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MORPHOMETRIC VARIATION OF REINDEER REMAINS (*RANGIFER TARANDUS* LINNAEUS, 1758) FROM LATE PLEISTOCENE CAVE LOCALITIES IN POLAND

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Abstract: The paper deals with the morphometric analysis of remains of the reindeer *Rangifer tarandus* Linnaeus, 1758 from 20 Late Pleistocene cave localities in Poland. In most of the localities, the species was the most abundant component of the large mammal fauna; the remains came from individuals, killed by predators, including man. The measurements of the remains were compared with those of reindeer from localities in Germany, Moldova, Ukraine and Russia. The measurements of the reindeer from Poland were intermediate between the smaller and more slender reindeer from north-western Europe and the larger reindeer from southern and eastern Europe; the antlers from the localities studied mainly represented the tundra form of *Rangifer tarandus*. The forest form of the species was represented by a few antlers. With respect to the ages of individuals, the reindeer from the Polish sites belonged to the age classes of under 2 years, 5–6 years and 6–7 years.

Key words: *Rangifer tarandus*, morphometry, Late Pleistocene, Poland.

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INTRODUCTION

During the Vistulian (Weichselian) Glaciation, the reindeer was a typical representative of the periglacial fauna in Eurasia. Its distribution range extended from northern Spain and the British Isles in the west, through Central Europe and the European part of Russia, to Siberia and Beringia in the east (Markova *et al.*, 1995; Kahlke, 1999). At the end of the main stadial of the Vistulian, the reindeer colonised new areas, which previously had been covered by the ice-sheet. Numerous remains of *Rangifer tarandus* Linnaeus, 1758 were found in Poland (Kowalski, 1959; Czyżewska, 1989). At the end of the Pleistocene, the reindeer was the most common ungulate in northern Poland.

Apart from the paper by Czyżewska and Usnarska (1980), there is no comprehensive morphometric analysis of reindeer remains from Poland in recent literature. This paper is an attempt to fill this gap. Its objective was to present, for the first time, a complete morphometric analysis of the species' remains from cave sites of Late Pleistocene in Poland. Unfortunately, at the present stage of such studies, most of the reindeer fossil record comes from sites of unknown or unclear stratigraphy, thus precluding detailed, statistical comparisons and recognition of morphometric variation, associated with environmental changes and the time of deposition. Most of the finds from Poland (Table 1) come from the Grudziądz Interstadial, MIS 3.

GEOLOGICAL SETTING

The material of *Rangifer tarandus* examined comes from sites, located in the Kraków–Częstochowa Upland (Cave IV in Birów Hill, the caves Komarowa, Deszczowa, Dziadowa Skała, Nietoperzowa, Stajnia, Jasna Strzegowska, Jasna Smoleńska, Skałka Łysa z Bramą, Schronisko Pośrednie, Lisia Jama Górna, Łokietka, Wschodnia, Mroczna), Obłazowa Cave in the Orawa–Nowy Targ Basin, Raj Cave in the Holy Cross Mountains and Naciekowa and Północna Duża caves in the Kaczawskie Mountains.

