowski 2010; Niska 2011; Kołaczek *et al.* 2012; Majecka 2014; Badura *et al.* 2017; Hrynowiecka *et al.* 2018, 2021; Kupryjanowicz *et al.* 2018, 2021; Żarski *et al.* 2018; Sobczyk *et al.* 2020; Roman *et al.* 2021; Pidek *et al.* 2022). Remains of invertebrates are quite common in these sediments, those of fishes, amphibians and reptiles are less abundant, and only scarce mammalian remains were found there (Römer 1879a, b, 1883; Ślósarski 1882a, b, 1883, 1884; Gürich 1885, 1905, 1913; Hermann 1911, 1913; Pax 1921; Krause 1925; Lubicz-Niezabitowski 1926, 1929; Pawłowski 1929; Zeuner 1934; Gołąb and Urbański 1938; Schroeder 1930; Juhnke 1932; Kowalski 1951, 1954, 1958, 1959; Czyżewska 1962; Kubiak 1965, 2001; Borsuk-Białynicka and Jakubowski 1972; Skompski 1977, 1983, 1996; Mamakowa 1976, 1988, 1989; Bałuk *et al.* 1979; Hebig 1978; Jakubowski 1988, 1996; Lorek 1988; Borisova 2005; Alexandrowicz and Alexandrowicz 2010; Pawłowska 2015a, b; Badura *et al.* 2017; Fedorowicz and Lorek 2019; Marciszak *et al.* 2019a–c; Sobczyk *et al.* 2020; Stefaniak *et al.* 2020, 2021a, b, 2022, 2023a, b; Alexandrowicz *et al.* 2022).

Especially noteworthy are the finds of large skeletal parts of the forest elephant *Palaeoloxodon antiquus* from Leszno Street in Warsaw in 1962 and the Jóźwin KWB quarry in Konin in the 1980s (Jakubowski 1988, 1996; Fedorowicz and Lorek 2019), as well as almost complete skeleton of Merck's rhinoceros *Stephanorhinus kirchbergensis* from Gorzów Wielkopolski (Badura *et al.* 2017; Sobczyk *et al.* 2020; Stefaniak *et al.* 2020, 2021a–c, 2023a, b).

Further information has been provided due to the multiproxy study of cave deposits, among which levels belonging to the Eemian interglacial were also identified. Remains of a few reptilian taxa, numerous birds and mammals were found there, including those of small mammals suitable for palaeoecological reconstructions (e.g., Madeyska 1981; Nadachowski 1989; Socha 2014, etc.).

The aim of this study is to present an overview of all available data on the vertebrate fauna from the Eemian Interglacial, both from open-air localities and cave sites, and to show their importance for biostratigraphy and palaeoecological reconstruction of this stage of the Quaternary.

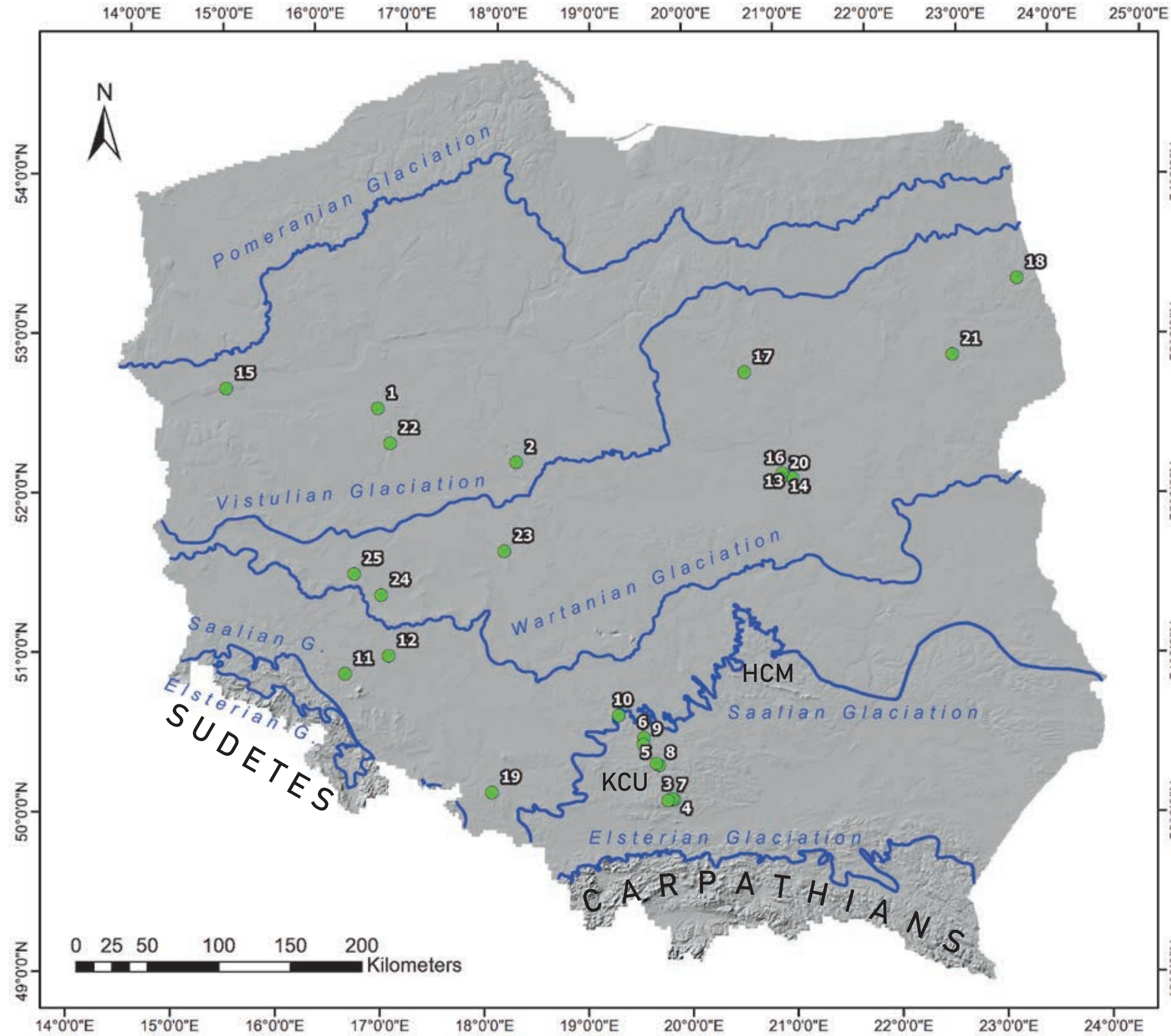
GEOLOGICAL SETTING

Vertebrate remains of the Eemian Interglacial came from 16 open-air localities and eight cave sites in the territory of Poland (Text-fig. 1). These localities are briefly described below.

Open-air sites

Gorzów Wielkopolski (52°43′51″N, 15°14′18″E). A profile of 22 m of sediments in Gorzów Wielkopolski (NW Poland) was unveiled during road construction works (Text-fig. 1: 15). It contains a complex series of lacustrine sediments consisting of gyttja intersected by peats and sands. The maximum thickness of lacustrine sediments is 11 m. These sediments rest on Wartanian fluvioglacial deposits and are covered by a few meters of Weichselian fluvioglacial and glacial sediments (Sobczyk *et al.* 2020). The lower lake complex represents a section of the Eemian Interglacial (MIS 5e), whereas the peat layer and the upper lake complex were formed during the Early Weichselian (MIS 5c–a). Disintegrated upper peat layer and the uppermost level of gyttja were deposited during the Interpleniglacial (MIS 3) (Badura *et al.* 2017; Sobczyk *et al.* 2020; Stefaniak *et al.* 2020, 2021a–c, 2023a, b; Alexandrowicz *et al.* 2021; Mirosław-Grabowska *et al.* 2022).

Szeląg near Poznań (52°25′43″N, 16°57′05″E). A Pleistocene sequence comprising lacustrine sediments of



Text-fig. 1. Location map of sites vertebrate fossils of the Eemian Interglacial in the territory of Poland and Scandinavian Ice Sheet (SIS) limits superimposed (SIS limits modified after Marks 2011): **1** – Oborniki; **2** – Konin Brown Coal Mine; **3** – Ciemna Cave; **4** – Łokietka Cave; **5** – Jasna Strzegowska Cave; **6** – Deszczowa Cave; **7** – Nietoperzowa Cave; **8** – Biśnik Cave; **9** – Dziadowa Skała Cave; **10** – Komarowa Cave; **11** – Imbramowice; **12** – Wrocław Hallera street 1; **13** – Siekierki, Wisła River; **14** – Szczęśliwice; **15** – Gorzów Wielkopolski; **16** – Warszawa, Leszno Street; **17** – Ciechanów; **18** – Sokółka; **19** – Pawłowiczki, county Koźle; **20** – Warszawa, Szczęśliwice (2); **21** – Zdrody (Nowe); **22** – Szeląg (Poznań); **23** – Nędzerzów (Kalisz); **24** – Żmigród on the Barycz River; **25** – Lechitów (Góra). Abbreviations: HCM – Holy Cross Mountains; KCU – Kraków-Częstochowa Upland.

the last interglacial was discovered there. Mollusc remains were reported by Lubicz-Niezabitowski (1929), Pawłowski (1929), Gołąb and Urbański (1938), Sawicki (1955), Woldstedt (1955), Środoń (1956), Skompski (1977), Alexandrowicz and Alexandrowicz (2010).

Konin Brown Coal Mine (52°19′21″N, 18°14′55″E). Numerous remains of the Quaternary fauna, both invertebrates and mammals, were found within the “Jóźwin” open-air pit of the Konin lignite mine (Text-fig. 1: 2). In February 1984, an almost complete skeleton of a male forest elephant was found there, deposited in sediments of the Eemian Interglacial. The remains included large skull fragments with teeth, a mandible, an almost complete axial skeleton, ribs, a right thoracic limb, and large parts of the right and left pelvic limbs. Other parts of the skeleton were destroyed. The elephant bones lay within silts and fine-grained sands interlayered with a peat layer and gyttja. Deeper in the profile, fine-grained sediments have been replaced by mix-grained sands, gravels and tills representing the Odranian glaciation *sensu* Lindner and Grzybowski (1982). Remains of the forest elephant as well as mammoth fossils were also found and collected in the "Marants" and "Kazimierz Biskupi" open pit mines. Noteworthy, the upper second premolar and pelvic bone of the Merck's rhinoceros *Stephanorhinus kirchbergensis* were also found very close to the forest elephant skeleton (see Fedorowicz and Olszak 1988; Gorczyca 1988; Jakubowski 1988; Lorek 1988; Maćkowiak 1988; Stankowski 1988, Fedorowicz and Lorek 2019 for more details).

Oborniki (52°38′41″N, 16°48′51″ E). Numerous remains of Pliocene and Pleistocene mammals came from the middle terrace of the Warta River (Chłapowski 1905; Wahnschapffe 1914; Krause 1925; Lubicz-Niezabitowski 1926; Schroeder, 1930; Kowalski 1959; Pawłowska 2015).

Imbramowice (50°58′6″N, 16°34′0″E). A fragment of rhino right mandible with five teeth was discovered at a brickyard in 1904 (Gürich 1905, 1913). Determining the exact age of the carbonate sediments containing organic material and rhinoceros bones remained problematic. In the early twentieth century, it was thought that they represented Mazovian/Holsteinian Interglacial dated at MIS 11c (Juhnke 1932). Later research (Kaczmarska 1976; Mamakowa 1976, 1989; Mirosław-Grabowska and Gąsiorowski 2010) allowed the determination of the age of these deposits as the Eemian Interglacial (MIS 5e). Lacustrine deposits (11 m) rest there on sediments of the Odranian glaciation. Palynological analysis clearly indicates the Eemian age of the remains. In later years, numerous remains of molluscs, cladocerans, fishes, rodents together with four teeth of the forest elephant were found in gyttja (Juhnke 1932). More recently a left hemimandible of an immense brown bear *Ursus arctos taubachensis* was found at Imbramowice (Marciszak and Lipecki 2020).

