

Polish Pliocene and Quaternary deer and their biochronological implications

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ABSTRACT

This work summarises the state of the art of the studies on the fossil cervids of Poland, from the Miocene through to the present, with an extensive reference to the faunas of the rest of Eurasia and the World. It deals with more than 5500 remains of 16 species from 68 localities. The study intends to give an overview on the taxa present in Poland. The primary focus is on the evolution and stages of dispersal of Cervidae in the frame of the environmental changes that took place across Central Europe. The authors propose to place the bioevents of cervids in the Western European Plio-Pleistocene mammalian biochronological framework, which includes the Ruscinian, Villafranchian, Galerian and Aurelian Mammal Ages. The cervid remains are shown to have great biochronological significance.

1. Introduction

The deer fossils of Poland have been the subject of scientific interest since the late 19th century. The earliest publications were purely descriptive and dealt with faunal assemblages or isolated finds. The earliest monographs are Czyżewska's (1959, 1960, 1968, 1981) studies on fossil Cervidae from the Pliocene site Węże 1. After these pioneering contributions, Czyżewska (1989) published the first comprehensive paper on all artiodactyls; this monumental study included a list of sites and plentiful descriptions of fossil remains. This valuable publication, however, is written in Polish, and is thus inaccessible to a broader audience. Moreover, in Czyżewska's (1989) study there is no reference to any biochronological scheme and the lists of taxa from numerous sites, especially those of Quaternary and Holocene age, are often incomplete.

Pliocene deer remains from Central and Eastern Europe, including Poland, were studied and revised by Croitor and Stefaniak (Stefaniak, 1995, 2001; Croitor and Stefaniak, 2009). Nearly all the Middle Miocene to Recent cervid remains from both open and cave sites in Eurasia were described in detail and revised in a monograph published by Stefaniak (2015). In this study, the fossil deer were analysed in the context of the global faunal and climatic changes. Stefaniak (2015) provided the stratigraphic sequence of all the Eurasian sites that yielded deer remains. In the present study, we try to place the deer fossils from Poland in a biochronological framework based on the detailed data

contained in Stefaniak (2015). The biochronological divisions of the Neogene and Quaternary of Poland are those provided by Kowalski, 1990, 2001, Nadachowski (1982, 1990a, b, 1998, 2001), Nadachowski et al. (1989), Rzebik-Kowalska (1994a,b, 2003, 2005, 2014), Wołoszyn (1987, 1989), which are based on small mammal fossils present also in other Plio-Pleistocene European mammalian communities (Azzaroli, 1977; De Giuli et al., 1983; Mein, 1990; Bonifay, 1996; Gliozzi et al., 1997; Sala et al., 1992; Abbazzi, 1995, 2004; Azzaroli, 1953; Palombo et al., 2000; Kotsakis et al., 2003; Masini and Sala, 2007; Nomade et al., 2014).

2. Methods

We provide the distribution and biochronological positioning of Polish extinct mammalian assemblages that include cervids remains as well as information on the occurrence of elephantids, perissodactyls and other artiodactyls. Figs. 1 and 2 present distribution of sites with cervid remains from the Neogene to the Holocene in Poland, whereas Figs. 3–5 show biostratigraphy of cervid remains in Poland compared with other European sites from the Pliocene to the Holocene. Tables 1–3 include current views on the stratigraphy of Pleistocene layers in selected Polish sites. In Table 4, we compared the distribution of Cervidae from the Pliocene to Holocene on the territory of Europe and in Table 5, we presented number of identified specimens (NISP) and minimum number of individuals (MNI) of cervids from Pliocene to the beginning

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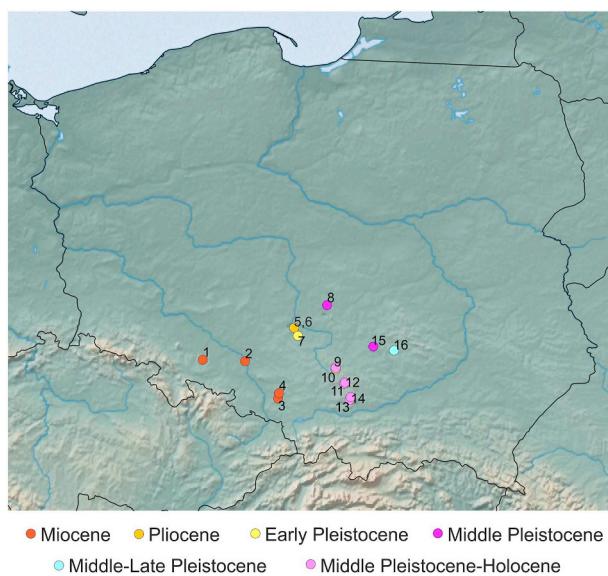


Fig. 1. Location of Polish sites with deposits from the Miocene, the Pliocene, the Early Pleistocene and the Middle Pleistocene to the Holocene, in which cervid remains were found. 1-Przeworno, 2-Opole, 3-Stanica, 4-Sośnicowice, 5-Węże 1, 6-Węże 2, 7-Rębielice Królewskie 1, 8-Bałchatów, 9-Deszczowa Cave, 10-Żabia Cave, 11-Biśnik Cave, 12-Jasna Strzegowska Cave and Wschodnie Rock-shelter, 13-Nietoperzowa Cave, 14-Tunel Wielki Rock-shelter and Pod Tunelem Wielkim Rock-shelter, 15-Kozi Grzbiet, 16-Sitkówka.

of the Holocene in the localities of Poland.

The geologic timescale and subdivisions adopted in this paper were based on the International Chronostratigraphic Chart (v2018/08) approved by the International Commission on Stratigraphy (<http://www.stratigraphy.org/index.php/ics-chart-timescale>), which places the Miocene/Pliocene boundary at 5.33 Ma, and the Pliocene/Quaternary boundary at 2.58 Ma (Steininger et al., 1990; Gibbard and Head, 2009; Gibbard et al., 2010; Cohen et al., 2018).

The now widely accepted biochronological division of the Neogene terrestrial faunas was originally proposed by Mein (1990), who defined MN and MQ (Mammal Neogene, Mammal Quaternary, respectively) biozones. Mein's (1990) biochronological scheme is based on the first appearance, last occurrence and highest abundance of the taxa. Mein's scheme was later complemented by many other papers focused on the evolution of small mammals (mainly Cricetidae, Arvicolidae, Muridae). Yet another scheme, also based on Mein's assumptions, was presented by Guérin (1982, 1990), who defined MNQ zones (Mammal Neogene Quaternary), numbered in order of age, from the oldest to the youngest. Guérin's MNQ zones are based on three parameters: 1) evolutionary degree; 2) composition of the mammal assemblages (in terms of genera and species); 3) first appearance (FAD – First Appearance Datum) and the last appearance (LAD – Last Appearance Datum) of new taxa.

The biochronology of the Western European Pliocene and Quaternary Mammal Ages is similar to that based on small mammals but is built on large mammalian assemblages (Fig. 3). The Ruscinian (zones MN14–15, 5.33–3.2 Ma) and Villafranchian (zones MN16–17, 3.2–1.0–0.9 Ma) Mammal Ages are dated to the Pliocene and Late Pliocene-Early Pleistocene, respectively (Steininger et al., 1990; Gliozzi et al., 1997; Rook and Martinez-Navarro, 2010). The Villafranchian is followed by the Epivillafranchian, which dates to the late Early and early Middle Pleistocene (1.2–0.9 Ma) (Kahlke R.D., 2006, 2007; 2009; Rook and Martinez-Navarro, 2010; Bellucci et al., 2015). The Galerian (1.0–0.5–0.4 Ma) includes the early half of the Middle Pleistocene. Finally, the Aurelian Mammal Age correlates with the late Middle Pleistocene and Late Pleistocene (Azzaroli et al., 1988; Gliozzi et al., 1997; Sardella et al., 1998; Caloi and Palombo, 1997; Petronio et al., 2011; Kahlke, 2014) (Figs. 3–5).

The taxonomy of Cervidae follows Czyżewska (1968), Groves and Grubb (1987, 1990, 2011), Grubb (2000), Croitor and Stefaniak (2009), Stefaniak (2015), Croitor (2018). We also used the results of phylogenetic analyses including ancient DNA (Flerov, 1952; Czyżewska, 1968; Vislobokova, 1990, 1992, 2008a, b, 2012a, b; Vislobokova and Hu, 1990; Vislobokova and Kalmykov, 1994; Geist, 1998; Randi et al., 1998; Pitra et al., 2004; Gilbert et al., 2006; Hassanin et al., 2012; Doan et al., 2017, 2018; Mennecart et al., 2017). Palaeoecological reconstructions were drawn from Flerov (1952), Janis and Scott (1987), Vislobokova (1990), Stefaniak (1995, 2001, 2015), Köhler (1993), Geist (1998), Croitor and Stefaniak (2009), and Croitor (2018).

In Figs. 3–5 we include a compilation of $\delta^{18}\text{O}$ curves from four 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 (NGRP2) (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).

3. Results

Cervid remains were found in more than sixty Polish localities: six of them are dated to the Neogene (four are attributed to the Miocene and two to the Pliocene), two sites were correlated to the Early Pleistocene, two localities were attributed to the middle Pleistocene; and more than fifty major cave and open site localities are dated to the late part of the Middle Pleistocene and to the Late Pleistocene (Figs. 1–5). The over 5500 cervid remains considered for this analysis belong to 3 subfamilies, 6 tribes, 17 genera and 25 lower-rank taxa (16 species, one of which new to the fauna of Poland).

3.1. Neogene – Early Pleistocene (Ruscinian, early and middle Villafranchian) – Figs. 1–3

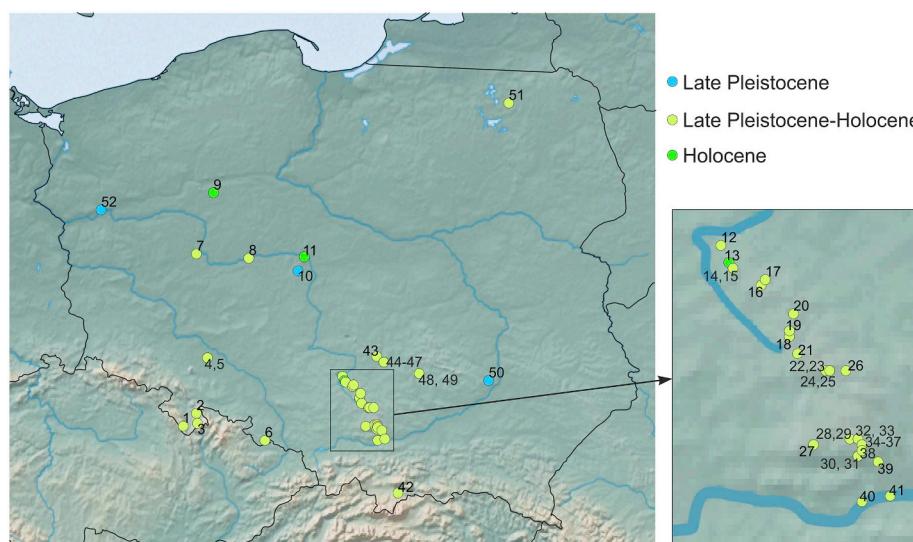
The earliest known cervid remains from Poland date back to the Middle Miocene (zones MN 7–8) and belong to *Euprox furcatus* (Hensel, 1859). Remains of the species were found in 4 Silesian localities (Fig. 1). In two of them (Opole and Przeworno), *E. furcatus* is accompanied by numerous remains of other vertebrate taxa (Kubiak, 1975, 1981a, b, 1982, 1989a, b; Kowalski, 1990; Czyżewska and Stefaniak, 1994a, b; Czyżewska, 1989; Stefaniak, 2015).

3.1.1. Pliocene (late ruscinian, MN15) – Węże 1 site

In the Pliocene, the number of cervid taxa rose to eight. The Late Ruscinian fauna is represented at Węże 1 site (MN15; 3.3–4 Ma) (Figs. 1 and 3, Table 5). Deer remains are dominant among those of large herbivores.

The numerous Early Pliocene deer remains from Węże 1 (MN 15) belong to 4 species: *Muntiacus polonicus* Czyżewska (1968), *Praeelaphus warthae* (Czyżewska, 1968), *Arvernoceros cf. ardei* (Croizet et Jobert, 1828) and *Procapreolus moldavicus* (Janovskaya, 1954). A few remains, i.e., a mandible fragment with teeth, two isolated upper teeth and fragments of a hind limb, belonging to a 5 months old individual, were described as a new species, *Muntiacus polonicus* (Czyżewska, 1968). The most abundant cervid remains in Węże 1 belong to the ancestral roe deer *Procapreolus moldavicus*. Individuals up to a maximum of 2 years of age are dominant. A group of slightly less abundant remains from Węże 1 belong to the medium-sized (body mass up to more than 120 kg) *Praeelaphus warthae* (Czyżewska, 1968).

Besides the cervid remains, the fauna of Węże included a few remains of odd-toed ungulates, which are represented by teeth of a young specimen of the rhinocerotid *Dichotolus megarhinus* (Christol, 1835) (Czyżewska, 1958; Kubiak, 1989a), and of an adult equid, probably belonging to the genus *Hipparium* De Christoll, 1832.