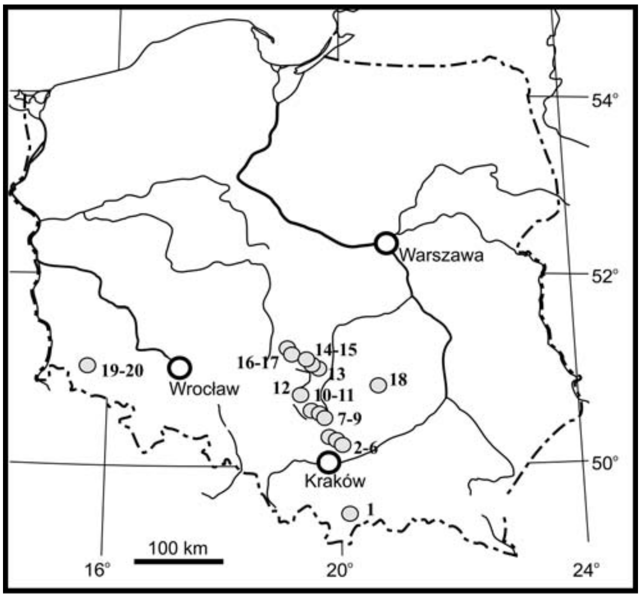

Fig. 1. Reindeer sites in Poland. 1. Obłazowa Cave; 2. Zbójecka Cave; 3. Nietoperzowa Cave; 4. Łabajowa Cave; 5. Łokietka Cave; 6. Koziarnia Cave; 7. Jasna Strzegowska and Lisia Jama caves; 8. Mroczna Cave in Pośrednica; 9. Rock shelters near Strzegowa I and II; 10. Zegar Cave; 11. Jasna Smoleńska Cave; 12. Cave IV in Birów Hill; 13. Cave in Dziadowa Skała; 14. Deszczowa Cave; 15. Stajnia Cave; 16. Shelter III in the Sokole Hills; 17. Komarowa Cave; 18. Raj Cave; 19. Północna Duża Cave; 20. Naciekowa Cave

Localities

The remains of the species came from 20 cave localities in the Kraków–Częstochowa Upland, Nowy Targ Basin, Holy Cross Mountains and Kaczawskie Mountains (Fig. 1). All the remains came from deposits, dated as Late Pleistocene (Eemian Interglacial, various phases of the Vistulian Glaciation).

Obłazowa Cave (Jaskinia Obłazowa; 49°25′N/ 20°09′E) (Late Pleistocene – Holocene, Early and Middle Vistulian – Holocene, MIS 5a–d – MIS 1). Obłazowa Cave is situated in Obłazowa Cliff (Skała Obłazowa), in the southwestern part of it, on the River Białka in the Pieniny Mountains. The excavations started in 1985 and are still continuing. Layer VIII (Gravettian) contained a complex of Gravettian stone artefacts, some human remains and a famous boomerang-shaped object, made from mammoth tusk (Valde-Nowak *et al.*, 1987). The diverse complex of 22 layers, uncovered during the exploration, included sands, cave loams with varied content of limestone rubble and gravels, deposited from the Early Glacial until the Holocene. The excavations yielded numerous mollusc and vertebrate remains; these were the subject of numerous publications (e.g., Valde-Nowak *et al.*, 1995, 2003).

Zbójecka Cave (Jaskinia Zbójecka; 50°1′N/19°4′E) (Late Pleistocene – Holocene, Vistulian – Holocene). The cave is situated in the Sąspowska Valley (Dolina Sąspowska) in the Jamki Gorge (Wąwóz Jamki), in the Ojców National Park. Preliminary excavations were conducted by J. Zawisza in 1871. In 1872, the deposit was exploited for manure by O. Grube; he gave the bone remains to F. Römer, who analysed them (Römer, 1883). Unfortunately, there is no information on the stratigraphy and chronology of the site.

Nietoperzowa Cave (Jaskinia Nietoperzowa; 50°11′N/ 19°46′E) (late Middle Pleistocene – Holocene, Saalian – Holocene, Q3 – Holocene, MIS 6 – MIS 1). The cave is located in the upper part of the Będkowska Valley (Dolina Będkowska), in the Kraków Upland. Nietoperzowa Cave contains spacious, horizontal chambers and is among the longest caves in the Kraków–Częstochowa Upland (326 m long). The excavations in the cave started in the 19th century. Earlier, the deposits had been excavated for manure. In 1956–1963, excavations were carried out by W. Chmielewski's team (Chmielewski, 1975). The deposits in the cave include 17 layers, mostly with bone remains and archaeological artefacts. The stratigraphy, from the end of the Warta Glaciation (Saalian) and certainly from the Eemian Interglacial to the Holocene has been described, among others, by Madeyska-Niklewska (1969), Chmielewski (1975) and most recently by Krajcarz and Madeyska (2010). The archaeological artefacts include Middle and Upper Palaeolithic finds. Among others, the Jerzmanowice culture was first described from this cave (Chmielewski, 1975). The few faunistic papers have dealt with both small and large mammals (Kowalski, 1961; Wojtal, 2007).