Wrocław-Hallera Street (51°N, 17°E). Archaeological sites at Hallera Street in Wrocław were explored in 1995 and 2000–2008 (Wiśniewski *et al.* 2023). The deposits are composed mainly of sands, gravels, loams, silts and fossil soils linked with the Vistulian glaciation (MIS 5d–MIS 2). Several settlement levels from the Middle Palaeolithic (Moustierian, Micoquian) were found together with animal and plant remains. The remains of Merck's rhinoceros came from older sediments, possibly belonging to the Eemian Interglacial (Wiszniowska *et al.* 2002b, 2005a; Wiśniewski 2006; Wiśniewski *et al.* 2009; Stefaniak *et al.* 2021a; Wiśniewski *et al.* 2023).

Pawłowiczki, county Koźle (50°14′29″N, 18°02′46″E). A well-preserved skull of the woolly rhinoceros was found in Pawłowiczki on the Głubczyce Plateau in 1877. According to the description, the remains were most probably found in a sand pit eastward of the village. The skull was found at a depth of 6.5 m in a layer of yellowish-grey clay sands (Römer 1879a, b; Gürich 1885; Pax 1921, Zeuner 1934; Kowalski 1959; Pawłowska 2015b; Marciszak *et al.* 2019a). In addition, many other skeletal remains of the same rhino individual, including ribs, scapula fragments, and a pelvis, were found there (Römer 1879a, b; Gürich 1885). After the reconstruction, the calvarium from Pawłowiczki became the main attraction of the mineralogical museum of the University of Wroclaw. A picture of this skull exhibited in the Geological Institute of the University of Wroclaw was published by Zeuner (1934). Currently, there is a part of a pelvis and possibly undetermined scapula and rib fragments described by Römer (1879a), as well as a skull fragment in the collection. However, it is not sure whether it is the skull fragment described above; its post-war fate remains unknown (Marciszak *et al.* 2019a). In addition, a right mandible fragment of *Ursus arctos taubachensis* was found there (Marciszak and Lipecki 2020).

Siekierki, Wisła River (52°12′29.56″N, 21°05′0.7″E). Remains of Pleistocene animals were found in the Vistula River near the village of Siekierki in 1970. Among them, there are a skull and mandible of the Merck's rhinoceros, bones of an unspecified rhinoceros, two horse skull fragments, five aurochs' horns, antlers of the red deer and reindeer (Borsuk-Białynicka and Jakubowski 1972).

Warszawa, Leszno Street (52°14′16.7″ N, 20°58′37.9″E). Skeletal fragments of a male forest elephant *Palaeoloxodon antiquus* were found during earthworks to construct a water pipeline in Leszno Street in 1962. They included fragments of the mandible, skull, axial skeleton and a few limb bones (Jakubowski 1996; Kubiak 2001; Pawłowska 2015b).

Warszawa, Szczęśliwice (52°12′27″ N, 20°57′28.08″E). Numerous Pleistocene animal remains from gyttja dated to the Eemian Interglacial have been found there since at least the late 19th century (Ślósarski 1882a, b, 1883, 1884; Czyżewska 1962; Jakubowski 1996; Borsuk-Białynicka and Jakubowski 1972; Kubiak 2001; Pietrzykowski 2014; Pawłowska 2015a, b).

Ciechanów (52°52′54″ N, 20°36′38″ E). The remains of a female forest elephant (skull fragments with M3, mandible fragment with m3, vertebrae, incomplete pelvic limb bones) were found during the construction of a water supply system between the villages of Kalisz and Przewojowo in 1981 (Jakubowski 1996; Kubiak 2001; Pawłowska 2015 and references therein).

Sokółka (53°24′25″N, 23°30′00″ E). Mandible fragments of *Palaeoloxodon antiquus* with milk teeth (dm3) were found in a gravel layer in 1968. These bones probably came from the sediments of an ancient fossil lake (Ruprecht 1971; Kubiak 2001; Niska and Kołodziej 2015; Pawłowska 2015b; Rychel 2021).

Zdrody near Białystok (52°56′50″N, 22°46′52″E). Animal remains were found in the sediments of a kem terrace. The age of these fossils had been previously estimated as the Middle Polish (Odranian) glaciation. Remains of small mammals, amphibians and molluscs were collected in sands interbedded with calcareous silts (Bałuk *et al.* 1979; Szyndlar 1984; Nadachowski 1989, 1990; Rzebik-Kowalska 1989, 1994, 2006, 2009; Młynarski and Szyndlar 1989; Kowalski 2001).

Nędzerzów near Kalisz (51°45′45″N, 18°08′22″E). Lacustrine and riverine deposits of the Eemian Interglacial in the Kalisz region were described by Malkiewicz (2002). Nędzerzów is located in the eastern part of Kalisz city (Winiary), within an abandoned open pit mine. Material from this locality is now deposited in the Berliner Museum für Naturkunde (Germany).

Żmigród on the Barycz River (51°28′13″N, 16°54′18″E). The site comprises lacustrine deposits, from which Skompski (1983) described the remains of molluscs, beetles, fish and rodents.

Lechitów near Góra (51°35′50″N, 16°37′21″E). This site is located 20 km west of Rawicz (Kondracki 1994). The geological features of this area were presented in detail by Czerwonka *et al.* (1997) and Malkiewicz (1998). A series of organic sediments is associated with a palaeolake that existed there from the end of the Saalian Glaciation until the Eemian Interglacial. In addition to these organic series, there are riverine sediments of the Weichselian Glacial (Malkiewicz 1998, 2002).

Cave sites

Biśnik Cave (50°25′35″N, 19°39′54″E; Middle Pleistocene–Holocene, end of Q3–Holocene, Röpersdorf – Schöningen (Lublinian) Interglacial and Saalian Glacial (Krzna Glacial – Holocene, MIS 7/8–1)). Biśnik Cave is in the rock Biśnik in the Wodąca Valley near the village of Smoleń in the Częstochowa Upland. The cave has several interconnected chambers and rock shelters, filled initially with deposits. Systematic studies started there in 1991 (Cyrek 1997, 1998, 2002, 2009, 2013; Wiszniowska *et al.* 2002a; Cyrek *et al.* 2009, 2010, 2014; Stefaniak and Marciszak 2009; Stefaniak *et al.* 2009a–c; Socha 2014; Krajcarz *et al.* 2014a, b, 2016). The profile includes 20 layers with bone remains and Palaeolithic man's tools (except for layer 20). Biśnik Cave is one of the oldest cave sites in Poland, with traces of occupancy by Palaeolithic man. Hitherto, a total of 23 settlement levels, from the Middle Palaeolithic till the Middle Ages, were distinguished there. The stratigraphy of the cave is still debatable. The "old stratigraphy" (Cyrek *et al.* 2009) assumed the continuity of most strata. A new approach (Krajcarz *et al.* 2014a) assumed that this sequence is intercalated by sedimentary gaps and was subject to partial redeposition (Table 1). The animal remains represent 160 taxa dated in the range from the Lublinian Interglacial up to the Holocene (Wiszniowska *et al.* 2002a; Socha 2009, 2014; Stefaniak and Marciszak 2009; Cyrek *et al.* 2010; Van Asperen and Stefaniak 2011; Marciszak *et al.* 2011, 2019b, 2020; Marciszak 2012, 2014; Tomek *et al.* 2012; Croitor *et al.* 2014; Krajcarz *et al.* 2014a; Made *et al.* 2014; Marciszak and Socha 2014; Piskorska and Stefaniak 2014; Socha 2014; Piskorska *et al.* 2015; Stefaniak 2015; Stefaniak *et al.* 2020; Marciszak and Lipecki 2022; Mazza *et al.* 2022; Ratajczak-Skrzatek *et al.* 2022). The Eemian Interglacial includes part of layer 15 as well layers 14 and 13 (Cyrek 2013).

Nietoperzowa Cave (50°11′38.33″N, 19°46′28.24″E; late Middle Pleistocene–Holocene, MIS 6–1). The cave is in the upper part of the Będkowska Valley in the Kraków Upland. It has a spacious horizontal chamber and is one of the longest (326 m) caves in the Kraków-Wieluń Upland. The excavations started there in the nineteenth century (Römer 1883). In 1956–1963, the cave was excavated by W. Chmielewski's team (Chmielewski 1975; Madeyska 1981; Wojtal 2007; Socha and Stefaniak 2008; Krajcarz and Madeyska 2010). The deposits include 17 layers, most comprising bone remains and archaeological artefacts. The stratigraphy of the deposits, including the period from the end of the Warta Glaciation (Riss) and certainly the Eemian Interglacial till the Holocene, was described, among others, by Chmielewski

MIS	Western Europe		Poland		Cyrek *et al.* 2010	Krajcarz *et al.* 2014	Gąsiorowski *et al.* 2014	Marciszak and Socha 2014	Socha 2014
1	Holocene		Holocene		1a–b	1a–b	–	1a–b	1a–b
2	Weichselian	Late Weichselian	Vistulian	Main Stadial LGM	2–1	2–1	7–1	1	3–1
3/2		–		–	–	–	–	–	7–4
3		Interpleniglacial		Grudziądz Interstadial	4–3	7–5	11–8	11–2	11–8
4		Older Pleniglacial		Świecie Stadial	8–5	8–7	?12	?12	?12
5a		Early Weichselian		Gniew Interstadial	9	9	–	–	–
5b				Toruń Stadial	10	10a–10	–	–	–
5c					11	11	?13	13	?13
5d					12	13–12	–	–	–
5e	Eemian		Eemian		13	15–13	?13	14	13
6	Drenthe (+Warthe)		Odranian (+Wartanian)		14	18–15	14 15 ?17–16	15	15–14
7	Röpersdorf-Schöningen		Lublinian		15; ?16	19a–19	–	18	18
8	?Saalian		Krznian		19–18	19d, c, b	18	19	19
9	Dömnitz-Reinsdorf		Zbójnian		19c, b, a	–	–	19ad	–
10	Fuhne		Liwecian		–	–	–	–	–

Table 1. Stratigraphy of the Biśnik Cave according to various sources.

(1975), Madeyska-Niklewska (1969), Madeyska (1981, 1982, 2006), Madeyska and Cyrek (2002) and Wojtal (2007) (Table 2). The archaeological artefacts represent the Middle and Upper Palaeolithic levels and the Holocene (Chmielewski 1975; Cyrek 2006; Wojtal 2007). A few publications are focused on the study of reptiles, birds and mammals from this cave (K. Kowalski 1961; Wójcik 1971; Madeyska 1982; Nadachowski 1982, 1989; Szyndlar 1984). The list of large mammals from the cave was provided by Wojtal (2007). The last interglacial deposits are represented by layers 12 and 13 (Table 2).

Deszczowa Cave (50°35′19″N, 19°32′28″E; late Middle Pleistocene–Holocene, MIS 6–1). The cave is located on the northern slope of Mt. Popielowa in the Kroczyckie Rocks, Częstochowa Upland. It has the form of a narrow karst crevice. Cave deposits were studied from 1989 to 1997 (Cyrek *et al.* 2000; Cyrek 2009). The excavations revealed 11 layers, with an estimated age (based on stratigraphy and animal remains) from the Saalian Glaciation, various phases of the Vistulian Glaciation and the Holocene (Cyrek *et al.* 2000; Nadachowski *et al.* 2000, 2009; Madeyska and Cyrek 2002; Wojtal 2007; Cyrek 2009; Madeyska 2009; Stefaniak *et al.* 2009a; Krajcarz and Madeyska 2010) (Table 2). Traces of human presence from the Middle Palaeolithic till the Holocene were discovered (Cyrek *et al.* 2000; Cyrek 2009). Cave deposits contain animal remains of more than 190 taxa, characteristic of the Middle Pleistocene, Vistulian Glaciation till the Holocene (Cyrek *et al.* 2000; Nadachowski *et al.* 2000, 2009; Lorenc 2006a, b, 2007, 2008, 2013; Wojtal 2007; Stefaniak *et al.* 2009a, d). In this cave, Eemian Interglacial deposits are represented by layer 4 (Table 2).