37-Ciasna Cave, 38-Ciemna Cave, 39-Maszycka Cave, 40-Piekary, 41-Spadzista Str. In Kraków, 42-Obłazowa Cave, 43-Stajnia Cave, 44-Łagorzata, Trwoga Paleontologa, Cisowe 1 and 2 Rock-shelters, 45-Mt. Połom, 46-Naciekowa Cave, 47-Północna Duża Cave, 48-Raj Cave, 49-Zwoleń, 50-Wilczyce, 51-Dudka, 52-Gorzów Wielkopolski.

3.1.2. Late Pliocene (Early Villafranchian, MN16) – Węże 2 site

The early Villafranchian fauna is represented in Węże 2 site (Sulimski, 1962; Kowalski, 1989, 1990; Czyżewska, 1989; Nadachowski et al., 1989; Stefaniak, 1995, 2001). The large mammal remains from the site are very fragmented and include only isolated teeth and a few limb bone specimens. The assemblage from Węże 2 included four deer species (two small, one medium-sized, and one large). The presence of the Ruscinian *Procapreolus moldavicus* is uncertain because of the scarcity of remains (only a left M_2). The most abundant species is another Ruscinian representative, *Croizetoceros ramosus* (Croizet et Jobert, 1828; Heintz, 1970, 1974; Korotkevich, 1970, 1988; Azzaroli et al., 1988; Azzaroli, 1992; Vislobokova, 1990, 2008a, b). The third species was a medium-sized taxon *Metacervocerus pardinensis* (Croizet et Jobert, 1828). Another taxon, known only from a single fragment of upper molar, is a large deer identified as *Arvernoceros cf. ardei* (Croizet et Jobert, 1828). *Croizetoceros ramosus* from Węże 2 shows low variability. Its measurements fall within the upper range of variation of the species from Western Europe (Heintz, 1970; Stefaniak, 1995). For this reason, it can be referred to as the subspecies *Croizetoceros ramosus* (Heintz, 1970, 1974). *Metacervocerus pardinensis* from Węże 2 falls within the variation range of *M. pardinensis* from Western Europe (Heintz, 1970; Spaan, 1992).

Besides the cervid remains, only a few fragments of teeth of an unidentified rhinocerotid, and of enamel and limb bones of an elephantid (?*Anancus*) were found in the site. Like Węże 1, Węże 2 is the partial infilling of a vertical cave. Its cervid fauna differs significantly from that of Węże 1 and includes species characteristic of the Late Pliocene, of the Villafranchian, and of the zone MN16 (Table 4).

3.1.3. Middle Villafranchian (end of MN 16 - beginning of the Early Pleistocene) - Rębielice Królewskie 1 site

The fauna of this period is represented at Rębielice Królewskie 1, near Kłobuck (end of zone MN 16 – the beginning of the Early Pleistocene) (Mossoczy, 1961; Kowalski, 1989, 1990; Nadachowski, 1989, 1990b; 1998; Nadachowski et al., 1989; Stefaniak, 2001). This fauna included ancestral lemmings and ptarmigans (Bochenński, 1989; Kowalski, 1989; Nadachowski, 1990b). The cervid fauna grew poorer *Croizetoceros ramosus* persisted, and the new large deer of the genus, *Eucladoceros*, which was widespread in the Villafranchian of Eurasia, finally appeared (Table 4).

The most abundantly represented cervid is the large deer *Eucladoceros* sp. (Table 5). Its specimens are dimensionally within the

Fig. 2. Location of Polish sites with deposits from the Late Pleistocene to the Holocene, in which cervid remains were found. 1-Solna Jama Cave, 2-Radochowska Cave, 3-Niedźwiedzia Cave, 4-Wrocław-Oporów, 5-Hallera Str. in Wrocław, 6-Dzierżysław 35, 7-Krosinko, 8-Pyzdry, 9-Ostrówki and Borowa, 10-Turek, 11-Koło, 12-I Rock-shelter in Srocko (Borsucza Cave, Sosnowiecka Cave), 13-Zamkowa Dolna Cave, 14-III Rock-shelter (Wilcze I Rock-shelter) in the Sokole Mts, 15-Komarowa Cave, 16-Wiercica Cave, 17-Rock-shelters V, VI and VII in Złoty Potok, 18-Okiennik Rock-shelter, 19-Dziadowa Skała Cave, 20-Krucza Skała Rock-shelter, 21-Cave IV on Mt. Birów, 22-Zegar Cave, 23-Jasna Smoleńska Cave, 24-Mroczna Cave, 25-I and II Rock-shelters near Strzegowa (Zaciszna Cave, Pod Oknem Cave), 26-Nad Jaskinią Zegar Rock-shelter, 27-Gorenicka Cave, 28-Rock-shelter above Niedostępna Cave, 29-Sąpowska Zachodnia Cave, 30-Mamutowa Cave, 31-Wierzchowska Góra Cave, 32-Koziarnia Cave, 33-Łokietka Cave, 34-Sadlana Cave, 35-Zbójęcka Cave, 36-Bramka Rock-shelter,

range of variation of both *Eucladoceros dicranios* (Nesti, 1841) and *Eucladoceros ctenoides* (Nesti, 1841), which prevents from assigning the remains to either of the two species. Rębielice Królewskie is the first and, till now, the only locality of *Eucladoceros* sp. in Poland (Heintz, 1970; Azzaroli and Mazza, 1992; Spaan, 1992; Vos et al., 1995; Titov, 2008; Stefaniak, 2015).

Rębielice Królewskie has characteristics (karst crevices) similar to those of Węże 2, which explains the small amount of large mammal remains and the high degree of fragmentation of the material from the two localities.

3.2. Early Pleistocene and early Middle Pleistocene (late Villafranchian and beginning of the Galerian) – Figs. 3–4

3.2.1. Early Pleistocene (Late Villafranchian, MNQ1) – Żabia Cave site

Late Early Pleistocene cervids have been found only in Żabia Cave. The sample is largely dominated by *Dama cf. farnetensis* (Azzaroli, 1992), which is the only member of *Dama* in the Early and Middle Pleistocene of Poland (Table 5). The morphology and size of the teeth and bones fall within the range of variation of both *D. vallonensis* and *Metacervocerus rhenanus* from the late Early and early Middle Pleistocene of Europe (Stefaniak, 2015).

A group of new incomers from Asia, which became characteristic of the Eurasian Quaternary, includes the elk *Cervales carnutorum* (Laugel, 1862) and the roe deer *Capreolus* sp. (Czyżewska, 1989; Kowalski, 1990; Stefaniak, 2001; Stefaniak et al., 2009a, b; Nadachowski et al., 2011; Made et al., 2014) (Table 4). *Cervales carnutorum* was a large-sized cervid. It marks the first occurrence of elk in Poland. Żabia Cave is the oldest locality of fossil elk in Poland, and the only locality where the species has hitherto been found (Stefaniak, 2015) (Table 5). At Żabia Cave, the elk remains are less numerous than those of *Dama cf. farnetensis*.

Capreolus sp. is represented by a few remains of a size close to that of *Capreolus cusanoides* H. D. Kahlke (2001) from the Early Pleistocene of Untermassfeld. Żabia Cave provided also the first and oldest occurrences of an equid and a large bovid in Poland.

3.3. Latest early and early Middle Pleistocene (Galerian, MNQ1-MNQ2) – Figs. 1–4

No Polish sites but Żabia Cave include Lower Pleistocene deposits with large mammal remains; sites with small mammal remains are also

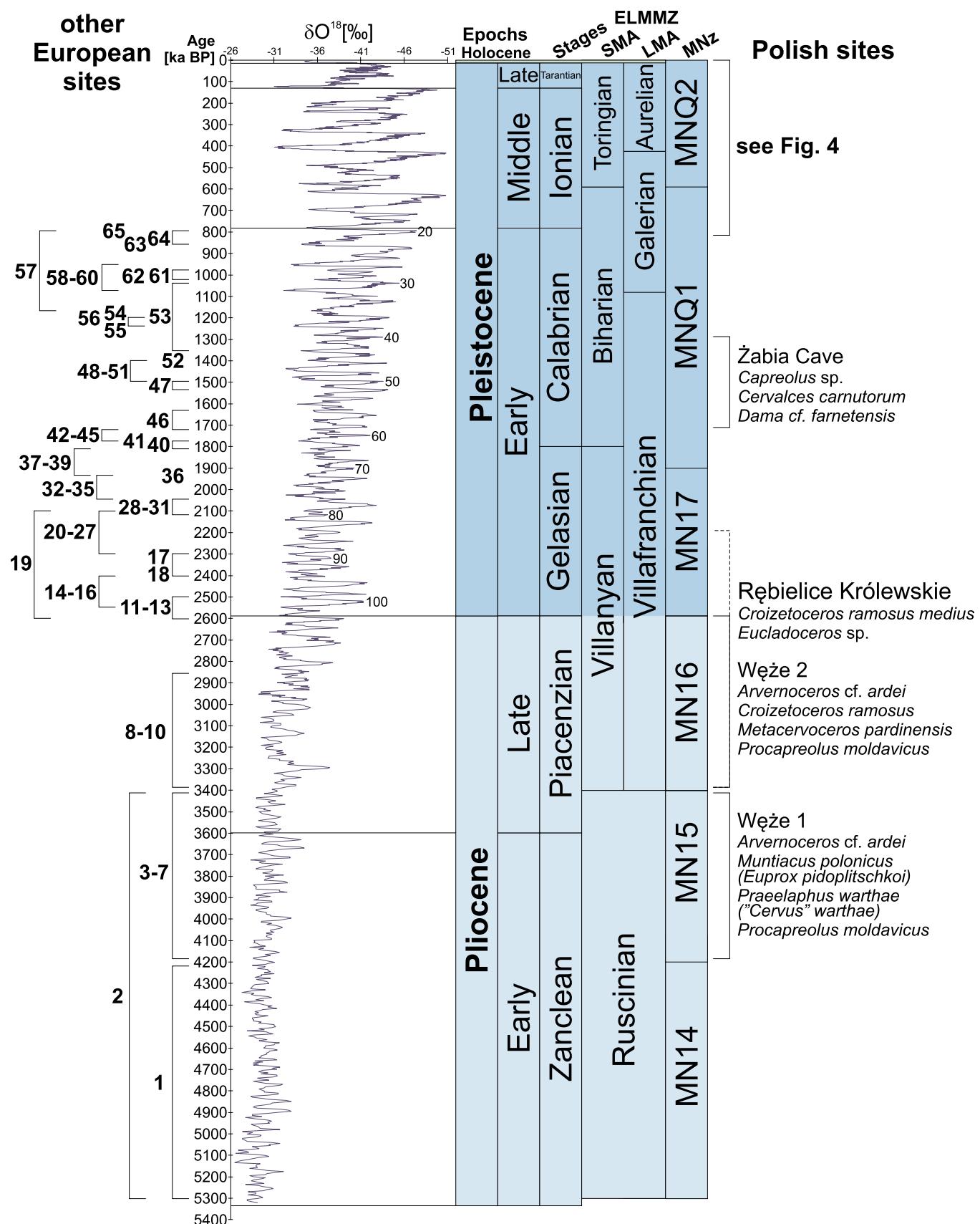


Fig. 3. Biostratigraphy and occurrence of cervid remains in Polish and other European sites in the Pliocene and the Early Pleistocene. ELMMZ, European Land Mammal Mega Zones; SMA, Small Mammal Ages; LMA, Large Mammal Ages; MNz, Mammal Neogene zonation; MIS, Marine isotope stages. Selected Marine isotope stages (MIS) were shown for the Early Pleistocene. The description of the other European sites (shown as numbers) is given in Appendix A.