Łabajowa Cave (Jaskinia Łabajowa; 50°11′N/ 19°46′E) (Late Pleistocene – Holocene, Early Vistulian – Holocene, MIS 5d – MIS 1). The cave is located at Bębło (commune Wielka Wieś). It is situated in a group of cliffs called Łabajowa Cliff (Łabajowa Skała), in the upper part of the Będkowska Valley, at the confluence of three gorges. The length of the cave is 40 m, and the entrance is at 410 m a.s.l. (Römer, 1883; Kowalski, 1951; Szelerewicz and Górny, 1986).

Łokietka Cave (Jaskinia Łokietka; 50°13'N/19°48'E) (Late Pleistocene – Holocene, Early Vistulian – Holocene, MIS 5d – MIS 1). Łokietka Cave is situated on Chełmowa Hill (Góra Chełmowa) in the Valley of Prądnik in Ojców National Park. The cave is 320 m long. The excavations were started by J. Zawisza and S. Czarnocki. The 20th century excavations began in 1998. During the work, eight to five layers of cave loams, loess and humus were uncovered in two profiles. On the basis of the archaeological finds and bone remains, the stratigraphy was estimated as the Eemian, various phases of the Vistulian and the Holocene. The archaeological artefacts represented various Palaeolithic cultures (Micoquian–Prondnikian, Levalloisian–Mousterian, Jerzmanowician) (Lipecki *et al.*, 2001; Wojtal, 2007).

Koziarnia Cave (Jaskinia Koziarnia; 50°13′N/ 19°48′E) (Late Pleistocene – Holocene, Early Vistulian – Holocene, MIS 5d – MIS 1). The cave is located in Ojców, in the Sąspowska Valley in Ojców National Park. Like in Nietoperzowa Cave, the deposits were exploited for manure. The excavations were conducted by W. Chmielewski in 1958–1963. The profile studied was composed of 21 layers of cave loams, with rubble of a diverse nature, sands and Holocene humus. The deposits contained numerous animal remains and archaeological artefacts from the period of the Jerzmanowician and Micoquian–Pradnikian cultures. The stratigraphy and a preliminary description of the animal re-