Dziadowa Skała Cave (50°32′46″N, 19°31′58″E; Upper Pleistocene–Holocene, Eemian–Holocene, MIS 5e–1). Dziadowa Skała Cave is situated in the Podlesickie Rocks, near the village of Skarżyce. The excavations there were conducted by W. Chmielewski between 1952 and 1954. Nine layers were uncovered; their stratigraphy was estimated to cover the period from the Eemian Interglacial until the Holocene. Sediments from the last interglacial have been found in strata 4-3c-a. (Dylik *et al.* 1954; Chmielewski 1958; K. Kowalski 1958; Madeyska 1981; Lorenc 2006a, b, 2007, 2008; Wojtal 2007; Stefaniak *et al.* 2009a, d) (Table 2). Archaeological artefacts found in the cave were relatively scarce and represent Palaeolithic cultures (Chmielewski 1958; Wojtal 2007; Cyrek 2009). Animal remains include those of birds and mammals (Chmielewski 1958; K. Kowalski 1958; Madeyska 1981; Nadachowski *et al.* 1989; Bocheński 1990; Lorenc 2006a, b, 2007, 2008; Wojtal 2007; Stefaniak *et al.* 2009a, d; Bocheński *et al.* 2012).

Jasna Strzegowska Cave (50°24′56″N, 19°41′29″E; end of Middle Pleistocene–Holocene, Saalian–Holocene, ?MIS 6–1). Jasna Strzegowska Cave and the rock shelter Wschodnie are situated in the rock Jamy near the village of Strzegowa Kolonia. The cave has been known for a long time. L. Sawicki conducted excavations there in 1947–1949. In 1991, K. Cyrek studied Jasna Cave to verify the results of Sawicki.

<table>
<tr><th>MIS</th><th colspan="2">Western Europe</th><th colspan="2">Poland</th><th>Nietoperzowa Cave[1]</th><th>Deszczowa Cave[2]</th><th>Dziadowa Skała Cave[3]</th><th>Jasna Strzegowska Cave[4]</th><th>Łokietka Cave[5]</th><th>Ciemna Cave[6]</th><th>Komarowa Cave[7]</th></tr>
<tr><td>1</td><td colspan="2">Holocene</td><td colspan="2">Holocene</td><td>1</td><td rowspan="2">XI–IXa</td><td>9</td><td>7a–7</td><td>1</td><td>1.2–1.1</td><td>A</td></tr>
<tr><td>2/1</td><td rowspan="8">Weichselian</td><td>Late Weichselian</td><td rowspan="8">Vistulian</td><td>Late Vistulian</td><td>2</td><td>–</td><td>–</td><td>–</td><td>2.12–2.11</td><td>B</td></tr>
<tr><td>2</td><td>Late Weichselian</td><td>Main Stadial LGM</td><td>3</td><td>6a–6</td><td>8–7</td><td>6a–6</td><td>C</td><td>2.2</td><td>C</td></tr>
<tr><td>3</td><td>Interpleniglacial</td><td>Grudziądz Interstadial</td><td>4–8</td><td>–</td><td>6</td><td>–</td><td>–</td><td>5–2.3</td><td>D</td></tr>
<tr><td>4</td><td>Older Pleniglacial</td><td>Świecie Stadial</td><td>9</td><td rowspan="5">5
4</td><td>–</td><td>–</td><td>D</td><td>8–6</td><td>F–E</td></tr>
<tr><td>5a</td><td rowspan="4">Early Weichselian</td><td>Gniew Interstadial</td><td rowspan="2">10</td><td>–</td><td rowspan="2">5</td><td rowspan="4">5–3</td><td rowspan="5">16–9
18–16
11–7</td><td rowspan="2">G; Ft; Jt</td></tr>
<tr><td>5b</td><td rowspan="3">Toruń Stadial</td><td>–</td></tr>
<tr><td>5c</td><td rowspan="2">11a–11b</td><td>–</td><td rowspan="2">4</td><td rowspan="2">Ftx</td></tr>
<tr><td>5d</td><td>–</td></tr>
<tr><td>5e</td><td colspan="2">Eemian</td><td colspan="2">Eemian</td><td>12–13</td><td>IV</td><td>4–3c–a</td><td>2</td><td>6</td><td>Gtx</td></tr>
<tr><td>6</td><td colspan="2">Drenthe (+Warthe)</td><td colspan="2">Odranian (+Wartanian)</td><td>14–16</td><td>–</td><td>–</td><td>–</td><td>–</td><td>19–17</td><td>–</td></tr>
<tr><td>7</td><td colspan="2">Röpersdorf-Schöningen</td><td colspan="2">Lublinian</td><td>–</td><td>–</td><td>–</td><td>–</td><td>–</td><td>–</td><td>–</td></tr>
<tr><td>8</td><td colspan="2">?Saalian</td><td colspan="2">Krznian</td><td>–</td><td>III</td><td>–</td><td>–</td><td>–</td><td>–</td><td>–</td></tr>
</table>

Table 2. Stratigraphy of the other cave sites discussed in the paper. References: [1] Krajcarz and Madeyska 2010; [2] Krajcarz and Madeyska 2010, Lorenc 2013; [3] Wojtal 2007, Lorenc *et al.* 2013; [4] Mirosław-Grabowska and Cyrek 2009; [5] Wojtal 2007; [6] Valde-Nowak *et al.* 2014; [7] Nadachowski *et al.* 2009; Lorenc 2013.

The deposits (eight layers) are similar to those of Biśnik Cave and represent a series of cave loams, loesses, sands and humic levels. The last interglacial deposits are represented by layer 2 (Table 2). Besides bone remains, the excavations yielded numerous flint artefacts representing four Palaeolithic and one Neolithic level (Sawicki 1949, 1953; Mirosław-Grabowska and Cyrek 2009; Stefaniak *et al.* 2009a). Most cave and rock shelter material, including the bone remains, have never been studied in detail.

Łokietka Cave (50°12′06.10″N, 19°49′07.56″E; Upper Pleistocene–Holocene, lower Vistulian–Holocene, MIS 5e–1). Łokietka Cave is situated on Mt. Chełmowa in the Prądnik Valley in the Ojców National Park. The first studies in the cave were conducted by J. Zawisza in 1872 and S. Czarnocki in 1896 and 1899. The excavations were resumed in 1998. From five to eight layers of cave loams, loesses and humus were uncovered in two profiles. Based on the archaeological finds and bone remains, the age of the fossil-bearing deposits was estimated as covering the Eemian, various phases of the Vistulian and the Holocene. In this cave, Eemian interglacial deposits are represented by layer 6 (Table 2). The archaeological artefacts represented various Middle Palaeolithic cultures (Micoquian-Pradnikian, Levalloisian-Mousterian, Jerzmanowician) (Sobczyk and Sitlivy 2001a, b; Lipecki *et al.* 2001; Wojtal and Patou-Mathis 2003; Wojtal 2007).

Ciemna Cave (50°11′48.95″N; 19°49′54.29″E; Upper Pleistocene–Holocene, lower Vistulian–Holocene, MIS 5d–1). Ciemna Cave is in the massif of Mt. Koronna on the left slope of the Prądnik Valley in Ojców; it has the most prominent chamber among caves of the Kraków-Wieluń Upland. The cave has been known for a long time. The first excavations were conducted there in 1898–1912 by S. Czarnowski, and then by S. Krukowski in 1918–1919. Subsequent systematic excavations took place in 1963–1968. Material from this cave has never been analysed in detail. In recent years, new excavations started, directed by K. Sobczyk. The results of stratigraphic, archaeological and palaeontological studies were described by Krukowski (1939–1948), S. Kowalski (1967, 1971, 2006), Madeyska (1981, 2006), Nadachowski (1982, 1990) and Valde-Nowak *et al.* (2014). There are 18 layers of cave loams, loesses and humus; the entire series is aged from the end of the Odranian Glaciation until the Holocene and the Eemian levels are represented by the layers 16–9, 18–16, and 11–7 (Table 2). Archaeological artefacts represent Micoquian-Pradnikian culture and Neolithic settlement (S. Kowalski 1967, 1969, 1971, 2006; Cyrek 2006; Valde-Nowak *et al.* 2014). Wojtal (2007) described large mammals from this cave.

Komarowa Cave (50°43′47″N, 19°17′31″E; Upper Pleistocene–Holocene, Eemian, Vistulian–Holocene; ?MIS 5e–1). Komarowa Cave is situated in the Sokole Mts. (Częstochowa Upland) on the northern slope of Mt. Puchacz. The studies in the cave started in 1997 and have been continued until 2001. The complex profiles of the deposits inside the cave (16 layers) and on the terrace in front of it (11 layers) were composed of loams, limestone rubble, sands, silts and humus. The layer on the terrace included eolic sands, limestone rubble, loams and silts, and humus. The deposits contained numerous animal remains and artefacts of the Middle (2 phases) and Upper Palaeolithic (several settlement phases), Neolithic and Middle Ages. The stratigraphy of the site, fauna and palaeoecology were described by Gierliński *et al.* (1998), Ochman (2003), Tomek and Bocheński (2005), Rzebik-Kowalska (2006), Nadachowski *et al.* (2009) and Stefaniak *et al.* (2009a, d). In this site, sediments belonging to the Eemian interglacial are represented by the layer Ftx (terrace layers) (Table 2). Wojtal (2007) described in detail the taphonomy of bone remains.

MATERIAL AND METHODS

The article presents an overview of all vertebrate remains from sixteen open-air localities and eight cave sites, the deposits of which were accumulating during the Eemian Interglacial in the present-day territory of Poland. The cave sites are in the Kraków-Wieluń Upland, while the open-air localities are dispersed throughout the country (Text-fig. 1). The presence of animal remains of this age from cave sites in the Sudetes and Holy Cross Mts. has not been previously recorded. Only taxa found in strata whose age was determined as equal to the Eemian interglacial are described. Many cave sites do not have a clear stratigraphy, but a broader discussion is beyond the scope of this study. The information about different groups of vertebrates is arranged here in systematic order. Habitat preferences of mammals were defined according to the data provided by the International Union for Conservation of Nature (2023), and climatic preferences are given based on the data from Madeyska (1981), Hernández Fernández (2001), Bocheński *et al.* (2012), and Kahlke (2014).