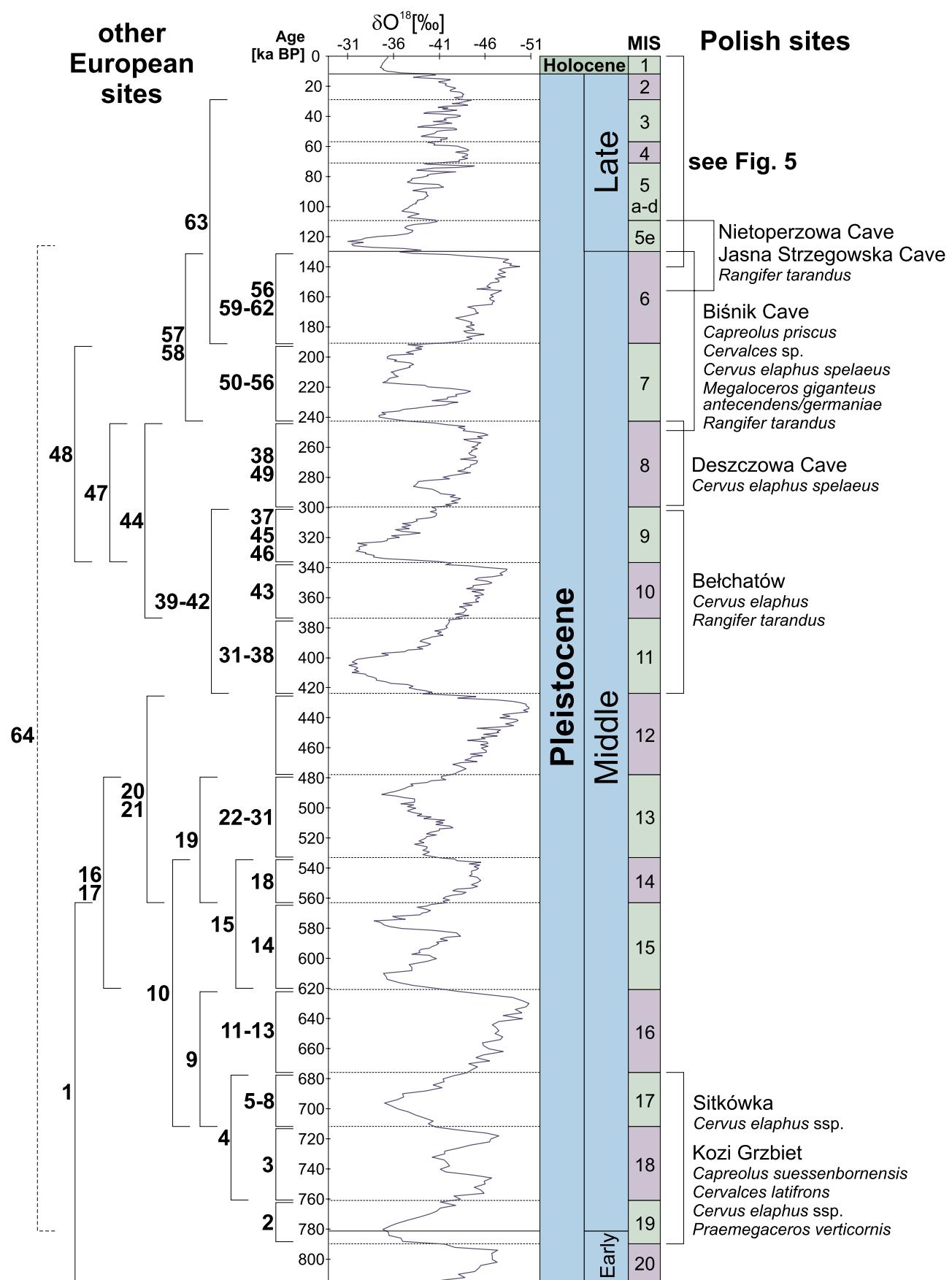


Fig. 4. Biostratigraphy and occurrence of cervid remains in Polish and other European sites of the Middle Pleistocene. MIS, Marine isotope stages. The description of the other European sites (shown as numbers) is given in [Appendix A](#).

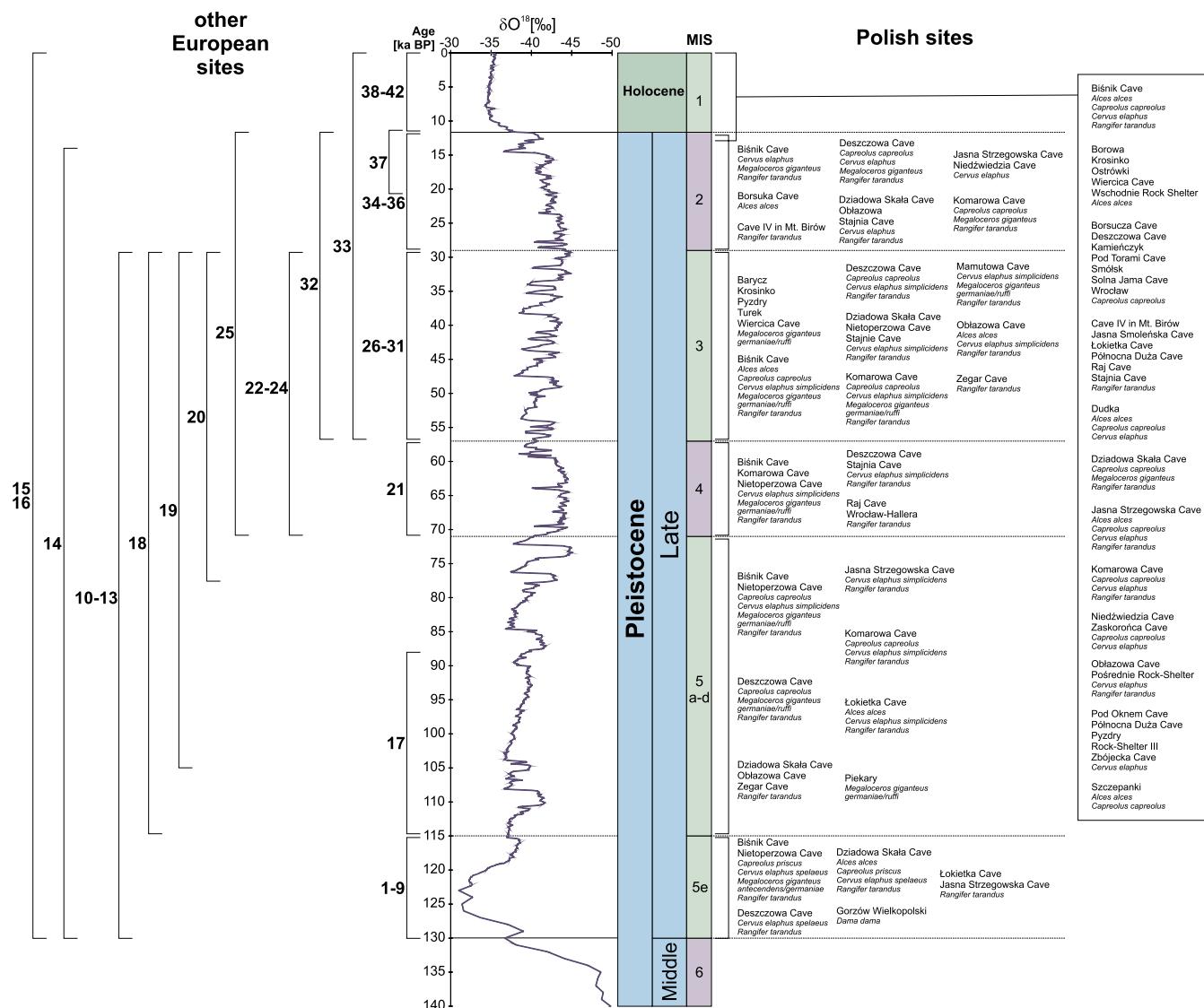


Fig. 5. Biostratigraphy and occurrence of cervid remains in Polish and other European sites of the Late Pleistocene and the Holocene. MIS, Marine isotope stages. The description of the other European sites (shown as numbers) is given in [Appendix A](#).

very few (Wiszniewska, 1989; Wyrost, 1989; Nadachowski, 1990a, 1998, 2001; Nadachowski et al., 1989). A stratigraphically younger site with the remains of vertebrates and cervids is Kozi Grzbiet near Kielce, which is dated to the MIS 19-17 (Middle Pleistocene, Podlasian Inter-glacial; Cromerian II-III) (Table 2). In this locality the following cervid species were discovered: *Cervus elaphus* ssp., *Praemegaceros verticornis* (Dawkins, 1872), *Capreolus suessenbornensis* H. D. Kahlke, 1956 and *Cervalces latifrons* (Johnson, 1874). The cervid remains found at Kozi Grzbiet include only teeth and, in the case of *Cervus elaphus* ssp. and *Capreolus suessenbornensis*, a few limb bone fragments. This site was a part of a now destroyed cave. Kozi Grzbiet is the oldest known locality with *Cervus elaphus* Linnaeus, 1758 in Poland. The specimens are of average size for a red deer. Kozi Grzbiet is also the only known site in Poland where remains of the giant deer *P. verticornis* were discovered. The measurements of the teeth fall within the lower range of variation of the representatives of this species from Süssenborn and Mosbach; it is considerably smaller than the specimens from Voigstede, Tiraspol and Moldova. This indicates that a smaller representative of the genus *Premegaceros* lived in Poland, possibly because of the presence of forest habitats. It is worth noting that also *Megaloceros giganteus* from the late Middle Pleistocene and Late Pleistocene of Biśnik Cave is smaller than other representatives of this species. The best represented cervid at Kozi

Grzbiet is *Capreolus*. An isolated tooth and a few limb bone fragments belonged to two large individuals; they are approximately the size of the specimens from Miesenheim I, Süssenborn and Mosbach. This is the only occurrence of *Capreolus suessenbornensis* in Poland (Stefaniak, 2015) (Table 5).

Fossil elk species are represented by the largest member of the group: *Cervales latifrons*. Only a fragment of P2, of an individual in the stage of tooth-replacement, was found in Kozi Grzbiet (MIS 18-17). It is similar in size to the specimens from Voigstede (MIS 17) and to one specimen from Mosbach (MIS 14-13), which are the typical representatives of *Cervales latifrons* from that period of the Middle Pleistocene (Stefaniak, 2015) (Table 4).

A second middle Pleistocene locality is Sitkówka near Chęciny, where a large *Cervales latifrons* was found, of a size similar to the representatives from Süssenborn (MIS 16). Kozi Grzbiet and Sitkówka are the only localities in Poland where this species is reported (Table 5).

3.4. Late Middle Pleistocene - Late Pleistocene (Aurelian, post Galerian, MNQ2) – Figs. 2, 4 and 5

There are six cervid species found in Polish late Middle Pleistocene deposits: *Cervus elaphus*, *Megaloceros giganteus* (Blumenbach, 1799),

Table 1

Stratigraphy of Biśnik Cave according to various sources (after Stefaniak, 2015).

Marine Isotope Stages	Western Europe	Poland	Biśnik Cave ¹	Biśnik Cave ²	Biśnik Cave ³	Biśnik Cave ⁴	Biśnik Cave ⁵
MIS 1	Holocene	Holocene	1a-b	1a-b		1a-b	1a-b
MIS 2	Weichselian	Late Weichselian	2-1	2-1	7-1	1	3-1
MIS 3/2	Weichselian	Interpleniglacial/Late Weichselian	Vistulian Main Stadial LGM	Grudziądz Interstadial/ LGM			7-4
MIS 3	Weichselian	Interpleniglacial	Vistulian Grudziądz Interstadial	4-3	7-5	?12, 11-8	11-2
MIS 4	Weichselian	Older Pleniglacial	Vistulian Świecie Stadial	8-5	8-7	?12	?12
MIS 5a	Weichselian	Early Weichselian	Vistulian Gniew Interstadial	9	9		
MIS 5b	Weichselian	Early Weichselian	Vistulian Toruń Stadial	10	10a-10		
MIS 5c	Weichselian	Early Weichselian	Vistulian Toruń Stadial	11	11	?14, ?13	13
MIS 5d	Weichselian	Early Weichselian	Vistulian Toruń Stadial	12	13-12		13
MIS 5e	Eemian		Eemian	13	15, 14, 13	15, ?14, ?13	13, 14, 15
MIS 6	Drenthe (+ Warthe)	Odranian (+ Wartanian)	14	18, 17, 16, 15	17, 16, 15	15	15, 14
MIS 7/6	Röpersdorf – Schöningen/ Drenthe (+ Warthe)	Lublinian/Odranian (+ Wartanian)					18
MIS 7	Röpersdorf – Schöningen	Lublinian	15; ?16	19a-19	18	18, 19	18
MIS 8/7	Saalian/Röpersdorf – Schöningen	Krznian/Lublinian		19d, c, b		19	19
MIS 8	? Saalian	Krznian	19-18			19, 19a-d	19
MIS 9	Dömnitz – Reinsdorf	Zbójnian	19c, b, a			19a-d	
MIS 10	Fuhne	Liwecian				19a-d	

Data are given according to: 1 – Cyrek et al., 2010; 2 – Krajcarz et al., 2014; 3 – Gąsiorowski et al., 2014; 4 – Marciszak and Socha, 2014; 5 – Socha, 2014.

Table 2

Stratigraphy of the other Pleistocene localities described in this paper (after Stefaniak, 2015).