Table 1

List of reindeer remains from sites studied in Poland

Site	Mandible	Teeth	Antler fragments	Humerus	Radius & ulna	Metacarpus	Carpal bnes	Femur	Tibia	Metatarsus	Tarsal bones	Phalanx I	Phalanx II	Phalanx III	Fragments of bones	TOTAL
Obłazowa Cave MIS 5a-d; MIS 5a–d – MIS 4		9											1		1	11
Obłazowa Cave MIS 4 – 3; MIS3		11					3			1	1	1		2		19
Obłazowa Cave MIS 3–2; MIS 3–1	1	4									1					6
Obłazowa Cave MIS 2–1		5										3				8
Zbójecka Cave MIS ?						1										1
Nietoperzowa Cave MIS 5e – MIS 5c		5	1	1			3				5	2	3		2	22
Nietoperzowa Cave MIS 4; MIS 3/MIS 4			2				3				1	1	1			8
Nietoperzowa Cave MIS 3		12					5				6	3	3			29
Łabajowa Cave MIS ?						1										1
Łokietka Cave MIS 5a–e		6					3		2		4					15
Łokietka Cave MIS1		1														1
Koziarnia Cave MIS ?				1												1
Jasna Strzegowska Cave MIS 6 – MIS 5e; MIS 5c, d			3		1							1			1	6
Jasna Strzegowska Cave MIS 3–1		5	2			2		2	4	1	5	3				24
Jasna Strzegowska Cave MIS 1		2		1					1		1					5
Jasna Strzegowska Cave MIS ?		1														1
Lisia Jama Cave MIS 3 – 1		1	3	1	3			1			5	2			1	17
Wschodnie Rock Shelter MIS ?		5	7		2			2	3			1			1	21
Mroczna Cave MIS ?					1					2					2	5
Cave IV in Birów Hill MIS 3-2		99	325	12	30	24	32	2	12	25	46	58	26	3	6	700
Cave IV in Birów Hill MIS2; MIS 2 – MIS 1		1	17			1	2	4			2		2		1	30
Jasna Smoleńska Cave MIS 2 – MIS 1					1											1
Zegar Cave MIS 5d – MIS 3		16	2	1						1						20
Cave in Dziadowa Skała MIS 5e; MIS 5a–d – MIS 3		3	2		2	1	1				1	2				12
Cave in Dziadowa Skała MIS 3 – 2		10				2	8				9	8	4		1	42
Cave in Dziadowa Skała MIS 2 – 1		1				1	4				3	4	2		2	17
Deszczowa Cave MIS 4; MIS 4 – 3		1					1				1			1		4
Deszczowa Cave MIS 3 – MIS 2		44	57	1	6	4	22		5	2	33	12	20	7	3	216
Rock Shelter in Sokole Hills MIS ?		5	3			1				2	1	4				16
Komarowa Cave MIS 5a–d														1		1
Komarowa Cave MIS 4; MIS 4/ MIS 3		21				4	4				2	3	3	2		39
Komarowa Cave MIS 3-2; MIS 3; MIS 2		176	1		3	12	19		6	7	44	33	21	17		339
Komarowa Cave MIS 2-1; MIS 1		7	3		1	2	5			1	3	2	3	1		28
Stajnia Cave MIS 4			5			1	1			1						8
Stajnia Cave MIS 3; MIS 3/ MIS 2		18	75	2		6	9	11	6	1	9	5	4	1	1	148
Stajnia Cave MIS 2		36	11		1	2	1	2		2	3	3	1			62
Stajnia Cave MIS 1		22	15		4	2		4	1	1	7	9				65
Stajnia Cave MIS ?		45	14		1	3	1	1	1	3	2	5	1			77
Naciekowa Cave MIS ?											1					1
Północna Duża Cave MIS ?	1															1
Raj Cave MIS 4; MIS 4/ MIS 3		47	551	2	6	1	16	2	4	2	12	14	1		2	660
Raj Cave MIS 1			4								1		1			6
Łysa z Bramą Rock Shelter MIS ?		6	1	1					1			2				11
TOTAL	2	625	1104	23	63	37	143	31	46	51	211	183	98	35	24	2704