RESULTS OF THE STUDY

Fishes

Six fish-bearing localities dating back to the Eemian interglacial (MIS 5e) are known to date from the territory of Poland (Table 3). Fish remains from Szeląg near Poznań, Nędzerzów near Kalisz and Żmigród on the Barycz River were briefly reported by Lubicz-Niezabitowski (1929), Skompski (1977, 1983) and Hebig (1978), while those from Imbramowice, Lechitów and Gorzów Wielkopolski have been recently described in detail and interpreted in terms of environmental changes by Stefaniak *et al.* (2021b). All fish-bearing localities of that age comprise palaeolacustrine communities. Fish remains were buried in the alluvium in a natural way, as evidenced by their taxonomic and anatomical diversity (Casteel 1976). The presence of 13 fish species representing six families (Acipenseridae, Cyprinidae, Salmonidae, Esocidae, Gobiidae, and Percidae) was revealed in the general sample. Among them, carp fishes were the most diverse (eight species), while other families were each represented by a single species. In addition, several specimens belong to closely indeterminate family-rank taxa. The roach, rudd, pike and perch, followed by the bream and tench,

Taxon	Localities					
	Szeląg near Poznań[1]	Nędzerzów near Kalisz[2]	Żmigród on the Barycz River[3]	Imbramowice[4]	Lechitów near Góra[4]	Gorzów Wielkopolski[4]
Acipenser sturio	+	–	–	–	–	–
Leuciscus sp.	–	–	–	+	–	–
Rutilus rutilus	–	+	+	+	+	+
Scardinius erythrophthalmus	+	+	–	+	–	+
Chondrostoma sp.	–	–	–	–	–	+
Alburnus alburnus	–	+	–	–	+	–
Abramis brama	–	+	–	+	–	+
Carassius carassius	–	+	–	–	–	+
Tinca tinca	+	+	–	–	–	+
Cyprinidae gen. et sp. indet.	–	–	–	+	–	+
Coregonus cf. *lavaretus*	–	–	–	–	–	+
Salmonidae gen. et sp. indet.	–	–	–	–	–	+
Esox lucius	+	+	–	+	–	+
?*Neogobius* sp.	–	–	–	–	–	+
Perca fluviatilis	+	+	+	+	–	+

Table 3. Fish remains in materials from localities of the Eemian Interglacial in the territory of Poland. References: [1] Lubicz-Niezabitowski 1929; [2] Hebig 1978; [3] Skompski 1983; [4] Stefaniak *et al.* 2021b.

were the most common components of the Eemian fish assemblages. At the same time, all other species appeared only once or twice in the fossil record of that age (Stefaniak *et al.* 2021b).

The fish assemblage from Szeląg near Poznań most likely inhabited a river with a gravel bottom suitable for spawning the Atlantic sturgeon. The presence of phytophilous forms indicates the development of macrophytes. Fishes from Nędzerzów near Kalisz lived in an open lake, some parts of which were overgrown and favourable for the rudd, tench, crucian carp, pike, and perch.

The fishes of Imbramowice also inhabited a slow-flowing lake with a sandy-silty bottom and well-developed aquatic vegetation. Most of the identified species are phytophilous, laying eggs on the underwater parts of plants. The roach, bream, and perch fed mainly on invertebrates, while aquatic vegetation predominates in the diet of the rudd. The presence of the tench and crucian carp indicates overgrowth of the reservoir and an increase in its trophism (Stefaniak *et al.* 2021b).

The bleak identified in Lechitów near Góra suggests a lacustrine environment. The Eemian fish community of Gorzów Wielkopolski inhabited an open lake probably connected with a river, as evidenced by the presence of the dace, nase, and goby (Stefaniak *et al.* 2021b). Some parts of this reservoir were overgrown (considering a large number of phytophilous fishes, in particular roach, rudd, bream, crucian carp, tench, pike, and perch) and characterised by slow-flowing water.

Amphibians and reptiles

Remains of amphibians and reptiles occurred in deposits of only two localities of the Eemian Interglacial (Table 4). Zdrody is a unique site where numerous amphibians were found. The latter are represented by anuran taxa, which are common in the recent fauna of Poland and were represented in the Pliocene and Lower Pleistocene fossil record: European green toad *Bufotes viridis*, the common frog *Rana temporaria*, the moor frog *Rana arvalis* and unspecified *Rana* sp. (Bałuk *et al.* 1979; Młynarski and Szyndlar 1989). Reptilian remains of Eemian age were found only in the Nietoperzowa Cave and are represented by the grass snake *Natrix natrix*, remains of which are well known and widely distributed in Quaternary deposits, and the common European viper *Vipera berus*. Considering the low diversity of amphibians and reptiles, it is impossible to provide any palaeoecological information except for the presence of a water reservoir near the Nietoperzowa Cave in the past (Madeyska 1982; Szyndlar 1984; Młynarski and Szyndlar 1989).

Taxon	Localities	
	Zdrody[1]	Nietoperzowa Cave
Bufotes viridis	+	–
Rana temporatia	+	–
Rana arvalis	+	–
Rana sp.	+	+
Natrix natrix	+	?+[2]
Vipera berus	–	+[3]

Table 4. Amphibian and reptilian remains in materials from localities of the Eemian Interglacial in the territory of Poland. References: [1] Bałuk *et al.* 1979; [2] Madeyska 1982; [3] Szyndlar 1984.

Birds

Bird remains in deposits of the Eemian Interglacial occurred only in material from cave sites. They were assigned to 47 taxa, of which 44 species were identified while three others were described using open nomenclature. Most of the identified bird taxa occurred in Poland during the Middle and Late Pleistocene and were typical representatives of Holocene avifaunal assemblages. At present, ptarmigans do not occur in this area, and some other bird species have become rare in the extant avifauna of Poland (Table 5), e.g., the Ural owl *Strix uralensis*, the Eurasian dotterel *Eudromias morinellus*, the ruff *Calidris pugnax*, the Alpine swift *Tachymarptis melba*, the northern hawk-owl *Surnia ulula* and representatives of the genus *Gallinago* (Nadachowski *et al.* 2000, 2009; Tomek and Bocheński 2005; Bocheński *et al.* 2012). Analyzing their ecological adaptations, 19 taxa represented during the Eemian Interglacial are associated with forests. In addition, there are 14 water-related taxa, eight species usually nested in rocks and caves, two species occur in open areas, while seven forms are associated with tundra and swamp environments. The large number of forest and water-related forms confirms the presence of forests, water reservoirs and wetlands in the area of the Kraków-Częstochowa Upland, as well as the development of open areas (Bocheński 1974, 1988, 1990, 2001; Madeyska 1982; Tomek and Bocheński 2005; Nadachowski *et al.* 2000, 2009; Stefaniak *et al.* 2009a; Bocheński *et al.* 2012).

Small mammals

Seven taxa of small mammals were recognised in the deposits of the Łokietka Cave, correlated with the Eemian Interglacial (Table 6): *Sicista betulina*,

Taxon	Localities						
	Nietoperzowa Cave	Jasna Strzegowska Cave	Biśnik Cave l. 15	Biśnik Cave l. 14–13	Dziadowa Skała Cave	Deszczowa Cave	Komarowa Cave
Anser anser/albifrons	–	–	–	–	–	+	–
Aythya fuligula	–	–	–	–	–	–	–
Spatula querquedula	–	–	–	+	–	–	–
Anas crecca/Spatula querquedula	–	–	+	–	–	+	–
Anas platyrhynchos	–	–	+		–	+	–
Coturnix coturnix	–	–	+	–	–	–	–
Lagopus lagopus	–	+	+	+	–	+	–
Lagopus muta	–	+	+	–	–	+	–
Lagopus sp.	–	–	+	–	–	+	–
Tetrao urogallus	–	+	+	+	+	+	–
Lyrurus tetrix	–	–	+	+	+	+	–
? (originally: *Tetrao/Lagopus*)	–	–	–	+	–	–	–
Galliformes indet.	–	–	–	+	–	–	–
Tachymarptis melba	–	–	–	+	–	–	–
Crex crex	–	–	+	–	–	–	–
Pluvialis squatarola	–	–	–	–	–	+	–
Pluvialis apricaria	–	–	+	–	–	+	–
Eudromias morinellus	–	–	–	+	–	–	–
Vanellus vanellus	–	–	+	–	–	–	–
Limosa limosa	–	–	–	–	–	+	–
Calidris pugnax	–	–	–	+	–	–	–
Scolopax rusticola	–	–	–	+	–	–	–
Gallinago media	–	–	–	–	–	+	–
Gallinago gallinago	–	–	–	–	–	+	–
Tringa glareola	–	–	–	–	–	+	–
Buteo sp.	–	+	–	–	–	–	–
Surnia ulula	–	–	–	+	–	–	–
Asio flammeus	–	–	–	+	–	–	–
Strix aluco	–	–	–	+	–	–	–
Strix uralensis	–	–	–	+	–	–	–
Dendrocopos major	–	–	+		–	–	+
Falco tinnunculus	–	–	–	–	–	+	–
Pyrrhocorax sp.	–	–	–	+	–	–	–
Nucifraga caryocatactes	–	–	+	–	–	–	–
Corvus monedula	–	–	+	+	–	+	–
Corvus monedula/*Pyrrhocorax* sp.	–	–	+	–	–	–	–
Corvus corax	–	–	–	+	–	–	–
Corvidae (small) indet.	–	–	–	–	–	–	–
Coccothraustes coccothraustes	–	–	–	+	–	–	–
Choris chloris	–	–	–	+	–	–	–
Loxia pytyopsittacus	–	–	+	–	–	–	–
Loxia curvirostra	–	–	–	+	–	–	–
Loxia sp.	–	–	+	–	–	–	–
Fringillidae indet.	–	–	–	+	–	–	–
Alauda arvensis	–	–	–	+	–	–	–
Acrocephalus arundinaceus	–	–	–	+	–	–	–
Hirundo/Cecropis	–	–	+	+	–	–	–
Aegithalos caudatus	+	–	–	–	–	–	–
Regulus regulus	+	–	–	–	–	–	–
Turdus viscivorus	–	–	+	–	–	–	–
Turdus philomelos	–	–	–	+	–	–	–
Turdus sp.	–	–	–	–	–	–	+
Turdidae indet.	–	–	+	–	–	–	–
Aves indet.	–	–	+	+	–	–	–

Table 5. Bird remains in materials from localities of the Eemian Interglacial in the territory of Poland (after Bocheński *et al.* 2012, modified).

Taxon	Localities							
	Nietoperzowa Cave	Łokietka Cave	Biśnik Cave l. 15	Biśnik Cave l. 14–13	Dziadowa Skała Cave	Deszczowa Cave	Komarowa Cave	Zdrody
Erinaceus roumanicus	–	–	+	+	–	–	–	–
Crocidura obtusa	–	–	+	+	–	–	–	–
Neomys fodiens	–	–	–	+	–	–	–	–
Sorex araneus	+	–	+	+	–	–	+	–
Sorex minutus	–	–	+	+	–	–	+	–
Sorex minutissimus	–	–	–	+	–	–	–	–
Sorex runtonensis	–	–	+	+	–	–	+	–
Sorex thaleri	–	–	+	–	–	–	–	–
Sorex caecutiens	–	–	–	–	–	–	–	+
Talpa europaea	+	–	+	+	–	–	+	+
Talpa minor	–	–	–	+	–	–	+	–
Eptesicus nilssonii	–	–	+	–	–	–	+	–
Eptesicus serotinus	–	–	+	–	–	–	+	–
Barbastella barbastellus	–	–	+	–	–	–	–	–
Barbastella cf. *schadleri*	–	–	–	–	–	–	+	–
Rhinolophus hipposideros	–	–	–	–	–	–	+	–
Plecotus auritus	–	–	+	+	–	–	+	–
Plecotus cf. *austriacus*	–	–	–	–	–	–	+	–
Nyctalus sp.	–	–	–	–	–	–	+	–
Vespertilio murinus	–	–	–	–	–	–	+	–
Myotis bechsteinii	–	–	–	–	–	–	+	–
Myotis emarginatus	–	–	–	–	–	–	+	–
Myotis brandtii	–	–	+	+	–	–	+	–
Myotis daubentonii	–	–	+	–	–	–	+	–
Myotis mystacinus	–	–	+	+	–	–	+	–
Myotis mystacinus/brandtii	–	–	–	–	–	–	+	–
Myotis nattereri	–	–	–	–	–	–	–	–
Myotis dasycneme	–	–	–	–	–	–	+	+
Myotis sp.	–	–	–	+	–	–	+	–
Chiroptera indet.	+	–	–	–	–	–	–	–
Castor fiber	–	–	–	–	–	+	+	–
Sciurus vulgaris	–	–	+	+	–	–	–	–
Spermophilus superciliosus	–	–	+	+	–	–	+	–
Spermophilus citelloides	–	–	+	+	–	–	+	–
Dryomys nitedula	–	–	–	+	–	–	–	–
Glis glis	–	–	+	+	+	–	+	–
Muscardinus avellanarius	–	–	–	–	–	–	+	–
Allactaga major	–	–	–	+	–	–	–	–
Sicista betulina	–	–	+	+	–	–	–	+
Arvicola amphibius	+	+	+	+	–	–	+	–
Dicrostonyx cf. *simplicior*	–	–	–	–	–	+	+	–
Dicrostonyx cf. *henseli/torquatus*	–	–	+	+	–	–	–	–
Lagurus lagurus	–	–	–	+	–	–	–	–
Lemmus lemmus	–	–	+	+	–	+	+	–
Microtus agrestis	+	–	+	+	–	–	–	+
Microtus arvalis	–	–	–	+	–	–	–	–
Microtus arvalis/agrestis	–	+	–	–	–	+	+	–
Microtus subterraneus	–	+	+	+	–	–	+	+
Microtus sp.	–	+	–	–	–	–	–	–
Stenocranius gregalis	+	–	+	+	–	+	+	–
Alexandromys oeconomus	+	+	+	+	–	+	+	–
Clethrionomys glareolus	+	+	+	+	–	+	+	+
Chionomys nivalis	+	–	–	–	–	–	–	–
Cricetulus migratorius	–	–	+	+	–	–	+	–
Cricetus cricetus	–	–	+	+	–	–	+	–
Apodemus flavicollis/sylvaticus	–	+	+	+	–	–	+	–
Apodemus cf. *agrarius*	–	–	–	–	–	–	+	–
Apodemus sp.	+	–	–	–	–	–	–	–
Hystrix brachyura	–	–	+	+	–	–	–	–
Ochotona pusilla	–	–	+	+	–	–	–	–
Lepus europaeus	–	–	+	+	–	–	–	–
Lepus timidus	–	–	–	+	–	–	–	–
Lepus sp.	–	–	–	–	–	+	–	–
Oryctolagus cuniculus	–	–	–	+	–	–	–	–