Marine Isotope Stages	Western Europe	Poland	Kozi Grzbiet	Nietoperzowa Cave ¹	Deszczaowa Cave ²	Dziadowa Skała Cave ³	Mamutowa Cave ⁴	Jasna Strzegowska Cave ⁵	Zegar Cave ⁶
MIS 1	Holocene	Holocene		1	XI-IXa	9	1	7a-7	1
MIS 2/1	Weichselian	Late Weichselian	Vistulian Late Vistulian	2					
MIS 2	Weichselian	Late Weichselian	Vistulian Main Stadial	3	VIIIa-VIII	8-7	IX; 2g-2	6a-6	?5-2
MIS 3/2	Weichselian	Interpleniglacial/ Late Weichselian	Vistulian Grudziądz Interstadial/ LGM		VIIa-VII		III-VIII; 3		6
MIS 3	Weichselian	Interpleniglacial	Vistulian Grudziądz Interstadial	4-8	VI	6			
MIS 4	Weichselian	Older Pleniglacial	Vistulian Świecie Stadial	9	V				
MIS 5a	Weichselian	Early Weichselian	Vistulian Gniew Interstadial	10	V			5	
MIS 5b	Weichselian	Early Weichselian	Vistulian Toruń Stadial	10	V			4	
MIS 5c	Weichselian	Early Weichselian	Vistulian Toruń Stadial	11a-11b	V				
MIS 5d	Weichselian	Early Weichselian	Vistulian Toruń Stadial	11a-11b	V				
MIS 5e	Eemian		Eemian	12-13	IV	4-3c-a			
MIS 6	Drenthe (+ Warthe)	Odranian (+ Wartanian)		14-16				2	
MIS 7	Röpersdorf – Schöningen	Lublinian				III			
MIS 8	? Saalian	Krznian							
MIS 9	Dömnitz – Reinsdorf	Zbójnian							
MIS 10	Fuhne	Liwecian							
MIS 11	Holsteinian	Mazovian							
MIS 12	Elsterian	Sanian 2							
MIS 13	Cromerian IV	Ferdynandovian							
MIS 14	Cromerian IV	Ferdynandovian							
MIS 15	Cromerian IV	Ferdynandovian							
MIS 16	Glacial C	Sanian 1							
MIS 17	Cromerian III	Podlasian	2c-a						
MIS 18	Glacial B	Podlasian	2c-a						
MIS 19	Cromerian II	Podlasian	2c-a						
MIS 20	Glacial A	Podlasian							
MIS 21	Cromerian I	Podlasian							
MIS 22	Dorst	Nidanian							

Data are presented according to: 1 – Krajcarz and Madeyska, 2010; 2 – Krajcarz and Madeyska, 2010; Lorenc, 2013; 3 – Wojtal, 2007; Lorenc, 2013; 4 – Wojtal, 2007; Lorenc, 2013; 5 – Mirosław-Grabowska and Cyrek, 2009; 6 – Stefaniak et al., 2009c.

Capreolus priscus (Soergel, 1914), *Rangifer tarandus* (Linnaeus, 1758), *Cervalces* sp. and *Alces alces* (Linnaeus, 1758). The majority of the sites of this time period provided remains of four of these species (*C. elaphus*, *M. giganteus*, *C. priscus*, *R. tarandus*).

The oldest locality dated to the MIS 11 (the Mazovian Interglacial, Holstein) or 9 (the Zbójna Interglacial, Dömnitz-Reinsdorf Interglacial) is Belchatów mine, where reindeer and red deer are reported (Pawlowska et al., 2014). They represent the earliest occurrence of

Table 3

Stratigraphy of the other Pleistocene localities described in this paper (continued) (after Stefaniak, 2015).

Marine Isotope Stages	Western Europe		Poland		Łokietka Cave ¹	Ciemna Cave ²	Komarowa Cave ³	Stajnia Cave ⁴	Obłazowa Cave ⁵	Obłazowa Cave ⁶
MIS 1	Holocene		Holocene		1	1.2-1.1	A	A	I	I
MIS 2/1	Weichselian	Late Weichselian	Vistulian	Late Vistulian		2.12-2.11	B			
MIS 2	Weichselian	Late Weichselian	Vistulian	Main Stadial LGM	?	2.2	C	B6, B7, C6, C7, C18 C9	V-II	V-II
MIS 3/2	Weichselian	Late Weichselian	Vistulian	Grudziądz Interstadial/LGM				VII	VII	
MIS 3	Weichselian	Interpleniglacial	Vistulian	Grudziądz Interstadial		5-2.3	D	D3-1, D2B, E1	XI-VIII	XIX-VIII
MIS 4	Weichselian	Older Pleniglacial	Vistulian	Świecie Stadial		8-6	F-E	E1	XII	
MIS 5a	Weichselian	Early Weichselian	Vistulian	Gniew Interstadial	5-3	16-9	G; Ft; Jt	E2	XIX-XIII	
MIS 5b	Weichselian	Early Weichselian	Vistulian	Toruń Stadial		16-9	G; Ft; Jt	F	XIX-XIII	
MIS 5c	Weichselian	Early Weichselian	Vistulian	Toruń Stadial		16-9	FTx	G	XIX-XIII	
MIS 5d	Weichselian	Early Weichselian	Vistulian	Toruń Stadial		16-9	FTx		XIX-XIII	
MIS 5e	Eemian		Eemian		6	16-9	GTx			
MIS 6	Drenthe (+ Warthe)		Odranian (+ Wartanian)			19-17				
MIS 7	Röpersdorf – Schöningen		Lublinian							

Data are presented according to: 1 – Wojtal, 2007; 2 – Valde-Nowak et al., 2014; 3 – Nadachowski et al., 2009; Lorenc, 2013; 4 – Żarski et al., 2017; 5 – Valde-Nowak et al., 2003; 6 – Valde-Nowak and Nadachowski, 2014.

these species in Poland. The red deer dominated up until the end of the Middle Pleistocene among cervid fauna. This deer was relatively small-sized, on average, and may be attributed to *Cervus elaphus acoranatus* (Benide, 1937), which was widespread in Europe in the time period of MIS 12 – MIS 9 (Made et al., 2014) (Table 4).

A single fragment of red deer antler found in the deposits of Deszczowa Cave dates back to the time of the Krzna Glaciation (MIS 8) (Stefaniak, 2015). A considerable amount of information on cervid remains from Poland comes from Biśnik Cave (Table 1). Many years of excavations yielded numerous vertebrate remains, accompanied by many archaeological artefacts, from Middle – Upper Pleistocene and Holocene deposits (Cyrek, 2002; Wiszniewska et al., 2002; Cyrek et al., 2010, 2014; Socha, 2009; Stefaniak and Marciszak, 2009). The earliest cervid remains come from the boundary between layers 19 and 20, as well as from layer 19 which is dated to Krzna Glaciation/Lublin Inter-glacial/Lublin Interglacial, Röpersdorf-Schöningen Interglacial/Saalian, MIS 8/7 – MIS 7, i.e. ca. 200–250 ka. The fossil remains from these levels belong to the large red deer *Cervus elaphus spelaeus* (Owen, 1846), to an early *M. giganteus antecendens* (Berckhemer, 1937)/*M. giganteus germaniae* (Pohlig, 1892), *Cervalces* sp., as well as to *Capreolus priscus* and *Rangifer tarandus* (Croitor et al., 2014; Made et al., 2014). The red deer is dominant; the second most abundant species was the reindeer. Fewer remains belonged to roe-deer and giant deer and only one to elk.

3.5. Late Pleistocene (Aurelian, MNQ2) – Figs. 2 and 5

An isolated metacarpal bone of the extant fallow deer *Dama dama* (Linnaeus, 1758) was found together with an almost complete skeleton of the rhinoceros *Stephanorhinus kirchbergensis* (Jäger, 1839) in the Eemian interglacial sediments of a fossil lake near Gorzów Wielkopolski. This is the first and only finding of this rhinoceros in the Pleistocene of Poland (Badura et al., 2017).

Two subspecies of the giant deer, *Megaloceros giganteus germaniae* and *Megaloceros giganteus ruffi* (Nehring, 1891), were present in Poland during the last glaciation. The distribution of the elk in Poland shrank considerably in the Late Pleistocene. A few localities with remains of this species date from the beginning of the last glaciation and the Interplenivistulian. Also the roe deer, though initially more abundant than the elk, became increasingly rare; like the elk, it disappeared during the consecutive cold periods of the Vistulian and was scarce in the Interplenivistulian. Since the Older Plenivistulian, the reindeer became the dominant cervid and also one of the dominant large mammals. Considerable changes in the cervid fauna took place at the end of the Pleistocene and the beginning of the Holocene (Stefaniak,

2015).

The elk *Alces alces* appeared in Poland during the Eemian Interglacial; an isolated tooth was found in the deposits of Dziadowa Skała Cave. Cervid remains also occurred in the deposits of Nietoperzowa, Biśnik and Deszczowa caves. The remains from that period and from the layers dating to the beginning of Vistulian, found in cave deposits of Poland, include *Cervus elaphus spelaeus* and reindeer. The third most abundant species was the roe deer, which occurred in the Nietoperzowa, Biśnik and Dziadowa Skała caves. Isolated remains of the giant deer *Megaloceros giganteus antecendens/germaniae* were also found in Biśnik and Nietoperzowa caves. It is noteworthy that in these cave deposits the dominant species is the reindeer and the second most abundant species is the red deer (Table 5). In contrast to the end of the Middle Pleistocene, remains of roe deer are rare. The giant deer and the elk were scarce too (Stefaniak, 2015).

Cervid remains from the early Vistulian (Toruń Stadial and Gniew Interstadial), a period of drastic climate changes, were found in the deposits of numerous caves: Nietoperzowa, Łokietka, Piekar, Jasna Strzegowska, Biśnik, Zegar, Dziadowa Skała, Deszczowa, Komarowa and Obłazowa. Remains of red deer (*Cervus elaphus simplicidens*) occur in five of the listed caves (except Deszczowa and Obłazowa). The reindeer is also documented in five caves (Nietoperzowa, Łokietka, Jasna Strzegowska, Dziadowa Skała and Obłazowa). The giant deer was found in four of the caves: Nietoperzowa, Piekar, Biśnik and Deszczowa. At that time the modern elk species appeared; an isolated tooth was found in the deposits of Łokietka Cave. Also the modern roe deer appeared in the Late Pleistocene (Made et al., 2014): it was recorded from Nietoperzowa, Biśnik, Dziadowa Skała and Komarowa caves (Stefaniak, 2015) (Table 5).

The cool Świecie Stadial was characterised by an impoverishment of the cervid fauna. No elk or roe deer is recorded from that period in Poland. Cervid remains were found in MIS 4 layers of six caves: Nietoperzowa, Biśnik, Deszczowa, Stajnia, Komarowa and Raj, as well as in deposits of the same time period of the open sites of Wrocław-Hallera and Zwolen. Changes in abundance occurred in the other cervids; the reindeer became the dominant species. The red deer is reported at this time from all the localities listed above except Raj Cave (Stefaniak, 2015) (Table 5).

The Grudziądz Interstadial (Interplenivistulian, MIS 3) was a period of climate warming and amelioration, but also of great climate fluctuations. Cervid remains were found in deposits of that time period present in ten caves (Nietoperzowa, Biśnik, Deszczowa, Stajnia, Komarowa, Raj, Mamutowa, Zegar, Wiercica and Obłazowa), as well as in a number of open sites (Krosinko, Turek, Pyzdry, Barycz and others).

Table 4
Spatial and temporal distribution of Cervidae taxa in Europe.