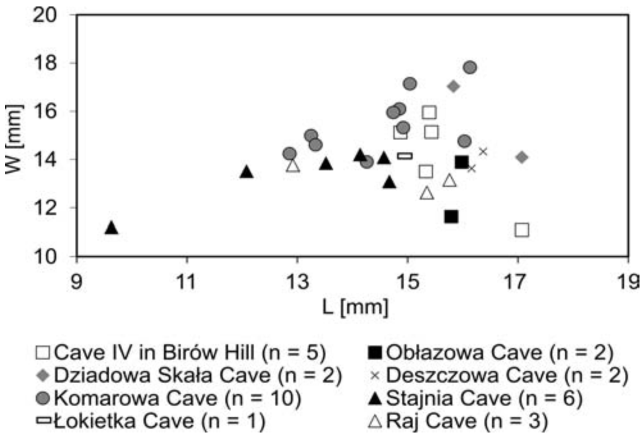

Fig. 2. Measurements of P_4 of *Rangifer tarandus* from the Polish sites

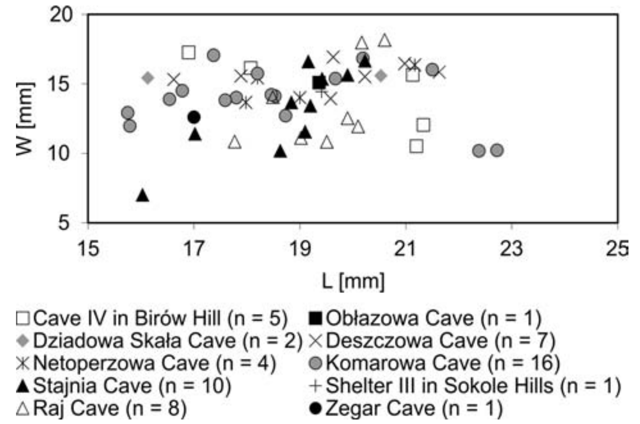

Fig. 3. Measurements of M_3 of *Rangifer tarandus* from the Polish localities

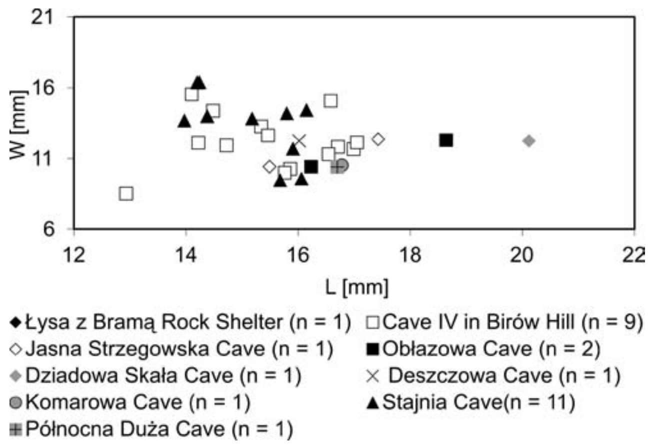

Fig. 4. Measurements of P_4 of *Rangifer tarandus* from the Polish localities

mains and archaeological finds are in Römer (1883), Kowalski (1951), Chmielewski (1958), Madeyska-Niklewska (1969) and, above all, in Chmielewski *et al.* (1967).

Group caves: Jasna Strzegowska (Jaskinia Jasna Strzegowska) and **Lisia Jama caves, Wschodnie Rock Shelter** (Schronisko Wschodnie), (50°2´N/19°4´E) (end of Middle Pleistocene – Holocene, Saalian – Holocene, MIS 6 – MIS 1). Jasna Strzegowska Cave and Wschodnie Rock shelter are situated in the Jamy Cliff, near the village of Strzegowa Kolonia. They have been known for a long time. In 1947–1949, L. Sawicki conducted systematic excavations in the area. In 1991, K. Cyrek examined Jasna Cave to verify Sawicki's results. Its deposits (8 strata) were similar to those in Biśnik Cave, composed of a series of cave loams, loess, sands and humic levels. During the excavations, in addition to bone remains, numerous flint artefacts were found, representing the Palaeolithic (Mousterian Aurignacian, and Gravettian) and one Neolithic level (Sawicki, 1949, 1953; Mirosław-Grabowska and Cyrek, 2009; Stefaniak *et al.*, 2009).

Mroczna Cave in Pośrednica (Jaskinia Mroczna w Pośrednicy; 50°2´N/19°4´E) (Late Pleistocene – Holocene, Middle Vistulian – Holocene, MIS 3, 2 – MIS 1). Mroczna Cave is located in Pośrednica Hill (Góra Pośrednica) near Strzegowa. As at Jasna Strzegowska Cave, the deposits were excavated by L. Sawicki in 1949. He found a thick deposit, composed of loess and Holocene humus with bone remains.

Rock Shelters near Strzegowa I and II (Zaciszna Cave, Pod Oknem Cave – Jaskinia Zaciszna, Jaskinia pod Oknem, Łysa z Bramą Rock Shelter; 50°2´N/19°4´E) (Late Pleistocene – Holocene, Late Vistulian – Holocene, MIS 3, 2 – MIS 1). These rock shelters are located in the so-called Skałka Łysa z Bramą, near the village of Strzegowa. The deposits were excavated by Sawicki in 1949.

Jasna Smoleńska Cave (Jaskinia Jasna Smoleńska; 50°2´N/19°4´E) (Late Pleistocene – Holocene, Late Vistulian – Holocene, MIS 2 – MIS 1). The cave is located in the Wodąca Valley (Dolina Wodącej) near the village of Smoleń in the summit part of the Zegarowe Cliffs (Skały Zegarowe). L. Sawicki discovered traces of a Neolithic flint workshop in the cave. Preliminary excavations were conducted by B. Muzolf in 1997–1998. They revealed layers of loess and Holocene humus, with few archaeological artefacts (Palaeolithic, Neolithic, Bronze Age and Middle Ages), and animal bone remains (Muzolf, 1999; Wiszniowska, *et al.*, 2001, 2002, 2004; Stefaniak *et al.*, 2009).