Table 6. Small mammalian remains in materials from localities of the Eemian Interglacial in the territory of Poland.

Apodemus sylvaticus/flavicollis, *Arvicola amphibius*, *Clethrionomys glareolus*, *Microtus arvalis/agrestis*, *Alexandromys oeconomus*, *Microtus subterraneus*, and *Microtus* sp. (Lipecki *et al.* 2001). The layer six is characterized by the dominance of eurytopic (44%) and forest (43%) species and represents climate warming.

Comparison of climatic preferences shows that the small mammalian taxa mentioned above preferred to exist in a temperate climate (VI – typical temperate – nemoral broadleaf-deciduous forest). At the same time, *Microtus arvalis* and *M. subterraneus* represent forms that are restricted in their occurrence only to the temperate climate zone. A comparison of habitat preferences shows that these taxa can occur in forests, open areas, and near-water habitats. The species composition of rodents of the Łokietka Cave is typical for the extant central European fauna.

Sediments of layer IV of the Deszczowa Cave are correlated with the Eemian Interglacial (Cyrek *et al.* 2000; Nadachowski *et al.* 2009). Eight taxa of small mammals were identified within this layer: *Castor fiber*, *Clethrionomys glareolus*, *Alexandromys oeconomus*, *Microtus arvalis/agrestis*, *Stenocranius gregalis*, *Dicrostonyx* cf. *simpilcior*, *Lemmus lemmus*, and *Lepus* sp. (Table 6).

According to Cyrek *et al.* (2002), the accumulation of layer IV took place in a cool (cold?) climate with a predominance of open areas. According to Nadachowski *et al.* (2009), the accumulation of this layer corresponds to the Wartanian glaciation (MIS 6). On the other hand, Krajcarz and Madeyska (2010) indicate that the accumulation of this layer took place in warm and humid conditions during the Eemian Interglacial (MIS 5e). According to these authors, layer IV from Deszczowa Cave corresponds to layers 13 and 12 of Nietoperzowa Cave, whose accumulation is correlated with the Eemian Interglacial (Krajcarz and Madeyska, 2010). At the same time, the results of radiometric studies presented by Lorenc (2006a) indicate that the deposition of this layer took place during MIS 3 (42,800±1,900 BP). Analyses of the species composition of small mammals from this layer, presented by Cyrek *et al.* (2000) and Nadachowski *et al.* (2009), indicate the dominance of two taxa – *Dicrostonyx* cf. *simplicior* and *Stenocranius gregalis*. These taxa represent forms that do not occur in temperate climate conditions. In the case of *Dicrostonyx*, it represents a genus mostly restricted to arctic habitats. *Stenocranius gregalis*, on the other hand, represents a form inhabiting dry open areas in three types of climate. Among other taxa from this layer, characterized by a much smaller proportion (Cyrek *et al.* 2000; Nadachowski *et al.* 2009), *Lemmus lemmus*, *Alexandromys oeconomus*, *Microtus agrestis* and *Clethrionomys glareolus* co-occur in a very cold (boreal) or cold climate (*Lemmus lemmus* and *Alexandromys oeconomus*).

According to Kowalski (1964), the deposition of layers 13 and 12 in Nietoperzowa Cave is correlated with temperate climate conditions, similar to modern ones. Ten taxa of small mammals were identified in the material from this locality: *Talpa europaea*, *Sorex araneus*, Chiroptera indet., *Clethrionomys glareolus*, *Arvicola amphibius*, *Chionomys nivalis* (only in the layer 13), *Microtus agrestis*, *Alexandromys oeconomus* (only in the layer 13), *Stenocranius gregalis* (only in the layer 12), and *Apodemus* sp. (Table 6). These taxa are characterized by diverse habitat and climatic preferences. Most of them coexist in the VI climatic zone (Typical temperate – nemoral broadleaf-deciduous forest). Only *Stenocranius gregalis*-represents a form that does not occur in this climate zone. This species was found in layer 12, which may indicate a change in climatic conditions, manifested by progressive cooling and increasing climate continentalization.

The problem of the stratigraphic correlation of layers 15–13 in Biśnik Cave is not fully solved (Krajcarz *et al.* 2014a; Socha 2014; Gąsiorowski *et al.* 2014). Assemblages of small mammals from these layers are characterized by a high level of diversity (Socha 2014). The remains of 35 taxa of small mammals were identified in layer 15, while 26 and 31 taxa were recognized in layers 14 and 13, respectively. Most of the identified taxa are characterized by the possibility of their occurring in two to four climatic zones, where they can inhabit various habitats. Most mammalian taxa found in these layers could have occurred in a temperate climate zone. The presence of taxa not occurring in the temperate climate zone, but characteristic of cold, boreal or continental climates, may indicate the deposition of these sediments in the periods preceding and following the Eemian climatic optimum. It is noteworthy that the remains of a porcupine *Hystrix brachyura* were found in layers 15 and 14. This species occurs in warm climate conditions.

The Eemian age of the layers 15–13 in Biśnik Cave is supported by the results of palaeoecological studies conducted based on rodent assemblages (Socha 2014). Associations of small mammals from these layers were characterized by high biodiversity and the dominance of taxa occurring in a temperate climate. A comparison of habitat preferences shows a mosaic of forest habitats and open areas in the vicinity of the study site during the deposition of these layers. The constant presence of water was a permanent element of the landscape of that time.

A decrease in the proportion of cold-adapted species or those associated with the continental climate (*Dicrostonyx*, *Lemmus*, *Stenocranius*) is observed in associations of small mammals from layers 15 and 14; it may indicate a gradual improvement of climatic conditions before the climatic optimum. On the other hand, the presence of a few cold-loving taxa in layer 13, as well as the appearance of taxa typical of continental climate species (*Lagurus*, *Allactaga*), may indicate deposition during the gradual development of the Scandinavian ice sheet. At the same time, high biodiversity may result from the situation where an extensive range of environments is available, typical for transitional climate conditions.

The remains of a single small mammalian species (*Glis glis*) were recorded in the Eemian deposits of Dziadowa Skala Cave (Table 6). Considering that *Glis glis* is a typical representative of the forest fauna, limited in its occurrence to a temperate climate, it can be assumed with high probability that the deposition of these sediments took place in the conditions of climate warming and the development of compact forest communities, represented by mixed deciduous forests.

Two layers in Komarowa Cave are correlated with the Eemian Interglacial. Both come from a sequence of sediments identified on the terrace in front of the entrance to Komarowa Cave (Nadachowski *et al.* 2009). A high taxonomic diversity of small mammals was recorded, which may either indicate that the deposition of these layers took place during a period of dynamic changes in environmental conditions or it may result from the mixing of organic remains in a dynamic environment of sedimentary deposits which constitute the foreground of the cave.

The small mammalian assemblages found in both layers represent mixed associations in terms of quality and quantity (Table 6). Both forms with high and low ecological valence occurred there. The coexistence of species with different ecological preferences may indicate the dominance of transitional climatic conditions. The reign of transitional climatic conditions is conducive to the development and coexistence of diverse natural environments, which is conducive to the growth of taxonomic diversity. Data presented by Nadachowski *et al.* (2009) confirm the high taxonomic diversity of small mammals in both Eemian layers of the Komarowa Cave. A comparison of the taxonomic composition of small mammals indicates that they correspond to the gradual evolution of conditions characterized by an increase in the climatic regime from the Gtx to the Ftx stratum.

The small mammalian assemblage of Zdrody (Table 6), in terms of the ecological preferences of its representatives, includes forms occurring today in Poland. All the identified taxa coexist in temperate climate conditions (Typical temperate – nemoral broadleaf-deciduous forest).

Carnivorans

The Eemian deposits comprising carnivore remains are relatively weakly represented in Polish biostratigraphy. Carnivores provide important biostratigraphic information, e.g. those from layers 3–4 of Dziadowa Skała Cave, layers 14–13 in Biśnik Cave or layers IV and V in Deszczowa Cave. Carnivore remains (especially those of ursids) are relatively numerous and well-represented in all these layers (Table 7). The remains of *Canis lupus* document the presence of a canid of moderately large and rather gracile stature, dimensionally comparable with the extant Polish grey wolf. Although the species composition of canids remained unchanged during the Late Pleistocene, there were marked fluctuations in *C. lupus* body size for the last 100 kyr (Made *et al.* 2014; Marciszak *et al.* 2021b, 2022, 2023). The body size of canids has been influenced by the harsh environmental conditions, with larger size potentially being a response to severely cold climates. In combination with the intense competition with other larger carnivores, such a response was very likely responsible for the substantial increase in the size of *C. lupus*. Particularly large and robust individuals usually appeared alongside normal-sized ones. In some localities, especially within the Sudetes (Jasna Radochowska, Obok Wschodniej Cave, Niedźwiedzia Cave) and those from Kraków-Częstochowa Upland (e.g., layers 7–5 of the Biśnik Cave), all wolf individuals were significantly larger than the extant *C. lupus* (Made *et al.* 2014; Marciszak *et al.* 2021b, 2022, 2023). The presence of these large wolves, identified as *Canis lupus spelaeus* (Goldfuss, 1823), is traditionally linked with the cooler phases of the Late Pleistocene. Their occurrence from multiple Polish sites is documented until the end of MIS 2. However, remains of *C. l. spelaeus* are missing in some Eemian layers (e.g., layers 3–4 of Dziadowa Skała, layers 14–13 in Biśnik Cave or the layer V in Deszczowa Cave). The size of specimens from these horizons corroborates well with those from other Eemian populations of Europe (Made *et al.* 2014; Marciszak *et al.* 2021b, 2023).

Numerous remains of *Martes martes* from the Eemian deposits are far less distant from the particularly large and robust Late Pleistocene pine marten.