Epochs (Large Mammal Complexes and ages)	Western Europe	Italy	Poland	Czech Republic, Slovakia, Hungary	Ukraine	Moldova, Romania	South-Western Europe	Southern Europe
Holocene 0.0117–0 My	<i>Cervus elaphus</i> <i>Dama dama</i> <i>Capreolus capreolus</i> <i>Alces alces</i>	<i>Cervus elaphus</i> <i>Capreolus capreolus</i> <i>Alces alces</i>	<i>Cervus elaphus</i> <i>Capreolus capreolus</i> <i>Alces alces</i>	<i>Cervus elaphus</i> <i>Capreolus capreolus</i> <i>Alces alces</i>	<i>Cervus elaphus</i> <i>Capreolus capreolus</i> <i>Alces alces</i>	<i>Cervus elaphus</i> <i>Capreolus capreolus</i> <i>Alces alces</i>	<i>Cervus elaphus</i> <i>Capreolus capreolus</i> <i>Alces alces</i>	<i>Cervus elaphus</i> <i>Megaloceros giganteus</i> <i>Alces alces</i>
Late Pleistocene (Aurelian) 0.126–0.117 My	<i>Cervus elaphus</i> <i>Megaloceros giganteus</i> <i>Dama dama</i> <i>Capreolus priscus/</i> <i>capreolus</i> <i>Alces alces</i> <i>Rangifer tarandus</i>	<i>Cervus elaphus</i> <i>Praemegaceros cazorii</i> <i>Megaloceros giganteus</i> <i>Dama dama</i> <i>Dama cariburgensis</i> <i>Capreolus priscus/</i> <i>capreolus</i> <i>Alces alces</i> <i>Rangifer tarandus</i>	<i>Cervus elaphus</i> <i>Megaloceros giganteus</i> <i>Dama dama</i> <i>Capreolus priscus/</i> <i>capreolus</i> <i>Alces alces</i> <i>Rangifer tarandus</i>	<i>Cervus elaphus</i> <i>Megaloceros giganteus</i> <i>Dama dama</i> <i>Capreolus priscus/capreolus</i> <i>Alces alces</i>	<i>Cervus elaphus</i> <i>Megaloceros giganteus</i> <i>Dama dama</i> <i>Capreolus priscus/capreolus</i> <i>Alces alces</i>	<i>Cervus elaphus</i> <i>Megaloceros giganteus</i> <i>Dama dama</i> <i>Rangifer tarandus</i>	<i>Cervus elaphus</i> <i>Megaloceros giganteus</i> <i>Cervales latifrons</i> <i>Rangifer tarandus</i>	<i>Cervus elaphus</i> <i>Megaloceros giganteus</i> <i>Cervales latifrons</i> <i>Rangifer tarandus</i>
Middle - Late Pleistocene (Aurelian) 0.4–0.0117 My	<i>Cervus elaphus</i> <i>Megaloceros giganteus</i> <i>Dama dama</i> <i>Capreolus capreolus/</i> <i>priscus</i> <i>Cervales latifrons</i> <i>Rangifer tarandus</i>	<i>Cervus elaphus</i> <i>Megaloceros giganteus</i> <i>Praemegaceros cazorii</i> <i>Dama dama</i> <i>Dama cariburgensis</i> <i>Cervales latifrons</i> <i>Capreolus capreolus</i> <i>Rangifer tarandus</i>	<i>Cervus elaphus</i> <i>Megaloceros giganteus</i> <i>Praemegaceros priscus</i> <i>Rangifer tarandus</i>	<i>Cervus elaphus</i> <i>Megaloceros giganteus</i> <i>Cervales latifrons</i> <i>Rangifer tarandus</i>	<i>Cervus elaphus</i> <i>Megaloceros giganteus</i> <i>Cervales latifrons</i> <i>Rangifer tarandus</i>	<i>Cervus elaphus</i> <i>Megaloceros giganteus</i> <i>Cervales latifrons</i> <i>Rangifer tarandus</i>	<i>Cervus elaphus</i> <i>Megaloceros giganteus</i> <i>Cervales latifrons</i> <i>Rangifer tarandus</i>	<i>Cervus elaphus</i> <i>Megaloceros giganteus</i> <i>Cervales latifrons</i> <i>Rangifer tarandus</i>
Middle Pleistocene (Galerian) 1 My–0.4 My	<i>Cervus elaphus</i> <i>Haplodoceros mediterraneus</i> <i>Eucladoceros giulii</i> <i>Praemegaceros dawkinsi</i> <i>Praemegaceros solilhacis</i> <i>Praemegaceros verticornis</i> <i>Prædama savini</i> <i>Megaloceros giganteus</i> <i>Dama clactoniana</i> <i>Capreolus suesseniensis</i> <i>Cervales latifrons</i> <i>Rangifer tarandus</i>	<i>Cervus elaphus</i> <i>Praemegaceros verticornis</i> <i>Praemegaceros solilhacis</i> <i>Praemegaceros</i> <i>piotaranoides</i> <i>Megaloceros giganteus</i> <i>Cervales latifrons</i> <i>suesseniensis</i> <i>Cervales latifrons</i> <i>Megaloceros giganteus</i> <i>Dama clactoniana</i> <i>Capreolus suesseniensis</i> <i>Cervales latifrons</i> <i>Rangifer tarandus</i>	<i>Cervus elaphus</i> <i>Praemegaceros verticornis</i> <i>Megaloceros giganteus</i> <i>Capreolus suesseniensis</i> <i>Cervales latifrons</i>	<i>Cervus elaphus</i> <i>Praemegaceros verticornis</i> <i>Megaloceros giganteus</i> <i>Capreolus suesseniensis</i> <i>Cervales latifrons</i>	<i>Cervus elaphus</i> <i>Praemegaceros verticornis</i> <i>Megaloceros giganteus</i> <i>Capreolus suesseniensis</i> <i>Cervales latifrons</i>	<i>Cervus elaphus</i> <i>Praemegaceros verticornis</i> <i>Megaloceros giganteus</i> <i>Capreolus suesseniensis</i> <i>Cervales latifrons</i>	<i>Cervus elaphus</i> <i>Praemegaceros solilhacis</i> <i>Megaloceros giganteus</i> <i>Praemegaceros</i> <i>piotaranoides</i> <i>Megaloceros giganteus</i> <i>Capreolus verticornis</i> <i>Megaloceros giganteus</i> <i>Cervales latifrons</i>	<i>Cervus elaphus</i> <i>Praemegaceros solilhacis</i> <i>Megaloceros giganteus</i> <i>Praemegaceros</i> <i>piotaranoides</i> <i>Megaloceros giganteus</i> <i>Cervales latifrons</i>
Early Pleistocene (Late Villafanchian) 1.8 (1.7) – 1 My	<i>Metacervocerus rhenanus</i> <i>Eucladoceros ctenoides</i> <i>Eucladoceros giulii</i> <i>Praemegaceros obscurus</i> <i>Dama valloneensis</i> <i>Cervales carinatum</i> <i>Cervales latifrons</i> <i>Rangifer tarandus</i> <i>Capreolus cusanoides</i> <i>Croizetoceros ramosus</i> <i>Arvernoceros sp.</i> <i>Cervales carinatum</i> <i>Cervales gallicus</i> <i>Rangifer tarandus</i>	<i>Metacervocerus rhenanus</i> <i>Praeelaphus lyra</i> <i>(australorientalis)</i> <i>Cervus nestii</i> <i>Praemegaceros obscurus</i> <i>Praemegaceros</i> <i>piotaranoides</i> <i>Eucladoceros ctenoides</i> <i>Dama eurygonos</i> <i>Dama vallorensis</i> <i>Arvernoceros sp.</i> <i>Cervales carinatum</i> <i>Cervales gallicus</i>	<i>Metacervocerus rhenanus</i> <i>Capreolus sp.</i> <i>Cervales carinatum</i>	<i>Metacervocerus rhenanus</i> <i>Arvernoceros sp.</i> <i>Eucladoceros giulii</i> <i>Praemegaceros obscurus</i> <i>Praemegaceros</i> <i>piotaranoides</i> <i>Dama eurygonos</i> <i>Cervales carinatum</i>	<i>Metacervocerus rhenanus</i> <i>Arvernoceros sp.</i> <i>Eucladoceros giulii</i> <i>Praemegaceros obscurus</i> <i>Praemegaceros</i> <i>piotaranoides</i> <i>Dama eurygonos</i> <i>Cervales carinatum</i>	<i>Metacervocerus rhenanus</i> <i>Arvernoceros sp.</i> <i>Eucladoceros giulii</i> <i>Praemegaceros obscurus</i> <i>Praemegaceros</i> <i>piotaranoides</i> <i>Dama eurygonos</i> <i>Cervales carinatum</i>	<i>Metacervocerus rhenanus</i> <i>Arvernoceros sp.</i> <i>Eucladoceros giulii</i> <i>Praemegaceros obscurus</i> <i>Praemegaceros</i> <i>piotaranoides</i> <i>Dama eurygonos</i> <i>Cervales carinatum</i>	<i>Metacervocerus rhenanus</i> <i>Arvernoceros sp.</i> <i>Eucladoceros giulii</i> <i>Praemegaceros obscurus</i> <i>Praemegaceros</i> <i>piotaranoides</i> <i>Dama eurygonos</i> <i>Cervales carinatum</i>
Early Pleistocene (Middle Villafanchian)	<i>Metacervocerus rhenanus</i> <i>Eucladoceros dicranios</i>	<i>Praeelaphus rhenanus</i> <i>Cervus bestii</i>	<i>Croizetoceros ramosus</i> <i>Eucladoceros sp.</i>	<i>Croizetoceros ramosus</i> <i>Eucladoceros sp.</i>	<i>Croizetoceros ramosus</i> <i>Eucladoceros sp.</i>	<i>Croizetoceros ramosus</i> <i>Eucladoceros sp.</i>	<i>Metacervocerus rhenanus</i> <i>Arvernoceros sp.</i> <i>Eucladoceros dicranios</i>	<i>Metacervocerus rhenanus</i> <i>Arvernoceros sp.</i> <i>Eucladoceros dicranios</i>

(continued on next page)

Table 4 (continued)

Epochs (Large Mammal Complexes and ages)	Western Europe	Italy	Poland	Czech Republic, Slovakia, Hungary	Moldova, Romania	South-Western Europe	Southern Europe
MN 16b - MN 17) 2.58–1.8 (1.7) My	<i>Cervales gallicus</i> <i>Croizetoceros ramosus</i>	<i>Eucitadoceros dicranios</i> <i>Cervales gallicus</i>				<i>Eucladoceros dicranios</i>	
Late Pliocene – Early Pleistocene (Early Villafanchian MN 16a) 3.6–2.58 My	<i>Procapreolus cusanus</i> <i>Croizetoceros ramosus</i> <i>Praeelaphus perrieri</i> <i>Metacervocerus pardinensis</i> <i>Arvenoceros ardei</i>	<i>Procapreolus cusanus</i> <i>Croizetoceros ramosus</i> <i>Praeelaphus lyra</i> <i>Metacervocerus pardinensis</i> <i>Arvenoceros ardei</i>	<i>cf. Muntiacus polonicus</i> <i>Croizetoceros ramosus</i> <i>Procapreolus moldanicus</i> <i>Metacervocerus ardei</i> <i>Cervidae gen. et sp. indet. I.</i> <i>(Arvenoceros ardei or Praeelaphus perrieri)</i>	<i>Muntiacus cf. polonicus</i> <i>Croizetoceros ramosus</i> <i>Procapreolus moldanicus</i> <i>Metacervocerus ardei</i> <i>Cervidae gen. et sp. indet. I.</i> <i>(Arvenoceros ardei or Praeelaphus perrieri)</i>	<i>Arvenoceros cf. ardei</i> <i>Procapreolus moldanicus</i> <i>Metacervocerus pardinensis</i>	<i>Arvenoceros</i> <i>Metacervocerus</i> <i>pardinensis</i>	<i>Eucladoceros</i> <i>Arvenoceros sp.</i> <i>Cervales gallicus</i> <i>Metacervocerus</i> <i>pardinensis</i>
Pliocene – Early Pleistocene (Ruscinian MN 15) 5.3–3.6 My	<i>Cervus australis</i> <i>Procapreolus cusanus</i> <i>Croizetoceros ramosus</i>			<i>Muntiacus polonicus</i> <i>(Euprox pidolitschkoii)</i> <i>Procapreolus moldanicus</i> <i>Praeelaphus warthae</i> <i>Arvenoceros cf. ardei</i>	<i>Muntiacus polonicus</i> <i>(Euprox pidolitschkoii)</i> <i>Procapreolus vesti</i> <i>Metacervocerus pardinensis</i> <i>Praeelaphus lyra</i> <i>Arvenoceros astralionalensis</i>	<i>Muntiacus polonicus</i> <i>(Euprox pidolitschkoii)</i> <i>Procapreolus moldanicus</i> <i>Metacervocerus pardinensis</i> <i>Praeelaphus lyra</i> <i>Arvenoceros vereschagini</i>	<i>Arvenoceros</i> <i>vereschagini</i>

During MIS 3 the elk and the roe deer returned to Poland. The dominant species was once again *Rangifer tarandus*, but the increasing numbers of the red deer and giant deer indicate that the conditions in the southern part of the country were favourable for the cervids. The second most abundant species was the red deer (found in the Nietoperzowa, Mamutowa, Biśnik, Dziadowa Skała, Deszczowa and Obłazowa caves). *Megaloceros giganteus* reached its maximum abundance in Poland during the MIS 3; its remains were found in four caves and four open sites. Isolated remains of the elk of that period were discovered in the deposits of Biśnik and Obłazowa caves. Remains of the roe deer were recovered from the MIS 3 deposits of Biśnik Cave (Stefaniak, 2015) (Table 5).

A new cooling occurred during the Last Glacial Maximum (LGM, MIS 2). The reindeer remained the dominant species and was the only cervid reported from the coldest interval of the LGM; its remains were found in seven caves (Biśnik, IV in Mt. Birów, Dziadowa Skała, Deszczowa, Stajnia, Komarowa, Obłazowa). The red deer was found in Biśnik, Dziadowa Skała, Deszczowa, Stajnia and Niedźwiedzia caves. The giant deer occurred in three caves (Biśnik, Deszczowa, Komarowa), but its remains are rare. Noteworthy is the presence of the elk, recorded from the deposits of Borsuka Cave near Cracow (Wilczyński et al., 2012), and of the roe deer, whose remains were found in Deszczowa and Komarowa caves. Forest-dwelling and more thermophilous species of cervids and of other vertebrates in periods of climate deterioration in the Quaternary are reported from the Kraków-Częstochowa Upland, which may confirm the refugial character of the area (Stefaniak et al., 2009a; Wilczyński et al., 2012; Stefaniak, 2015).

3.6. Holocene (MIS 1) – Figs. 2 and 5

At the end of the last glaciation (MIS 2/1 and MIS 1), the giant deer receded from Poland. An isolated tooth was found in Dziadowa Skała Cave. The roe deer occurred in the deposits of Biśnik, Dziadowa Skała and Komarowa caves and – probably at Dudka, an open site locality in northern Poland. The red deer was reported from Biśnik, Komarowa and Obłazowa caves. As in the preceding periods, the reindeer was the dominant species, albeit with lower total amounts; it was found in Łokietka, Jasna Strzegowska, Schronisko Pośrednie, Jasna Smoleńska, Cave IV in Mt. Birów, Dziadowa Skała, Stajnia, Komarowa, Obłazowa, Raj, Jaskinia Północna Duża caves (Stefaniak, 2015) (Table 5).

The elk re-colonised Poland at the end of the last glaciation. The earliest Holocene elk record comes from the south-eastern part of the country and is dated to about 12,000 years BP (Nadachowski, pers. com.). The next oldest localities for this species are Rusinowo, in Pomerania, where a ritual object dated to $10,700 \pm 60$ BP was discovered (Plonka et al., 2011; Plonka and Kowalski 2017; Stefaniak et al., 2017), and Dudka, where this species occurred in the Early Preboreal (Gumiński and Fiedorczuk, 1988; Gumiński, 1995, 1999, 2003, 2005a-c; Gautier, 2005b; Stefaniak, 2015).