Zegar Cave (Jaskinia Zegar; 50°25´N/19°40´E) (Late Pleistocene – Holocene, Early Vistulian – Holocene, MIS 5d – MIS 1). The cave is situated within the Zegarowe Cliffs, in the Wodąca Valley, near Smoleń. The first references to Zegar Cave date back to the 19th century. Like in many caves in the area, part of the deposits was transported to the nearby fields, and bones and archaeological artefacts were found in it. In 1997–1998, excavations were conducted by B. Muzolf. As a result, profiles were uncovered both within the cave and in front of it. The deposits inside the cave were composed of seven strata of cave loams, silts, sands, humus and dripstones. At the front, cave profiles of loess and humus were uncovered. The archaeological finds included Middle-Palaeolithic (Micoque–Prondnikian), Upper-Palaeolithic, Neolithic, Bronze Age, Roman period and Medieval tools. Animal remains were numerous (Muzolf, 1999; Wiszniowska, 1999; Wiszniowska *et al.*, 2001, 2002, 2004; Stefaniak *et al.*, 2009).

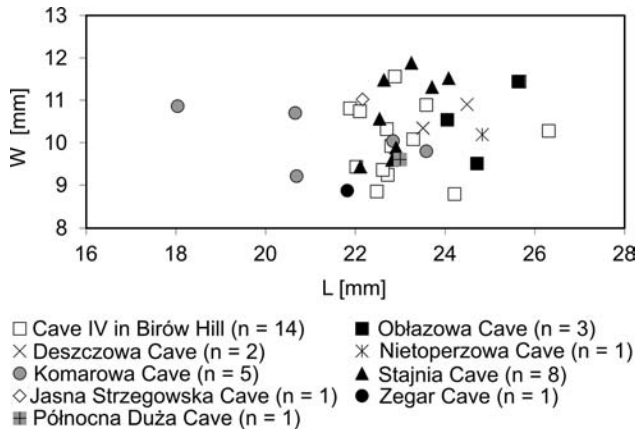

Fig. 5. Measurements of M_3 of *Rangifer tarandus* from the Polish sites

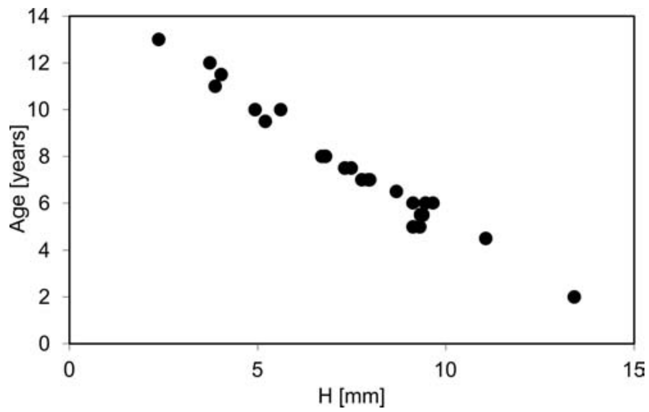

Fig. 6. Age against crown height of M_1 in *Rangifer tarandus* from the Polish sites

Cave IV in Birów Hill (Northern Rock Shelter in Birów Hill; Jaskinia IV na Górze Birów; 50°2´N/19°4´E) (Late Pleistocene – Holocene, Late Vistulian – Holocene, MIS 2 – MIS 1). The rock shelter is located on the northern slope of Birów Hill, near Podzamcze. The excavations in multi-culture localities around Birów Hill (Góra Birów) were conducted by B. Muzolf's team in the 1990s. They explored the deposit in the cave, revealing eight layers of silts, sands, loess and Holocene humus. Several cultural levels were discovered in the cave, from the Upper Palaeolithic (Aurignacian), Neolithic, Bronze Age and Łużyce to Przeworsk and Middle Ages (Mirosław-Grabowska, 1995; Muzolf *et al.*, 2009; Stefaniak *et al.*, 2009)