Taxon	Localities								
	Ciemna Cave l. 16-9	Nietoperzowa Cave l. 13-12	Imbramo-wice	Jasna Strzegowska Cave	Biśnik Cave l. 15	Biśnik Cave l. 14–13	Dziadowa Skała Cave l. 4-3	Deszczowa Cave l. IV-V	Komarowa Cave l. Gtx
Canis lupus lupus	+	+	–	–	+	+	+	+	+
Vulpes vulpes	+	+	–	–	+	+	+	+	+
Vulpes lagopus	–	–	–	–	+	+	–	–	–
Ursus spelaeus spelaeus	+	+	–	–	+	+	+	+	+
Ursus arctos taubachensis	+	+	+	–	+	+	+	+	+
Meles meles	+	+	–	+	+	+	+	+	+
Martes martes	+	+	–	+	+	+	+	+	+
Mustela putorius	–	+	–	–	+	+	+	+	+
Mustela erminea	–	+	–	–	+	+	–	+	+
Mustela nivalis	–	+	–	–	+	+	+	+	+
Panthera spelaea spelaea	–	+	–	–	+	+	–	+	+
Panthera pardus	–	–	–	–	+	–	+	–	–
Lynx lynx	–	–	–	–	+	–	+	–	–
Felis silvestris	–	+	–	–	+	+	+	–	–
Crocuta crocuta spelaea	–	–	–	–	+	+	+	–	+

Table 7. Carnivore remains in materials from localities of the Eemian Interglacial in the territory of Poland.

These specimens are comparable in size and morphology to the extant *M. martes* (Marciszak 2012; Marciszak *et al.* 2020). In any of the Eemian individuals of Polish *M. martes*, the m1 total length does not exceed 11.5 mm. This is the limiting value for this marten, above which individuals (males) are considered to be definitely above the average value for this species. On the other hand, males of *M. martes* from strata dating to the cold periods of the last glaciation (MIS 5–2) have a first molar longer than 11.5 mm. Among mustelids of the Eemian Interglacial, noteworthy is also the absence of typical cold-adapted species, e.g. *Gulo gulo* and *Mustela eversmanii*, usually present in layers accumulating during colder phases. Remains of the thermophilic *Meles meles* are usually correlated with warmer periods.

The remains of two forest species, *Lynx lynx* and *Felis silvestris*, are relatively common in Eemian deposits as compared to those in layers dated to MIS 5–2 (Wolsan 1989, 1993; Barycka 2008). While *L. lynx* can hunt and live in deep snow conditions, snow cover deeper than 20 cm and lying for a longer time is a limiting factor for *F. silvestris* (Mermod and Liberek 2002). The occurrence of this species in Polish sites is usually correlated with interglacial/interstadials, and it is well documented during the Holocene (Marciszak *et al.* 2017; Krajcarz *et al.* 2022). The remains of larger felids, e.g., *Panthera spelaea spelaea* and *Panthera pardus*, are also present in the Eemian deposits of Poland. Both species are ecologically flexible and might have occurred during glaciers and interglacials. The cave lion already occurred as the morphologically advanced chronosubspecies *P. s. spelaea*, the last in the evolutionary lineage. Most Polish lions from the Eemian strata are characterised by moderate and large sizes. Among them, however, we still observe a high proportion of large individuals as a remnant of the Middle Pleistocene (Marciszak *et al.* 2021). Leopard remains are rarer, but most individuals are also large, massive males. The cave hyena *Crocuta crocuta spelaea* is present in some Eemian strata in the territory of Poland. However, they are represented in such a small number and density as well as by primarily fragmentary material, that they cannot give any reliable information about the species in the respective timespan.

The typical individual of *Ursus spelaeus ingressus* from Polish sites is a very robust and large speleoid bear (Marciszak *et al.* 2020). Its skull, in lateral view, has a nearly horizontal sagittal crest and a very prominent, step-like frontal. Multiple-coned and enlarged tooth cusps, broadened molar crowns and the lack of additional premolars confirmed their full herbivorous specialisation. P4 morphotypes represented a multi-coned, broad type E, with enlarged main cusps. When the material from Eemian deposits is compared to those from other Late Pleistocene layers, the presence of evolutionary less advanced morphotypes and, on average, slightly smaller dimensions can be noted. Since genetic analyses were not performed so far for most of these localities, where it is most likely *U. s. spelaeus* and *U. s. ingressus* occurred side by side, in the following paper, we use the taxonomy in the rank of subspecies, since the level of difference between them does not exceed that between subspecies of the extant *U. arctos*, such as *U. a. beringianus* Middendorff, 1851 and *Ursus* *arctos piscator* Pucheran, 1855 (Baryshnikov and Puzachenko 2011). The results of the analysis demonstrate that the remains of both above species are present in some Polish sites like Biśnik, Komarowa and Radochowska Caves, where they are distinguishable by biometrical methods.

Even more symptomatic is the abundance of numerous remains of *Ursus arctos*, represented by the chronosubspecies *Ursus arctos taubachensis*, which was very specific and widespread during the Eemian Interglacial. The predominance of *U. arctos* over *U. spelaeus* sensu lato is a clear signal of the interglacial nature of these layers. Such a scenario is well documented in a number of European localities, where the remains of *U. arctos* outnumber the remains of *U. spelaeus* sensu lato in deposits dated to the Eemian or other interglacials. Those localities are Taubach (Portis 1878; Pohlig 1892; Soergel 1912, 1914; Rode 1931, 1935; Erdbrink 1953, 1967; Kahlke 1958, 1961, 1994, 1995; Kurtén 1977; Hemmer 1984; Dusseldorp 2009), Heppenloch (Fraas 1895; von Reichenau 1904, 1906; Freudenberg 1908, 1914, 1932; Adam 1975), Weimar-Ehringsdorf (Kurtén 1975), Chlupáč Cave (Mostecký 1961, 1963, 1969; Marciszak *et al.* 2022), layers 14–13 of Kůlna Cave (Musil 1970, 2010, 2018; Valoch *et al.* 1970; Valoch 1988), Grays Thurrock (Kurtén 1957, 1959), or Tornewton Cave (Kurtén 1957; Baryshnikov 2007).

Ursus arctos priscus was described as a huge bear, occurring during the late Middle–Late Pleistocene (last ca. 450 kyr), with a flat forehead, additional premolars (P1–P3/p1–p3), enlarged and unusually broad molars, bulkier metacarpals and metatarsals as well as some differences in muscle attachments on postcranial elements (Baryshnikov 2007; Rabeder *et al.* 2010; Marciszak *et al.* 2019a, b). Interglacial individuals were also very large, comparable in size and stature with the record-sized specimens of the extant subspecies of *Ursus arctos*, e.g. *Ursus arctos beringianus* Middendorff, 1851, *Ursus arctos middendorffi* Merriam, 1896 and *Ursus arctos gyas* Merriam, 1902. Specimens from glacials and stadials could have been even larger, being in fact, the largest late Middle and Late Pleistocene Eurasian carnivorans (Marciszak *et al.* 2019a, b). This large bear migrated from the East (Musil 1996; Sabol 2001a, b) and first appeared ca. 450 kya (Kurtén 1959; Baryshnikov 2007; Marciszak *et al.* 2019; Marciszak and Lipecki 2020; Marciszak *et al.* 2022). Earlier authors described bear remains from the Eemian Interglacial as representing an independent subspecies *Ursus arctos taubachensis* Rode, 1935 (Kurtén 1957, 1959, 1968, 1975, 1977; Mostecký 1961, 1963, 1969; Musil, 1996; Sabol 2001a, b; Wagner 2001). However, its taxonomic position has been revised, and it is now considered to be a synonym for *U. a. priscus* sensu lato (Baryshnikov 2007; Marciszak *et al.* 2019, 2022; Marciszak and Lipecki 2020).

Elephants and ungulates

Elephants in the territory of Poland during the Eemian Interglacial were represented by two taxa, the remains of which are known only from open-air localities. Among them, the most numerous are those belonging to the forest elephant *Palaeoloxodon antiquus* (Jakubowski 1988, 1996; Kubiak 1989b, 2001; Pawłowska 2015b). The find as mentioned earlier from Konin is one of the most complete finds in Europe. The remaining sites provide finds of limb bones and teeth (Jakubowski 1988, 1996; Kubiak 1989b, 2001; Pawłowska 2015b). The forest elephant was widely distributed in Europe during the interglacial periods, retreating to refugia during the glacial periods. It was associated with the forest environment, both in the temperate and Mediterranean zones. Numerous dwarf forms of this species have arisen on the islands of the Mediterranean. It became extinct during the MIS 3 period, although there are unconfirmed data that it may have survived up to the Holocene on islands of the Mediterranean Sea (Koenigswald 1991; Kolfschoten 2000; Stuart 2005; Pushkina 2007). The presence of this species in Poland is an indicator of forest environments.

The woolly mammoth *Mammuthus primigenius* occurred in two localities dated to the Eemian Interglacial (Szeląg and the Lignite Mine in Konin), although these deposits probably belong to the last glaciation. This species was widely distributed during the Middle Pleistocene and persisted up to the end of the Pleistocene, being essential part of the so-called *Mammuthus–Coelodonta* complex (Kozłowski and Kubiak 1972; Kubiak 1989b, 2001; Kahlke 1999, 2014; Nadachowski *et al.* 2011, 2015a, b, 2018; Markova *et al.* 2013; Pawłowska 2015b; Baca *et al.* 2017).

Odd-toed ungulates were represented in material from Polish localities of the last interglacial by three species: the wild horse *Equus ferus*, the woolly rhinoceros *Coelodonta antiquitatis* and Merck's rhinoceros *Stephanorhinus kirchbergensis*. Of them, the first two species occurred in open-air localities and cave sites, while the latter was found only in an open-air locality (Tables 8, 9).

Equus ferus was found in Szeląg near Poznań, Imbramowice and Siekierki, but as in the case of the woolly mammoth, its remains could have come

Taxon	Localities								
	Ciemna Cave	Nietoperzowa Cave	Łokietka Cave	Jasna Strzegowska Cave	Biśnik Cave l. 15	Biśnik Cave l. 14–13	Dziadowa Skała Cave	Deszczowa Cave l. IV	Komarowa Cave
Equus ferus	+	+	–	+	+	+	–	+	–
Coelodonta antiquitatis	–	–	+	?+	+	+	+	–	–
Sus scrofa	+	–	–	–	+	+	+	–	+
Cervus elaphus	+	+	–	+	+	+	+	–	+
Megaloceros giganteus	–	+	–	–	+	+	–	–	–
Capreolus capreolus priscus	+	+	–	–	–	+	+	+	–
Cervalces sp.	–	–	–	–	+	–	–	–	–
Alces alces	+	–	–	–	–	–	+	–	–
Rangifer tarandus	+	+	+	–	+	+	+	–	–
Bison priscus	+	–	–	–	+	+	+	–	–
Bos primigenius	–	–	–	–	+	–	+	–	–
Bos/Bison	+	+	–	–	–	–	+	–	+
Rupicapra rupicapra	+	–	–	–	+	–	–	–	–

Table 8. Large mammalian remains in materials from cave sites of the Eemian Interglacial in the territory of Poland.

Taxon	Localities									
	Oborniki	Szeląg near Poznań	Konin Brown Coal Mine	Imbramo-wice	Wrocław, Hallera street 1	Siekierki, Wisła River	Gorzów Wielko-polski	Warszawa Leszno street	Warszawa Szczęśli-wice	Ciecha-nów
Palaeoloxodon antiquus	+	–	+	+	–	–	–	+	+	+
Mammuthus primigenius	–	+	+	–	–	–	–	–	–	–
Equus ferus	–	+		+	–	+	–	–	–	–
Coelodonta antiquitatis	–	+	+	–	–	–	–	–	–	–
Stephanorhinus kirchbergensis	–	–	–	+	+	+	+	–	+	–
Cervus elaphus	–	+	–	–	–	+	–	–	–	–
Dama dama	–	–	–	–	–	–	+	–	–	–
Capreolus capreolus priscus	–	–	–	–	–	–	–	–	+	–
Rangifer tarandus	–	–	–	–	–	+	–	–	–	–
Bison priscus	–	+	–	–	–	–	–	–	+	–
Bos primigenius	–	+	–	–	–	+	–	–	+	–

Table 9. Large mammalian remains in materials from open-air localities of the Eemian Interglacial in the territory of Poland.

from the Vistulian strata. As for the cave sites, the remains of this species were found in the Eemian layers of the Ciemna Cave, Nietoperzowa Cave, Jasna Strzegowska Cave and Biśnik Cave (Tables 8, 9). The remains of this horse became numerous since the Middle Pleistocene and have been found throughout the country, although most of the sites are not well-dated. Most of the remains are teeth and bones of limbs. The horse is associated with open areas, but it could also inhabit forested areas or forest-steppes (Kubiak 1989a; Stefaniak *et al.* 2009a; Van Asperen and Stefaniak 2011; Nadachowski *et al.* 2015a, b).