The red deer and the roe deer became dominant during the Holocene. In contrast to the elk, fluctuations in their abundances are not well known. They inhabited the whole country. At present, the roe deer is observed to distribute in open areas and agricultural land (the so-called field roe deer). The fallow deer and the sika deer were introduced in historic times into Poland (Pucek, 1984).

4. Discussion and palaeoenvironmental considerations

4.1. Middle Miocene (Ruscinian, MN 7–8)

Palaeoenvironmental reconstructions of the Middle Miocene sites (Opole and Przeworno) indicate the presence of mosaic environments, with dry, open habitats, and moist tropical/subtropical forests (Böhme, 2003; Böhme et al., 2011; Glazek and Szynkiewicz, 1987). There are no Late Miocene and Early Pliocene cervid records from Poland, because during that time the area was covered by an epicontinental sea (Glazek

Table 5
Number of identified specimens (NISP) and minimum number of individuals (MNI) of cervids from Pliocene to the beginning of the Holocene in the localities of Poland.

Locality		Geological age	Species	NISP	MNI
Węże 1	MN 15		<i>Muntiacus polonicus Czajewska</i> (1968) <i>Prædaphus warthae</i> (Czajewska, 1968) <i>Arvenoceros cf. ardei</i> (Croizet et Jobert, 1828)	9 555 5	2 16 1 or 2
Węże 2	MN 16		<i>Procapreolus moldanicus</i> (Janowskaya, 1954) <i>Procapreolus ramosus</i> (Croizet et Jobert, 1828) <i>Metacervoceros pardensis</i> (Croizet et Jobert, 1828)	588 128 18	26 9 2
Rebielice Królewskie	MN 16/MN 17		<i>Arvenoceros cf. ardei</i> (Croizet et Jobert, 1828) <i>Croizatoceros ramosus</i> (Croizet et Jobert, 1828)	1 20	1 2
Żabia Cave	MIS 58-40		<i>Eucladoceros</i> sp. <i>Dama</i> cf. <i>fammeensis</i> (Azzaroli, 1992) <i>Cervales carinatum</i> (Lagel, 1862)	55 82 41	2 or 3 2 2
Kozi Grzbiet	MIS 19-17		<i>Capreolus</i> sp. <i>Cervus elaphus</i> ssp. <i>Præmegaceros vericornis</i> (Dawkins, 1872) <i>Cervales latifrons</i> (Johnson, 1874)	3 4 4 1	1 1 1 1
Sitkówka	MIS 19-17		<i>Capreolus stiessnenensis</i> H. D. Kahlke, 1956	13	1
Bielchatów	MIS 11 or 9		<i>Cervales latifrons</i> (Johnson, 1874)	2	2
Deszczowa Cave	MIS 8		<i>Cervus elaphus angulatus</i> Benide, 1937 <i>Rangifer tarandus</i> (Linnaeus, 1758)	4 1	2 or 3 1
Bisniki Cave	MIS 8/7-MIS 7		<i>Cervus elaphus spelæus</i> Owen, 1846 <i>Cervus elaphus spelæus</i> Owen, 1846 <i>Megaceros giganteus</i> Blumenbach, 1803	28 3	5 1
Bisniki Cave, Nietoperzowa Cave, Jasna Strzegowska Cave	MIS 6		<i>Cervales</i> sp. <i>Capreolus priscus</i> Soergel, 1914 <i>Rangifer tarandus</i> (Linnaeus, 1758) <i>Dama dama</i> (Linnaeus, 1758)	8 14 72	4 5 16
Gorzów Wielkopolski	MIS 5e		<i>Megaceros giganteus</i> Blumenbach, 1803	7	2
Bisniki Cave, Nietoperzowa Cave, Dziadowa Skala Cave, Deszczowa Cave	MIS 5e		<i>Cervales</i> sp. <i>Capreolus priscus</i> Soergel, 1914 <i>Rangifer tarandus</i> (Linnaeus, 1758) <i>Dama dama</i> (Linnaeus, 1758)	3 64 66	2 13 10
Bisniki Cave, Nietoperzowa Cave, Deszczowa Cave, Stajnia Cave, Deszczowa Cave, Komarowa Cave, Oblazowa Cave, Zwoleni Cave, Oblazowa Cave, Zwoleni	MIS 5a-d		<i>Megaceros giganteus</i> Blumenbach, 1803 <i>Ales alces</i> (Linnaeus, 1758)	31 1	11 1
Bisniki Cave, Nietoperzowa Cave, Deszczowa Cave, Stajnia Cave, Piekary Cave, Jasna Strzegowska Cave, Raj Cave, Wiercica Cave, Wiercica Cave, Deszczowa Cave, Komarowa Cave, Oblazowa Cave, Raj	MIS 3		<i>Capreolus capreolus</i> (Linnaeus, 1758) <i>Rangifer tarandus</i> (Linnaeus, 1758) <i>Cervus elaphus simplicidens</i> Guadelli, 1996	133 71 105	42 13 24
Bisniki Cave, Nietoperzowa Cave, Deszczowa Cave, Stajnia Cave, Raj Cave, Wiercica Cave, Deszczowa Cave, Komarowa Cave, Oblazowa Cave, Raj	MIS 4		<i>Megaceros giganteus</i> Blumenbach, 1803 <i>Ales alces</i> (Linnaeus, 1758) <i>Capreolus capreolus</i> (Linnaeus, 1758) <i>Rangifer tarandus</i> (Linnaeus, 1758) <i>Cervus elaphus simplicidens</i> Guadelli, 1996	41 2 17 105	23 2 7 24
Bisniki Cave, Nietoperzowa Cave, Mamutowa Cave, Zegar Cave, Wiercica Cave, Stajnia Cave, Oblazowa Cave, Raj			<i>Megaceros giganteus</i> Blumenbach, 1803 <i>Megaceros giganteus</i> Blumenbach, 1803 <i>Cervus elaphus simplicidens</i> Guadelli, 1996 <i>Ales alces</i> (Linnaeus, 1758)	91 9 2 2	3 42 43 23
Bisniki Cave, Nietoperzowa Cave, Mamutowa Cave, Zegar Cave, Wiercica Cave, Stajnia Cave, Oblazowa Cave, Raj			<i>Capreolus capreolus</i> (Linnaeus, 1758) <i>Rangifer tarandus</i> (Linnaeus, 1758)	3 624	1 47

(continued on next page)

Table 5 (continued)

Locality		Geological age	Species	NISP	MNI
Bisnik Cave, Borsuka Cave, Mt. Biorów Cave, Dziedowa Skala Cave, Deszczowa Cave, Komarowa Cave, Obłazowa Cave, Niedźwiedzia Cave	MIS 2		<i>Cervus elaphus simplicidens</i> Guadelli, 199	55	13
Bisnik Cave, Łokietka Cave, Jasna Strzegowska Cave, Jasna Smoleńska Cave, Pośrednia Rock-Shelter, Cave IV in Mt. Biorów, Dziedowa Skala Cave, Stajnia Cave, Komarowa Cave, Obłazowa Cave, Raj Cave, Północna Duża Cave, Dudka, Rusinowo	MIS 2/1		<i>Megaloceros giganteus</i> Blumenbach, 1803 <i>Ales alices</i> (Linnaeus, 1758) <i>Rangifer tarandus</i> (Linnaeus, 1758) <i>Cervus elaphus simplicidens</i> Guadelli, 1996 <i>Megaloceros giganteus</i> Blumenbach, 1803 <i>Ales alices</i> (Linnaeus, 1758) <i>Capreolus capreolus</i> (Linnaeus, 1758) <i>Rangifer tarandus</i> (Linnaeus, 1758)	17 4 1195 15 1 3 5 132	7 2 102 4 1 3 5 16

and Szynkiewicz, 1987).

4.2. Pliocene (late Ruscianian, MN15)

The Pliocene faunal assemblages from Węże 1 (MN15), which show numerous affinities with coeval ones from Ukraine (Table 4), the Caucasus, south-eastern Asia and North America, indicate warm Mediterranean climatic conditions, and the presence of both forested and open areas (Czyżewska, 1968, 1989; Kowalski K., 1989; Vislobokova, 1990). Many authors (Glazek et al., 1976; Glazek and Szynkiewicz, 1987; Kowalski K., 1989; 1990; Nadachowski et al., 1989) suppose that the Węże 1 fauna is of mixed age, ranging from the Late Miocene (or Early Pliocene) to the Late Pliocene – Early Pleistocene.

The Early Pliocene deer remains from Węże 1 belong to 4 species: *Muntiacus polonicus* Czyżewska (1968), *Praeelaphus warthae* (Czyżewska, 1968), *Arvernoceros cf. ardei* (Croizet et Jobert, 1828) and *Procapreolus moldavicus* (Janowska, 1954). Croitor (2018) transferred *M. polonicus* to the genus *Euprox* Stehlin, 1928, alongside *Eostyloceros pidoplitschkoi* Korotkevich (1964) and *Muntiacus pliocaemicus* Korotkevich (1965), known from Ukraine and southern Moldova (Table 4). The similarity of these two species to *Euprox* was pointed out in earlier publications (Croitor and Stefaniak, 2009; Stefaniak, 2015); they were also shown to have a sister-group relationship with Muntiacinae (Croitor, 2018; Heckengerg and Wörheide, 2019). Fejfar et al. (2016) described teeth and fore limb bones of two individuals of *M. cf. polonicus* from Hajnáčka (Slovakia, MN 16a). According to Croitor (2018), *Euprox pidoplitschkoi* occurred in Italy (an individual from Montopoli, with uncertain stratigraphic provenance), Romania, Bulgaria, Ukraine and Moldova (Table 4). Poland and Slovakia were located in the northernmost part of its range. In Croitor's view, *Euprox* survived till the Late Pliocene, when it became extinct due to climate cooling (Vislobokova, 1990; Croitor and Stefaniak, 2009).

P. moldavicus was larger than *P. cusanus* and smaller than *Crozetoceros ramosus*, although its range of dental measurements partly overlapped those of the latter species (Stefaniak, 2015). According to Stefaniak (2015) and Croitor (2018) *P. moldavicus* was the largest (estimated body mass 40–50 kg) representative of *Procapreolus*. It was distributed in Ukraine, Moldova and Poland (Table 4). In Węże 1 it was somewhat larger than its conspecifics from Ukraine and Moldova (Stefaniak, 2015; Croitor, 2018).

Czyżewska (1968) considered "*Cervus*" *warthae* close to the extant genus *Rusa*, an opinion shared by Vislobokova (1990) and Di Stefano and Petronio (2002). For these authors, "*Cervus*" *warthae* and "*Cervus*" *perrieri* are close to the evolutionary lineage of *C. elaphus*, based also on the teeth structure. Stefaniak (2001) included *Cervus*" *warthae* in the genus *Pseudodama* Azzaroli, 1992, in spite of the considerable differences, in size and morphology, between the two taxa. Di Stefano and Petronio (2002) suggested a close relationship with *Cervus magnus* Zdansky (1925) from the Early/Middle Pliocene of Eurasia. According to Croitor and Stefaniak (2009), despite some similarities to *Cervus*" *perrieri* and the palmation of the antlers, which occurs also in "*Pseudodama*" *lyra* Azzaroli (1992), the status of the species is unclear at the present state of knowledge. Based on its similarities to "*Cervus*" *perrieri* and the Italian *Pseudodama* *lyra* Azzaroli (1992), Croitor (2012) proposed to include *Cervus*" *warthae* in the genus *Praeelaphus* Portis, 1920, which was common in Europe from the Pliocene to the Early Pleistocene (Table 4). *P. warthae* was among the largest species of its genus, being second only to the western European *P. perrieri* Croizet et Jobert (1828) from the Late Pliocene sites in France and England (Croitor, 2018).

A few remains of those assigned by Czyżewska (1968) to *P. warthae* were attributed to *Arvernoceros cf. ardei* (Croizet et Jobert, 1828) by Croitor and Stefaniak (2009). According to Heintz (1970), Vislobokova (1981, 1990, 2011, 2012a, b) and Vislobokova and Hu (1990), the genus *Arvernoceros* was a member of the giant deer group and the ancestor of the genus *Megaloceros* Brookes, 1828. Di Stefano and Petronio

(2002) included *Arvernoceros* in the genus *Axis* C. H. Smith (1827). According to Croitor (2018), *Arvernoceros* was phylogenetically close to the genus *Rucervus* Hodgson, 1838, which comprised large cervids, up to 700 kg of weight, with very characteristic antlers. *Rucervus* was distributed throughout Europe, and as far east as the Caucasus, during the Early Pleistocene. Węże 1 is one of the oldest localities that yielded remains of this genus (Tables 4 and 5).