Cave at Dziadowa Skała (Jaskinia w Dziadowej Skale; 50°32´N/19°31´E) (Late Pleistocene – Holocene, Eemian – Holocene, Q2 – Holocene, MIS 5 – MIS 1). Cave at Dziadowa Skała is a horizontal cave, located in Skały Podlesickie, near the village of Skarżyce. The excavations were carried out by W. Chmielewski between 1952 and 1954. Nine layers were uncovered; their stratigraphy was estimated as the period Eemian interglacial – Holocene (Chmielewski, 1958; Kowalski, 1958; Lorenc, 2008; Stefaniak, *et al.*, 2009). Archaeological artefacts were very rare and represented Middle and Upper-Palaeolithic cultures (Chmielewski, 1958; Cyrek, 2009). Animal remains included numerous birds and mammals (Chmielewski, 1958; Kowalski, 1958; Lorenc, 2008; Wojtal, 2007; Stefaniak, *et al.*, 2009).

Table 2

Age determination based on wear of crown of M_1 of *Rangifer tarandus* from Upper Pleistocene sites in Poland

Site	Inventory number	Crown height (mm)	Age (months)	Age (years)
Cave IV in Birów Hill	GBJ 68/94/74	9.13	72	6
	GBJ 1/93/8	4.93	120	10
	GBJ 96/315/1	9.39	67	5.5
	GBJ 35/93/351	7.49	91	7.5
	GBJ 79/93/314	7.32	90	7.5
	GBJ 11/94/8	9.46	68	6
	GBJ 44/94/1	9.33	66	5.5
	GBJ 13/94/4	9.46	68	6
	GBJ illegible	3.73	140	12
	GBJ 84/7	8.69	78	6.5
	GBJ 2/93/10	7.95	86	7
	GBJ 62/93/1	9.31	59	5
	GBJ 273	2.37	157	13
	GBJ 96/315/1	9.39	67	5.5
	GBJ 35/93/35	7.49	91	7.5
	GBJ 79/93/31	7.32	90	7.5
Deszczowa Cave	81 (MF/23660)	13.41	22	< 2
	44 (MF/2339)	9.13	57	5
Komarowa Cave	5c/145/7	6.81	97	8
	3c/165	3.87	136	11
	16f/180	6.7	96	8
	4c/160/18	7.98	86	7
	13e/215/9	9.66	69	6
	15e/275	4.03	137	11.5
Stajnia Cave	197/94985	5.2	114	9.5
	197/1170	11.06	53	4.5
	197/5141	7.77	88	7
	197/4778	5.61	118	10
Łokietka Cave	No inventory number	6.78	96	8

Deszczowa Cave (Jaskinia Deszczowa; 50°34´N/19°31´E) (late Middle Pleistocene – Holocene, Saalian – Holocene, Q3 – Holocene, MIS 6 – MIS1). The cave is located on the northern slope of Popielowa Hill (Góra Popielowa) in Kroczyckie Hills (Skałki Kroczyckie), in the Częstochowa Upland. It has the form of a narrow karst crevice. The deposits were studied in 1989–1997 (Cyrek, *et al.*, 2000; Cyrek 2009; Krajcarz and Madeyska, 2010). Eleven layers were explored; on the basis of stratigraphic studies and animal bones, the age was estimated as the period from the Warta Glaciation and various phases of the Vistulian, until the Holocene (Cyrek *et al.*, 2000; Madeyska and

Table 3

List of sites with remains of reindeer *Rangifer tarandus*, based on literature review

Country	Locality	Reference
Germany	Gönersdorf	Turner, 1990
	Große Grotte	Weinstock, 1999
	Schweinskopf	Turner, 1990
	Stellmoor	Burdukiewicz, 1986; Bratlund, 1999; Weinstock 2000
	Salzgitter-Lebenstedt	Kleinschmidt, 1953; Behre and Plicht, 1992
	Wannen	Turner, 1990
Moldova	Brinzeni-1	Ganya, 1971; David and Pascaru, 2000; Croitor, 2010
	Cosauţi-1	David *et al.*, 2003; Croitor, 2010
	Rascov-7	Croitor, 2010
	Starye Duruitory	Carotenuto, 2009; Croitor, 2010
Poland	Maszycka Cave	Kozłowski *et al.*, 1993
Ukraine	-	David *et al.*, 2003
Russia	Ural	David *et al.*, 2003
Canada	Pokiak, Kugaluk, Barry	Morrison and Whitridge, 1997