Another characteristic representative of the mammoth steppe fauna was the woolly rhinoceros *Coelodonta antiquitatis* (Guérin 1980; Kahlke 1999, 2014, Markova *et al.* 2013). The remains of this species have been described from four cave sites (Łokietka Cave, ?Jasna Strzegowska Cave, Biśnik Cave, Dziadowa Skała Cave) and two open-air localities (Szeląg near Poznań, Konin Brown Coal Mine) (Tables 8, 9). As in the case of the woolly mammoth, they could have come from the Vistulian strata or from the levels accumulated at the beginning or end of the Eemian Interglacial. The presence of such cold-adapted species was also reported for small mammals and reindeer (Socha 2014; Stefaniak *et al.* 2009a; 2020). The woolly rhinoceros was widespread during the Middle and Upper Pleistocene. A total of 185 sites are known in Poland, 37 of which are caves, but, as in the case of the horse, most do not have precise stratigraphy. These were skulls and their fragments, as well as limb bones (Borsuk-Białynicka and Jakubowski 1972; Kubiak 1989a; Stefaniak *et al.* 2009a–c; Nadachowski *et al.* 2015a, b; Baca *et al.* 2017; Stefaniak *et al.* 2023b).

The remains of *Stephanorhinus kirchbergensis* are known from five open-air localities in Poland

(Table 9). Three of them (Imbramowice, Konin, Gorzów Wielkopolski) and probably Wrocław Hallera Street and Warszawa Szczęśliwice are confined to deposits of the Eemian Interglacial (MIS 5e) and thus are the earliest confirmed occurrences of this species in Poland. The other eight localities have no clear stratigraphy. 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). Noteworthy is the recent find of an almost complete skeleton of a female Merck's rhinoceros from Gorzów Wielkopolski, which, according to the results of osteometric studies, is one of the largest known individuals of the species (Stefaniak *et al.* 2023a). Other Polish finds include rhino skulls, mandibles and isolated 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, 2023; Badura *et al.* 2017; Marciszak *et al.* 2019a; Sobczyk *et al.* 2020; Stefaniak *et al.* 2021b, c, 2023b).

The wild boar *Sus scrofa* Linnaeus, 1758 is a typical interglacial species, the remains of which were considered very rare in the Quaternary of Poland (Czyżewska 1989). Only research in recent years has extended this knowledge. In the Eemian Interglacial, the occurrence of the wild boar was recorded from four cave sites: Ciemna Cave, Biśnik Cave, Dziadowa Skała Cave, Komarowa Cave (Table 8). It is represented mainly by teeth and fragments of limbs. The wild boar is a forest species, but it can also occur in more open areas (Czyżewska 1989; Wojtal 2007).

Deer in the Eemian Interglacial of Poland were represented by eight taxa, of which seven occur in cave sites, and the fallow deer *Dama dama* in Gorzów Wielkopolski (Tables 8, 9).

Remains of the red deer *Cervus elaphus* are known from the sediments of both cave sites (Ciemna Cave, Nietoperzowa Cave, Jasna Strzegowska Cave, Biśnik Cave, Dziadowa Skała Cave, Komarowa Cave) and open-air localities (Szeląg near Poznań, Siekierki, Wisła River). In Poland, *Cervus elaphus spelaeus* was recorded, which was the second most numerous species after the reindeer. Its remains include antlers and skull fragments, teeth, as well as limb bones and their fragments (Made *et al.* 2014; Nadachowski *et al.* 2015a, b; Stefaniak 2015; Stefaniak *et al.* 2020).

Gorzów Wielkopolski is the only site where fallow deer was recorded. The remains of this species are represented by a metacarpal bone found on the border of the gyttja and peat layers (Badura *et al.* 2017; Sobczyk *et al.* 2020; Stefaniak *et al.* 2020; 2021a–c; 2023a, b) (Table 9).

Giant deer has been present in Poland since the Middle Pleistocene. During the last interglacial, this species occurred only in cave sites (Nietoperzowa Cave and Biśnik Cave), and it was represented by *Megaloceros giganteus ruffi* (Nehring, 1891) – a form adapted to live on forest edges and forest-steppes; however, its remains are scarce and represented by isolated teeth and fragments of limb bones (Made *et al.* 2014; Nadachowski *et al.* 2015a, b; Stefaniak 2015, 2020).

The third species in terms of the number of remains found in cave sites was the extinct roe deer *Capreolus capreolus priscus*. The extant roe deer *Capreolus capreolus* first appeared at the beginning of the last glaciation (Stefaniak 2015, 2020). Its remains were recorded in Ciemna Cave, Nietoperzowa Cave, Biśnik Cave, Dziadowa Skała Cave and Deszczowa Cave (Made *et al.* 2014; Stefaniak 2015; Stefaniak *et al.* 2020). Roe deer remains were also found in the Warszawa Szczęśliwice site. This species was represented by teeth and their fragments and more or less well-preserved limb bones (Ślósarski 1882a, b, 1883, 1884; Stefaniak 2015).

Two teeth of the Middle Pleistocene elk *Cervalces* sp. were found in layer 15 of Biśnik Cave (Stefaniak 2015; Stefaniak *et al.* 2020). The elk *Alces alces* appeared in Poland during the Eemian Interglacial and Early Vistulian; an isolated tooth was found in deposits of Dziadowa Skała and Ciemna Cave (Nadachowski *et al.* 2015a, b; Stefaniak 2015; Stefaniak *et al.* 2020).

Reindeer *Rangifer tarandus* is the most numerous regarding the number of remains. It occurred in five cave sites (Ciemna Cave, Nietoperzowa Cave, Łokietka Cave, Biśnik Cave and Dziadowa Skala Cave) as well as in the interglacial strata of Warsaw Szczęśliwice (Ślósarski 1882a, b, 1883, 1884). The presence of this species may indicate a colder episode. Reindeer may occur, apart from tundra, in boreal forests (Stefaniak *et al.* 2012, 2020; Piskorska and Stefaniak 2014; Nadachowski *et al.* 2015a, b; Piskorska *et al.* 2015; Stefaniak 2015). Among the Bovidae, the most common species in Poland was the steppe bison *Bison priscus*. Its remains are present in almost all Quaternary sites, including those of Eemian age (Ciemna, Biśnik, Dziadowa Skała Caves, Szeląg near Poznań, Warszawa Szczęśliwice). Skulls and their fragments represent the remains of the bison, axial and postcranial bones (Kowalski 1959; Czyżewska 1989; Wojtal 2007; Stefaniak *et* *al.* 2009a; Nadachowski *et al.* 2015a, b; Ratajczak-Skrzatek *et al.* 2022).

The aurochs *Bos primigenius* was the least numerous among bovids during the Eemian Interglacial. This species was not very common in Poland during the Quaternary. Most of its remains have been found in open-air localities without a clear stratigraphic context (Kowalski 1959; Czyżewska 1989). The presence of aurochs in the Eemian Interglacial is documented in two cave sites and three open-air localities (Tables 8, 9). A fragment of the metatarsal and the left calcaneus were found in Dziadowa Skała Cave. The upper molar of this species was described from layer 15 of the Biśnik Cave, although its dating is uncertain (Krajcarz *et al.* 2014a, b; Mazza *et al.* 2022).

Data from large mammals (the presence of *Cervalces*) indicate the MIS 7 period (Lubawian Interglacial) (Stefaniak 2015; Stefaniak *et al.* 2020), which may confirm the mixed nature of this layer. In open-air localities, the remains of aurochs were found in Szeląg near Poznań, in the Vistula River near Siekierki and in Warsaw Szczęśliwice. Horns, fragments of skulls and limb bones were collected in these sites (Kowalski 1959; Czyżewska 1989, Wojtal 2007; Stefaniak *et al.* 2009a; Nadachowski *et al.* 2015a, b) (Tables 8, 9). The Alpine chamois *Rupicapra rupicapra* was a permanent fauna element in the Kraków-Częstochowa Upland and Sudetes during the Middle and Late Pleistocene. A handful of remains of this species were found in Ciemna Cave and Biśnik Cave (Table 8). The Alpine chamois usually migrated to uplands during cooler periods (Kowalski 1959; Czyżewska 1989, Wojtal 2007; Stefaniak *et al.* 2009a; Nadachowski *et al.* 2015a, b).

Due to the difficulties in distinguishing the remains of large Bovidae in cave sites, they have been marked as *Bos*/*Bison*. Such forms without close identification occurred in the Eemian deposits of Ciemna Cave, Nietoperzowa Cave, Biśnik Cave, Dziadowa Skała Cave and Komarowa Cave (Tables 8, 9). Small bovids have not yet been found in the Eemian deposits (Stefaniak *et al.* 2009a).

DISCUSSION

Fish assemblages from the Eemian Interglacial of Poland were quite similar in taxonomic composition to those of Chibanian and Tarantian age from central and eastern Europe (G. Böhme 2003, 2009, 2010, 2011; M. Böhme 2010; Rekovets *et al.* 2014; Kovalchuk 2017; Kovalchuk *et al.* 2017, 2021; Stefaniak *et al.* 2021a, b, 2022). Further development of the fish fauna in the Polish Lowland was favoured by the formation of numerous lakes after the melting of the ice sheet.

The avifauna of the Eemian sites confirms the paleoecological and paleoclimatic observations obtained from the remains of mammals. A large number of forest taxa and the presence of water-related forms indicate the development of forests and the presence of water reservoirs and wetlands in the Kraków-Częstochowa Upland. Caves and rock shelters created good conditions for the nesting and living of birds associated with this landscape. There were also forms related to the tundra environment, including ptarmigans and plovers, which is also typical for the Quaternary fauna of Poland (Bocheński 1974, 1988, 1990, 2001; Madeyska 1982; Tomek and Bocheński 2005; Nadachowski *et al.* 2000, 2009; Stefaniak *et al.* 2009a; Bocheński *et al.* 2012; Socha 2014).

Small mammalian assemblages that existed during the Eemian Interglacial are characterized by numerous taxa that now inhabit the temperate climate zone prevailing in Europe. On the other hand, the presence of taxa typical of a continental or arctic climate may indicate that these assemblages represent periods before or after the climatic optimum of the interglacial. This is related to dynamically changing climatic conditions. In the period before the climatic optimum, climate changes result from, among others, a decrease in the importance of anticyclonic circulation and the role of dry continental air masses in shaping the climatic and habitat conditions in front of the ice sheet, with a simultaneous increase in the importance of humid oceanic air masses. These phenomena are conducive to the gradual reconstruction of habitats, from dry open areas of steppe or tundra to dense forest communities dominated by mixed deciduous forests, shedding leaves for winter in the climatic optimum. At the same time, the frequency of occurrence of small mammalian taxa associated with open habitats decreased, with the simultaneous emergence and then increased in importance and dominance of eurytopic and forest taxa. Because of these events, in many sites, the co-occurrence of forest taxa and taxa currently restricted to open habitats in continental or arctic climate zones is observed in sediments correlated with the Eemian Interglacial (Kowalski 2001). However, in the periods after the climatic optimum, along with the increasing importance of anticyclonic circulation and dry continental air masses, on shaping the climatic conditions in front of the developing ice sheet, forest habitats dominating in the climatic optimum gradually give way to open habitats. At the same time, small mammalian assemblages were characterized by a gradual transformation from forest fauna to fauna dominated by taxa typical of open habitats in a continental or arctic climate. As in the pre-optimal period, this situation was conducive to the co-existence of forms with different ecological preferences.