The genera *Muntiacus* (*Euprox*) and *Procapreolus* are older cervids, known already from the Miocene. The genera *Praeelaphus* and *Arvernoceros* came to Europe from Asia during the Pliocene. *Praeelaphus warthae*, of the evolutionary lineage leading to *Cervus elaphus*, was a component of a new wave of immigrants from Asia. Poland was situated on one of the migration routes (northern corridor, north of the Caucasus and the Carpathian Arch) from Asia to Europe (Azzaroli et al., 1988; Fejfar et al., 1990; Heintz et al., 1990; Vislobokova, 1990, 2008a, b; Gliozzi et al., 1997; Di Stefano and Petronio, 1998a, 2002; Stefaniak, 2001; Rădulescu, 2005; Petronio et al., 2007, 2013; Croitor and Stefaniak, 2009; Valli, 2010; Croitor, 2012, 2014). The cervid assemblage confirms the Early Pliocene age of this part of the Węże 1 fauna.

The cervids included forest-dwellers, as well as taxa of forest edges and of more open habitats. Węże 1 was a characteristic natural trap (sinkhole). Wide open areas were present in the environs of Węże 1, as indicated by other faunal components associated with the cervids (e.g. horse remains - *Hipparrison*), but the environment was most probably mixed: karstic hills scattered in a mosaic of forests of various kinds and open habitats (Glazek and Szynkiewicz, 1987; Stefaniak, 1995).

4.3. Late Pliocene (Early Villafranchian, MN16)

The early Villafranchian fauna in Poland is represented at Węże 2 site (MN16). The cervids had pan-European distribution (Table 4); they were present also in Western, Southern, Central and Eastern Europe (Heintz, 1970; Heintz and Poplin, 1974; Guérin, 1982, 1990; Repenning, 1985; Azzaroli et al., 1988; Vislobokova, 1990, 2008a, b; Azzaroli, 1992; Palombo and Valli, 2003–2004; Rădulescu et al., 2003; Koustopoulos and Athanassiou, 2005; Rădulescu, 2005; Croitor, 2006a, 2009a, b, 2012, 2014; Brugal and Coior, 2007; Logvinenko, 2008; Croitor and Stefaniak, 2009; Rook and Martinez-Navarro, 2010; Valli, 2010; Kahlke et al., 2011; Baigusheva and Titov, 2013; Made et al., 2014; Fejfar et al., 2016). In the early Villafranchian, the Akchagyl transgression separated the faunas of Asia and Europe from one another (Vislobokova, 1990). A new Villafranchian species widespread in Europe (Heintz, 1970; Azzaroli et al., 1988; Azzaroli, 1992; Di Stefano and Petronio, 1998a; Vislobokova, 1990) is the medium-sized deer *Metacervocerus pardensis* (Croizet et Jobert, 1828) (Table 4). The morphology of these species and the accompanying fauna suggest a forest environment (Stefaniak, 1995) interrupted by open areas with presence of water bodies.

M. pardensis from Węże 2 belongs to an early stage of the radiation of the species. It was smaller than its counterparts from Eastern Europe and similar to the Western European ones (Heintz, 1970; Spaan, 1992; Vos et al., 1995, 2002; Stefaniak, 1995; Croitor and Bonifay, 2001; Kostopoulos and Athanassiou, 2005; Croitor, 2006a; Garrido, 2008; Titov, 2008; Abbazzi, 2010).

In the Early Villafranchian, the climate had deteriorated, compared to that of the Ruscinian (Shackleton and Opdyke, 1977; Shackleton et al., 1984; Stuchlik, 1987; Bonifay, 1990; Suc et al., 1995; Vislobokova, 2008a, b), and many thermophilous species became extinct, or were replaced by taxa typical of more temperate climatic conditions (Bonifay, 1990). The genera *Eucladoceros* Falconer, 1868 and *Praeelaphus* Portis, 1920 (Stefaniak, 2015), which were present in other parts Europe at that time, where not distributed in Poland (Table 4).

4.4. Beginning of the Early Pleistocene (Middle Villafranchian, end of MN 16)

Similarly to Węże 2, the fauna from Rębielice Królewskie indicates a relatively warm, Mediterranean climate, with open forest environment and constant presence of water bodies (Czyżewska, 1972; Glazek and Szynkiewicz, 1987; Kowalski, 1989, 1990; Nadachowski, 1989, 1990b; Stefaniak, 1995). However, the climate had become colder and wetter, as indicated by the appearance of taxa typical of cooler (boreal) climate and open areas. There were two species of deer at Rębielice Królewskie. The measurements of teeth and phalanges of *Croizetoceros ramosus* are within the variation range of the species from the Pliocene and Early Pleistocene localities of Europe (Table 4) and close to those from Les Étouaires, Puebla and Villaroya (Stefaniak, 2015). Because the fauna from Rębielice Królewskie is younger than that from Węże 2, this cervid can be considered a younger subspecies *C. ramosus medius* (Heintz, 1970, 1974).

The genus *Eucladoceros* evolved in Asia and colonised Europe in the Pliocene, where it survived to the Late Pleistocene (Table 4). Its members were large-sized animals, although smaller than the elk, with strongly developed, arborescent antlers. Most of the authors regarded the genus *Eucladoceros* as the ancestor of giant deer genus *Megaceroides* Jouleaud, 1914 (Abbazzi, 1995, 2004; Abbazzi and Masini, 1997; Azzaroli, 1994; Azzaroli and Mazza, 1992, 1993a, b; Lister, 1994; Croitor, 2006b). Lately, Croitor (2018) and Mennecart et al. (2017) suggested a close relationship of *Eucladoceros* with the genus *Przewalski* Flerov, 1930.

In all, five cervid taxa occurred in Poland in the Early and Middle Villafranchian. The genus *Procapreolus* was still present in the Early Villafranchian and became extinct at the end of that time period. *Croizetoceros ramosus* occurred in both the Early and Middle Villafranchian. The medium-sized *Metacervocerus pardensis* was present in the Middle Villafranchian, but it was absent from the fauna of Rębielice Królewskie. The genus *Eucladoceros* appeared in Poland in the Middle Villafranchian (Tables 4 and 5).

4.5. Early Pleistocene (late Villafranchian, MNQ1)

At the beginning of the Early Pleistocene, the faunal assemblages underwent profound changes; after the disappearance of the Akchagyl reservoir, new species immigrated into Europe from Asia, Africa and North America (Vislobokova, 1990). The successive cooling cycles (which lasted ca. 41 ka each) of the Pre-Tiglian (MIS 98–100) and Eburonian (MIS 56–62) caused the formation of the zone of boreal coniferous forests, mixed forests and steppes in Central Europe, and the zone of Arctic tundra and steppe-tundra in the northern part of the continent. In that period some holdover species, from earlier time periods, became extinct and were replaced by other species that characterised later periods of the Quaternary (Frenzel, 1967; Sadowska, 1987; Stuchlik, 1987; Azzaroli et al., 1988; Vislobokova, 1990, 2008a, b; Sher, 1992; Suc et al., 1995; Lister, 1996; Palombo et al., 2000; Sala et al., 1992; Palombo and Valli, 2003–2004; Mojski, 1993; Torre et al., 1992; Abbazzi, 2010; Rook and Martinez-Navarro, 2010; Kahlke et al., 2011). The only Late Early Pleistocene site with the remains of Cervidae in the territory of Poland is the Žabia Cave (MIS 58–40). The cave is a vertical karst well, at present more than 12 m deep, which likely acted as a natural trap during the Early Pleistocene. Most of the best preserved remains belong to small vertebrates; the remains of larger animals are badly fragmented (Stefaniak et al., 2009a, b; Nadachowski et al., 2011a; Stefaniak, 2015).

The occurrence of three deer taxa was described at this locality. The structure of the teeth indicates that *Dama* cf. *farnetensis* from Žabia Cave inhabited forests and their margins, feeding on tree and shrub leaves. The structure of its incisors, and especially the asymmetrical I_1 , indicates a wide spectrum of food items including grasses and other short-vegetation plants (Stefaniak, 2015).

C. carnutorum from Žabia Cave and from other localities was similar to the modern elk but larger than the ancestral elk *Cervales gallicus* (Azzaroli, 1952, 1953) and smaller than the Middle Pleistocene *Cervalces latifrons* (Johnson, 1874). The structure of its teeth and mandible suggest a mixed diet, including both tree and shrub leaves and herbaceous plants. The life style resembled that of the modern elk.

Capreolus sp. from Žabia Cave is the oldest occurrence of the taxon in Europe; it is only slightly younger than the roe deer from Dilska (Southern Georgia, ca. 2.1 Ma) (Kahlke, 1997, 2001; Valli, 2010; Kahlke et al., 2011; Stefaniak, 2015).

The remains of Cervidae and of other vertebrates in Žabia Cave's layer 15 date to the end of the Otwockian Glaciation (Eburonian; MIS 56–62) or to the beginning of the Celestynowian Interglacial (Waalian; MIS 36–52) (Early Pleistocene).

4.6. Latest early and early Middle Pleistocene (Galerian, MNQ1-MNQ2)

The cervid assemblage from Kozi Grzbiet has evident relationships with the fauna of other parts of Europe and Asia (Table 4). It indicates a forest environment interspersed with open areas, and a warm and humid climate with a tendency to deterioration. Species still present today such as the roe and red deer, appeared then for the first time. Besides the cervids, Kozi Grzbiet provided remains of wild boar, which co-existing with roe deer indicate that the fauna and forested habitats are to be referred to an interglacial cycle.

The fossil records from Kozi Grzbiet and Sitkówka include genera of the present-day fauna (*Cervus* and *Capreolus*), though represented by different species or subspecies. In the course of the Quaternary, *Praemegaceros verticornis* and *Cervalces latifrons* became extinct. There are no sites in Poland with the remains of large mammals in the period from MIS 17 to MIS 11 or MIS 9. Generally, localities with vertebrate fauna of the period between MIS 17 and MIS 11 are very rare in Poland (Nadachowski et al., 1989).

4.7. Late Middle Pleistocene – Late Pleistocene (Aurelian, post Galerian, MNQ2)

The last part of the Pleistocene (0.4 Ma till the beginning of the Holocene) was characterised by appearance of many extant species. At the end of the Cromerian, as a result of the considerable climate cooling between 480 and 400 ka (MIS 12), and at the beginning of the Aurelian, the Villafranchian taxa became extinct; also some Cromerian species disappeared: *Premegaceros verticornis*, *Megaloceros savini*, more ancestral subspecies of *Cervus elaphus* and the roe deer *Capreolus suessendorbensis*. Modern members of the red deer *Cervus elaphus angulatus* and *Cervus elaphus spelaeus*, roe deer *Capreolus priscus*, fallow deer, elk *Cervalces* sp. and *Alces cf. alces* appeared. There is noteworthy coexistence in Europe and Asia of two fallow deer species, i.e. *Dama clactoniana* and *Dama dama* (Di Stefano and Petronio, 1998b), and elks, i.e. *Cervalces latifrons* and *Alces alces* (Kurtén, 1968; Azzaroli, 1981, 1985, 1994; Churcher and Pinsof, 1987; Kahlke, 1990; Boeskorov, 2001; Breda and Marchetti, 2005; Breda, 2008; Nikolskyi, 2010).

Other European localities of this age are: Ehringsdorf, Ariendorf 3, Neumark Nord (Germany), Acquedolci (Italy – MIS 7–6), ?Vaufrey (France – MIS 7 or MIS 6), La Fage (France, MIS 7), and a part of layers from Kudaro Cave (Caucasus, MIS 10/9–MIS 7) (Baryshnikov and Nikolayev, 1982; Delpech, 1988; Turner, 1990; Baryshnikov, 1993; Gliozzi et al., 1997; Pfeiffer, 1998; Van der Made, 2004, 2010a-d, Van der Made et al., 2014).

The presence of *Cervalces* dates these layers to the end of the Middle Pleistocene. The last representative of *Cervalces* in Poland was *Cervalces* sp., which was present since the Odra Glaciation (Saalian).

A roe deer species, *Capreolus priscus*, not recorded from earlier periods in Poland, was relatively abundant at that time (Tables 4 and 5).

The giant deer *Megaloceros giganteus* (Vislobokova, 1990, 2011,

2012a, b, Lister, 1994; Gliozzi et al., 1997; Sardella et al., 1998; Palombo and Valli, 2003–2004; Made and Tong, 2008; Made et al., 2014) appeared and spread widely during this time period, but became extinct at the end of the Pleistocene in Europe and in the Holocene in Asia. The elk *Cervalces latifrons* migrated into North America through Beringia and became widespread there, but disappeared at the Pleistocene/Holocene transition both in Asia and North America. The genera *Axis*, *Cervus (Rusa)*, *Elaphurus*, *Muntiacus*, *Rangifer* and *Sinomegaceros* continued to exist in Europe and Asia. Representatives of the latter disappeared at the end of the Pleistocene in Asia. Numerous species of *Axis*, *Cervus*, *Dama*, *Elaphurus*, *Rangifer* and *Rusa* changed their ranges of distribution (Vislobokova, 1990).

The cervid community of the glacial and interglacial periods differ significantly from one another. During interglacial cycles, the red deer was the most abundant species, followed by the reindeer. In Poland cervid remains are particularly abundant from layers dating to the onset of the Odra Glaciation (Drenthe, MIS 6) as well as to the following Eemian Interglacial. In Poland, Biśnik, Nietoperzowa and Jasna Smoleńska caves provided rich collections of cervid remains of these time periods. During the Odra Glaciation reindeer increased in abundance, outnumbering forest-dwelling taxa, such as the red deer and roe deer. During the Eemian Interglacial, the reindeer still persisted, while the roe deer grew significantly more abundance, and the elk rarer (Stefaniak, 2015) (Tables 4 and 5).

4.8. Late Pleistocene (Aurelian, MNQ2)

During the last glaciation two related elk species, *Cervalces latifrons* and *Cervalces scotti* (Lydekker, 1898), occurred in North America, but they were geographically and ecologically separated one from another by the interposition of mountain ranges and of the Wisconsin ice sheet (Churcher and Pinsof, 1987; Guthrie, 1995).

The fallow deer *Dama dama* has a wider ecological tolerance than the older *Dama clactoniana*; in fact, it inhabited not only deciduous forests, but also mixed and coniferous ones together with open areas (Czyżewska, 1964). As suggested by Di Stefano (1996), as well as by Di Stefano and Petronio (1998b), the south-easternmost populations of *Dama clactoniana* gave origin to the Mesopotamian fallow deer (*Dama mesopotamica*), which during the Late Pleistocene was widely distributed in the Near East, extending to northern Iraq and southern Caucasus, Anatolia and north of Egypt. *Dama dama* finally replaced *Dama clactoniana*, which survived only to the Eemian. *D. dama* is present only at one Polish locality from the Eemian, which contrasts with findings in Western Europe, where this species is much more numerous (Di Stefano and Petronio, 2002) (Table 4) Its size was similar to that of fallow deer from the Middle Pleistocene site Neumark-Nord (Badura et al. 2017).

In the Polish sites from the Last Glacial Period, *Rangifer tarandus* is a dominant cervid. Its number increased at the beginning of this period and reached maximum in the LGM (Tables 4 and 5). This reindeer was intermediate in size between smaller West European forms and bigger East European representatives (Stefaniak, 2015). *R. t. arcticus* Richardson, 1829 dominated in Poland, whereas remains of another subspecies, *R. t. tarandus* (Linnaeus, 1758) are rare (Stefaniak, 2015).

Red deer *Cervus elaphus simplicidens* was less numerous than reindeer. Its remains increased only in the Interplenivistulan. In Poland during the Eemian, another deer subspecies also occurred, i.e. *C. e. spelaeus* but in the last glacial only *C. e. simplicidens* occurred. Its size is typical of this subspecies from other regions of Europe (Van der Made et al., 2014; Stefaniak, 2015).

The giant deer is relatively numerous in the territory of Poland beyond MIS 4. It reached the largest number in the Interplenivistulan (MIS 3). In Polish localities, the remains of *Megaloceros giganteus germaniae/ruffi* were found, whereas in Western Europe, *Megaloceros giganteus giganteus* (Blumenbach, 1799) occurred in a larger number. Based on the osteometric analyses, we can state that the Polish forms

were less massively built than those from Western Europe (Croitor et al., 2014; Van der Made et al., 2014; Stefaniak, 2015).

The modern roe deer occurred in the Vistulian very rarely. It was more numerous at the beginning of the glacial. *Capreolus capreolus* was not present in the periods of the ice sheet expansion and occurred in the Interplenivistulian as well as at the end of the glacial or only in the Holocene. More precise radiocarbon dating is necessary to solve this issue. The forms from the Vistulian Glaciation are close in size to those from the European localities of that period (Van der Made et al., 2014; Stefaniak, 2015).

At the Late Pleistocene/Early Holocene transition the elk *Alces alces* migrated into North America, where it replaced *Cervales latifrons*. The American counterpart of elk *Cervales scotti* also became extinct at that time (Heintz and Poplin, 1981; Azzaroli, 1983, 1985; 1994; Bubenik, 1986; Czyżewska, 1987; Guthrie, 1995; Kahlke H. D., 1990; Boeskorov, 2001; Nikolskyi, 2010).

4.9. Holocene (MIS 1)

At the beginning of Holocene, *Alces alces* reached its maximum distribution range; then, from the end of Boreal period, its range gradually began to shrink. With the expansion of deciduous forests and the climate warming of the Atlantic period, this species became extinct in South-Western Europe, persisting only in Central Europe. Human encroachment and climate changes led the elk to extinction in most of its earlier range at the end of Middle Age (Szymczyk, 1973a-c; Schmölcke and Zachos, 2005). At present, a slow westward expansion of the species is observed, and its limit of distribution runs across Poland (Szymczyk, 1973a-c; Schmölcke and Zachos, 2005; Stefaniak, 2015).

Other cervid species (red deer and roe deer) together with the wild boar dominate in the Holocene in Poland. Roe deer is much less numerous than red deer and wild boar (Wiszniewska, 1986; Wyrost, 1989, 1994; Wyrost and Chrzanowska, 1985 a-c).

In historic times, man largely affected the distribution and evolution of cervids. Decisive factors were the profound environmental changes resulting from land cultivation and animal breeding and hunting, which caused changes in the abundance and distribution of the species. Moreover, various cervids adapted to living in agricultural or other anthropogenic habitats (e.g. parks). Man also deliberately introduced various species (e.g. fallow deer in Central Europe, sika deer in Central and Eastern Europe, etc.; Nowak, 1991).

Most cervid remains were found in archaeological sites, in deposits dating to the end of the Middle Pleistocene, to the time of the Vistulian Glaciation and to the Holocene. Cervids were hunted by Palaeolithic and modern hominins, as indicated by numerous human-derived traces left on the bones. They provided not only meat and skins, but also raw material, such as antlers and bones, to make tools and ornaments; numerous images and burials of cervids may suggest that they were also objects of cult (Czyżewska and Usnarska, 1980; Wiszniewska, 1986; Wiszniewska et al., 2002; Cyrek, 2002; Wojtal, 2007; Cyrek et al., 2010, 2014). Cervids were also preferred targets for carnivores, as indicated by gnawing and digestion traces on the bones (Cyrek, 2002; Wojtal, 2007; Stefaniak and Wojtal, 2012).

5. Conclusions

Although fossils of cervids from Polish territory are not as numerous as those of small mammals, they are an important component of Neogene and Pleistocene fauna. They are also more abundant than perissodactyls and proboscideans as well as bovids. Therefore, they can be useful in palaeofaunistic, palaeoclimatic and palaeoenvironmental reconstructions as well as setting biochronology of both Neogene and Pleistocene sites in Poland; in some cases, they can be used even to date particular levels. They importantly enrich the European cervid fossils, especially from poorly recorded periods, Pliocene and Early Pleistocene.

The earliest cervid remains known in Poland date back to the Middle Miocene (zone MN 7–8) and belong to *Euprox furcatus*, a typical species of that time. The next oldest cervid remains date to the Early Pliocene (MN 15) and imply a warm and humid climate. Moreover, they indicate the presence of habitats with mixed and park forests, as well as open areas. These taxa (*Muntiacus polonicus*, *Praeelaphus warthae*, *Arvernoceros cf. ardei*, *Procapreolus moldavicus*) were also found in other sites of Central and Eastern Europe, but not in Western Europe (Table 4). It suggests more intense migrations of these cervids between the territory of Poland and the former regions than the latter. The Late Pliocene cervid remains in Poland are known only from one locality, i.e. Węże 2. It yielded evidence of 4 cervid taxa characteristic of zone MN 16: *Croizetoceros ramosus*, *Metacervocerus pardinensis*, *Arvernoceros cf. ardei* and *Procapreolus moldavicus*. The first two were reported from older deposits (MN 15) in Western and Eastern/Southern Europe, respectively, but not in Poland. It can suggest that these species migrated to Poland at the end of Pliocene. In contrast, the last two species are known from the older site Węże 1 in Poland and Węże 2 is their last occurrence. *Croizetoceros ramosus* and *Procapreolus moldavicus* from this site were somewhat larger than the Western European representatives of their genera. The cervids from Węże 2 were found in other sites of a similar age in the whole Europe, which indicates that these regions were faunistically related and characterised by similar environmental conditions (Table 4).

The cervid fauna found at Rębielice Królewskie is represented by two cervids: *Croizetoceros ramosus* and a representative of the genus *Eucladoceros*. The presence of a younger subspecies *Croizetoceros ramosus medius* dates this site to the Pliocene and Pleistocene boundary (MN 16/17). This taxon is a Pliocene holdover, which was also reported only in Western Europe, but not in areas located east and south of Poland. On the other hand, *Eucladoceros* is a cervid that was widespread at that time in the whole Europe (Table 4).

Early Pleistocene cervids found in Żabia Cave are characteristic of other European sites from the Late Villafranchian. The Polish fauna also witnessed considerable changes associated with climate cooling. Taxa from the Early Villafranchian became extinct and were replaced by those that survived into later periods of the Quaternary. The most abundant cervid was *Dama cf. farnetensis*, the only member of genus *Dama* in the Pleistocene of Poland. Large cervids were represented by one of the earliest elks, *Cervales carnutorum*; it is the earliest occurrence of elk in Poland. Żabia Cave also documents the earliest occurrence of the genus *Capreolus* in Poland (Table 5).

The infillings of Kozi Grzbiet and Sítkówka near Checiny provided early Middle Pleistocene cervid remains typical of other European sites of the comparable age (MIS 19–17, the Podlasian Interglacial, Cromerian II–III). This site records the first occurrences of *Cervus elaphus* ssp., *Praemegaceros verticornis*, *Cervales latifrons* and *Capreolus suessenbornensis* in Poland. *P. verticornis* was found in Western, Central and Eastern Europe but was not reported in southern parts of the continent, where other species of this genus were found, i.e. *P. solilhacus* and *P. pliotarandoides* (Table 4).

Cervids are not recorded in deposits of the MIS 16–12 age in Poland but are present in numerous localities of the later periods, from the Late Middle Pleistocene to the Holocene. The composition of the cervid assemblages generally corresponds well to those in other European sites of the same age. However, *Capreolus priscus* and *Capreolus capreolus* was reported in the Middle and Late Pleistocene sites in Poland, Western Europe and Italy as well as other Central European sites of the Late Pleistocene, but not in Eastern and Southern Europe. Similarly, *Alces alces* and *Rangifer tarandus* remains were not reported from the Pleistocene sites in Southern Europe. Only in the Holocene, these species have been widely distributed in the whole continent. It may indicate that not all regions of Europe offered the same optimal conditions in the Pleistocene for all cervid species. The territory of Poland was more similar to Western Europe in this respect (Table 4).

Rangifer tarandus appeared in Poland during MIS 11 or 9

(Bełchatów) and was the dominant cervid from the Late Pleistocene (the Świecie Stadial, Older Plenivistulian) till the beginning of the Holocene, replaced in abundance by the red deer *Cervus elaphus*. *Cervus elaphus angustidens*, earliest recorded in Bełchatów, survived till the end of Middle Pleistocene. Then in MIS 8, the large size red deer *Cervus elaphus spelaeus* appeared, which was replaced by a smaller subspecies, *Cervus elaphus simplicidens*, existing from the Eemian Interglacial till MIS 3. Since MIS 2, remains of the modern red deer are reported. An important component of the Pleistocene fauna was the giant deer, which is represented since MIS 8/7-7 till MIS 1 by two subspecies, *Megaloceros giganteus germaniae* and *M. g. rufi*. *Cervalces* sp. and *Capreolus priscus*, which were present since MIS 7-6 till the Eemian Interglacial, are important for the biochronology of Biśnik Cave, because they date cave's strata to the end of the Middle Pleistocene (Tables 1 and 5).

The modern elk *Alces alces* and the fallow deer *Dama dama* appeared in Poland in the Eemian Interglacial. The fossils of *Alces alces* are important from biochronological point of view, because this species occurred also in Europe in the same time. The distribution of the elk in Poland shrank considerably in the Late Pleistocene. A few localities with remains of this species date to the beginning of the last glaciation and the Interplenivistulian. A roe deer, *Capreolus priscus* occurred since MIS 7 to the Eemian Interglacial. After that it was replaced by a modern species *Capreolus capreolus*. Likewise, the roe deer, though initially more abundant than the elk, became increasingly rare; like the elk, it disappeared in the consecutive cold periods of the Vistulian and was scarce in the Interplenivistulian. The presence of recent elk and roe deer in Interplenivistulian layers indicates warming of climate and return of forest communities, as well as confirms the age of these deposits.

Considerable changes in the cervid fauna took place at the Pleistocene/Holocene transition. The giant deer became extinct, while the reindeer retreated to Northern Europe and Asia. The elk was the first to recolonise Poland, followed by the red and roe deer. Since the Middle Holocene, the abundance of the elk decreased, and the red deer and roe deer became the dominant species.

Human-derived modifications of cervid bones are met more frequently from the Middle Palaeolithic onward, indicating that cervids had the undesirable privilege of being one of the hominins' most popular prey. Cervids were becoming important sources of food and raw materials. During the Holocene, the increasing human impact on the environment, due to the development of agriculture, forest exploitation, hunting and the introduction of alien cervid species, such as the fallow deer and the sika deer, had significant consequences on cervid populations. The preserved faunal assemblages show that the Cervidae are very sensitive to environmental changes and reflect well the climate evolution of Poland and in general of Central Europe.

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Appendix A. Supplementary data

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