In most of the localities considered, where Eemian assemblages of small mammals were found, the co-occurrence of taxa characterized by different habitat and climatic preferences was observed. At the same time, the proportion of taxa typical of continental or arctic climate conditions in these localities was lower as compared to that in strata correlated with glacial periods (e.g., Nadachowski *et al.* 2009; Socha, 2014). The presence of taxa associated with the arctic or continental climate in the Eemian deposits (e.g., the Norway lemming *Lemmus lemmus*, the Arctic lemming *Dicrostonyx torquatus*, and the narrow-headed vole *Stenocranius gregalis*) has also been documented in materials from other European localities (Kowalski 2001). These species were typical representatives of the glacial fauna, and their dispersion from the north and east can be explained by specific climatic and habitat changes caused by the transgression of the ice sheet from higher to lower latitudes in the northern hemisphere. At the same time, the small mammalian assemblages of Europe were characterized by an apparent increase in biodiversity and the absence of one or two dominant taxa. This may indicate an improvement in climatic conditions and an increase in habitat diversity, which enables the coexistence of many species in the same area.

A large number of forest-related taxa and thermophilic species (e.g., *Meles meles*, *Martes martes*, *Lynx lynx*, *Felis silvestris*, *Sus scrofa*, *Alces alces*, *Capreolus capreolus priscus*), as well as the presence of species living on forest edges (e.g. *Ursus arctos taubachensis*, *Cervus elaphus spelaeus*, and *Bos primigenius*) corroborated the assigning of particular strata to the Eemian Interglacial (Chmielewski 1958; Kowalski 1958; Madeyska 1981; Lorenc 2006a, b, 2007, 2008; Wojtal 2007; Stefaniak *et al.* 2009a). In all these localities, in addition to the characteristic species, we can also observe the occurrence of chronosubspecies existed during MIS 5e. Among them, there are relatively large and gracile wolf *Canis lupus* ssp., cave hyena *Crocuta crocuta spelaea*, brown bear *Ursus arctos priscus*, large coronate red deer *Cervus elaphus spelaeus*, and robust roe deer *Capreolus capreolus priscus*. Even if the remains of some cold-adapted species like *Alopex lagopus* and *Rangifer tarandus* are present in the Eemian strata, it changed nothing. Both these species existed in Europe during the Eemian, but the density of their populations is lower than that during glacials and stadials (Kahlke 2014). The presence of these species can also be explained, especially in the case of *V. lagopus*, due to re-deposition: the upper part of layer four from Dziadowa Skała Cave was in contact with a disturbed layer 5 MIS 5a–d (Chmielewski 1958; Kowalski 1958).

The presence of cold-loving taxa in sediments dated to the Emian Interglacial is characteristic of birds and mammals. As mentioned above, this may indicate colder parts of the interglacial, as well as phenomena related to redeposition, or not entirely clear and legible stratigraphy, especially in the case of cave sites, and, of course, the wide ecological tolerance of some species (Nadachowski *et al.* 2009; Socha, 2009; 2014; Stefaniak *et al*. 2009a; Stefaniak 2015).

According to the literature data (von Koenigswald 1991; von Koenigswald and Heinrich 1999; Kolfschoten 2000; Pushkina 2007; von Koenigswald *et al.* 2019), the following indicator species of large herbivorous mammals, indicating a warm climate and forest environment, were represented during the Eemian Interglacial: the straight-tusked elephant *Palaeoloxodon antiquus*, Merck's rhinoceros *Stephanorhinus kirchbergensis*, *Hippopotamus amphibius*, wild boar *Sus scrofa*, fallow deer *Dama dama*, roe deer *Capreolus capreolus priscus*, and the European water buffalo *Bubalus murriensis*. Hippos and buffaloes do not occur in Poland, which may be explained by the shape of the ancient river network. The remains of these species are known from Germany.

The largest and the most spectacular species, *Palaeoloxodon antiquus*, occurred in at least seven open-air sites in Poland, including two containing skeletal fragments of large males from Konin and Warsaw and Merck's rhinoceros *Stephanorhinus kirchbergensis* in materials from five localities. However, material from some sites with undetermined stratigraphy could also come from this interglacial. The wild boar is known only from cave sites, and the fallow deer was only found in Gorzów Wielkopolski. Roe deer occurred in five cave sites and one open-air locality (Table 8). Other large mammals, e.g., horse *Equus ferus*, red deer *Cervus elaphus*, giant deer *Megaloceros giganteus*, elk *Alces alces*, aurochs *Bos primigenius* and steppe bison *Bison priscus*, could have been occurred both during interglacials and cooler climates. *Bison priscus* was also a characteristic species of the mammoth steppe. Tundra, steppe and mountain elements (e.g., woolly mammoth *Mammuthus primigenius*, woolly rhinoceros *Coelodonta antiquitatis*, reindeer *Rangifer tarandus*, the Alpine chamois *Rupicapra*

rupicapra) were also represented in the Eemian of Poland (von Koenigswald 1991; Kahlke 1999, 2014; von Koenigswald and Heinrich 1999; Kolfschoten 2000; Stefaniak *et al.* 2009a–c; Nadachowski *et al.* 2015a, b; Stefaniak 2015; Puzachenko *et al.* 2022).

Paradoxically, contrary to other Polish (especially Sudeten) cave sites, remains of ungulates are the most informative for the biostratigraphy of the Eemian Interglacial. *Rangifer tarandus* was the most abundantly represented in the fossil record of that time (Stefaniak 2015). Remains of this species are characterised by a slightly larger average size than those from other Polish localities, dated at MIS 5d–2 (Stefaniak 2015). A large coronate red deer *Cervus elaphus spelaeus*, which is a characteristic chronosubspecies within the evolutionary lineage of *Cervus elaphus* in Europe during the MIS 7–5e, was also represented in the territory of Poland during the Eemian Interglacial (Pohlig 1892; Lister 1987; Made *et al.* 2014; Stefaniak 2015). The remains of a smaller and less coronate form *Cervus elaphus simplicidens* are known from the younger layers, dated to MIS 5a–d (Guadelli 1996; Made *et al.* 2014; Stefaniak 2015). This chronosubspecies in Europe is characteristic of the period MIS 5d–3 (Made *et al.* 2014; Stefaniak 2015; Stefaniak *et al.* 2020). Similarly, the genus *Cervalces* in layer 15 of Biśnik Cave allows the dating of these sediments either as the Lubawian Interglacial (MIS 7) or the Wartanian Glacial (MIS 6). *Capreolus capreolus* was represented by the chronosubspecies *Capreolus capreolus priscus*, which was larger and slightly more robust than the extant roe deer (Stefaniak 2015). A clear tendency in the decreasing of size is observed in the evolution of the genus *Capreolus* – from *Capreolus suessenbornensis* through *C. capreolus priscus* up to the Late Pleistocene and Holocene *C. capreolus* (Made *et al.* 2014; Stefaniak 2015; Stefaniak *et al.* 2022).

This faunal assemblage is characteristic of the Eemian faunas of Europe (Kolfschoten 2000; Kindler *et al.* 2020) and resembles that of other localities dated at MIS 5e, e.g. Chlupáč Cave (Mostecký 1961, 1963, 1969; Marciszak *et al.* 2022), Kůlna Cave (Musil 1970, 1988, 2002, 2010, 2018; Valoch *et al.* 1970; Valoch 1988), Gröbern (Benecke *et al.* 1990; Hartung 1991), Lehringen (Sickenberg 1969), Neumark-Nord (Mania 1992; Pfeiffer 1998; Kindler *et al.* 2020), Rabutz (Soergel 1920; Toepfer 1958; Eissmann 1990), Schönfeld (Böhme 1991; Fischer 1991; Heinrich 1991), Taubach (Kahlke 1994; Bratlund 1999; Von Koenigswald and Heinrich 1999), Burgtonna (Mania 1973, Kahlke 1978), and Stuttgart-Untertürkheim (Schweigert 1991; Wenzel 1996).

Unfortunately, several species of hoofed mammals known from interglacial sites of western Europe, even in areas relatively close to Poland (e.g., Germany, Netherlands), are absent in this region. The remains of *Equus hydruntinus* Regalia, 1907, *Stephanorhinus hemitoechus* Falconer, 1859, *Hippopotamus amphibius* (Linnaeus, 1758) and *Bubalus murrensis* Berckhemer, 1927, known from western and southern Europe (Koenigswald 1991; Kahlke 1999; Kolfschoten 2000; Pushkina 2007; Musil 2010) have never been found in the territory of Poland. Presumably, this is due to paleoenvironmental reasons and the relatively small number of sites of this age.

CONCLUSIONS

The Eemian vertebrate fauna of Poland was quite diverse. Bone remains of about 150 species (including 13 fishes, three amphibians, two reptiles, 44 birds, and 88 mammals) have been found in deposits of this age (Table 10). This is especially noteworthy considering the short period (ca. 15 ka) covered by the Eemian. Most of the identified taxa have been recorded earlier based on material from the other Eemian localities in central and eastern Europe. Extinct taxa identified for the Eemian faunal assemblages of Poland were represented by several species of small mammals (*Crocidura obtusa, Sorex runtonensis, Talpa minor*, *Spermophilus superciliosus, S. citelloides*, *Dicrostonyx* cf. *simplicior*, *D.* cf. *henseli/torquatus*), large carnivorans (*Ursus spelaeus spelaeus*, *U. arctos taubachensis*, *Panthera spelaea spelaea*, *Crocuta crocuta spelaea*), elephants (*Palaeoloxodon antiquus*, *Mammuthus primigenius*) and ungulates (*Equus ferus*, *Coelodonta antiquitatis*, *Stephanorhinus kirchbergensis*, *Megaloceros giganteus*, *Capreolus capreolus priscus*, *Cervalces* sp., *Bison priscus*, *Bos primigenius*). These taxa were associated with open areas and inhabited the steppe and forest-steppe environments in a cold or temperate climate. Another group was represented by species that do not occur in the contemporary fauna of Poland since their ranges changed.

Group	Taxonomic level			
	Species	Genus	Family	Order
Fishes	13	13	6	6
Amphibians	3	2	2	1
Reptiles	2	2	2	1
Birds	44	36	18	10
Mammals	88	61	26	8
TOTAL	150	114	54	26

Table 10. Taxonomic richness of the Eemian vertebrate fauna of Poland.

Those are species associated with tundra (*Lemmus lemmus*, *Vulpes lagopus*, *Rangifer tarandus*), steppes (*Allactaga major*, *Lagurus lagurus, Ochotona pusilla*) and forests (*Panthera pardus*).

In addition, there was a large group of animals which included taxa occurring in the territory of Poland both during the Eemian Interglacial and at the present times. It was dominated by eurytopic species as well as those preferring forest habitats (e.g., *Sciurus vulgaris*, *Glis glis*, *Clethrionomys glareolus*, *Meles meles*, *Lynx lynx*, *Felis silvestris*, *Sus scrofa*, *Cervus elaphus*). Several species are restricted to open areas and near-water biotopes. The European fallow deer *Dama dama* was prehistorically native to Poland, as evidenced by the presence of its remains in Gorzów Wielkopolski. This species was re-introduced into a more significant portion of Europe (including Poland) before the Middle Ages.

Future research and field investigations should be focused on the evolution of the Eemian fauna of Poland concerning the Quaternary climate changes. The results of such studies will allow the clarification of the stratigraphic position of poorly dated faunas and a better understanding of environmental changes in Central Europe.

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