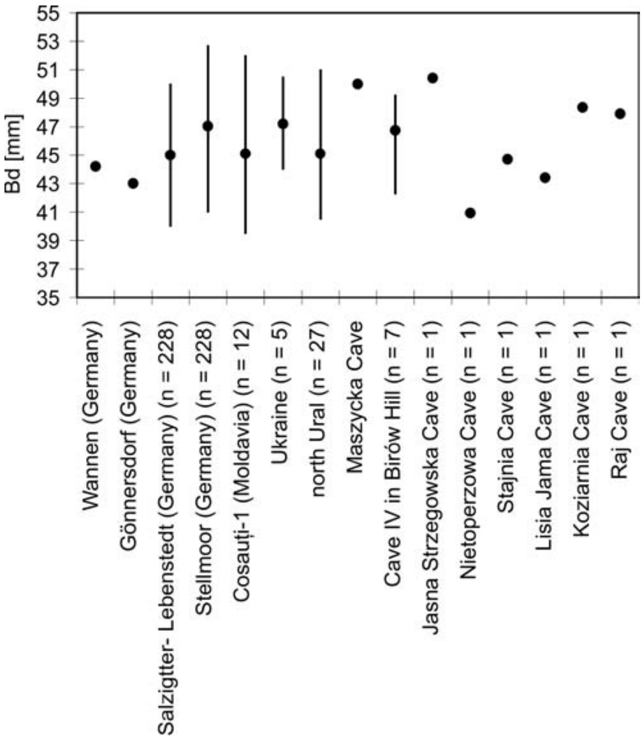

Fig. 7. Width of distal epiphysis of humerus in reindeer from Pleistocene localities of Poland, Germany, Ukraine, Moldova and Russia

Cyrek, 2002; Cyrek, 2009; Nadachowski, *et al.*, 2009; Stefaniak, *et al.*, 2009; Krajcarz and Madeyska, 2010). Traces of human occupancy from the Middle-Palaeolithic to the Mesolithic were found in the cave (Cyrek, *et al.*, 2000; Cyrek, 2009). The deposits contained numerous animal remains (more than 190 taxa), which were characteristic of the end of the Middle Pleistocene, Vistulian and Holocene (Cyrek, *et al.*, 2000; Wojtal, 2007; Nadachowski *et al.*, 2009).

Stajnia Cave (Jaskinia Stajnia; 50°61'N/19°48'E) Late Pleistocene – Holocene, Vistulian – Holocene; ?MIS 5d, MIS 3 – MIS 1). The cave is located in the northern part of the Częstochowa Upland, near Mirów, in the community of Niegowa. The excavations were conducted in 2008–2010 by M. Urbanowski. The deposit, composed of layers of sands, loams with various content of limestone rubble, silts and Holocene humus, contained Middle and Upper Palaeolithic tools, as well as teeth of Neanderthal man and animal remains (Urbanowski *et al.*, 2010)

Rock Shelter III in the Sokole Hills (Rock Shelter Wilcze I, Schronisko w Górach Sokolich III, Schronisko Wilcze I; 50°43´N/19°17´E) (Late Pleistocene – Holocene, Vistulian – Holocene; MIS 3 – MIS 1). The rock shelter is situated in the Sokole Hills in the Puchacz massif, near Komarowa Cave. Preliminary excavations were conducted in 1989–1991 by the team of P. Socha. The deposits were composed of sandy loams, sands and Holocene humus with bone remains; no archaeological artefacts were found (Stefaniak *et al.*, 2009).

Komarowa Cave (Jaskinia Komarowa; 50°43´N/ 19°17´E) (Late Pleistocene – Holocene, ?Eemian, Vistulian – Holocene; MIS 5e – MIS 1). It is located in the Sokole Hills (Częstochowa Upland), on the northern slope of the Puchacz massif. Studies in the cave started in 1997 (Gierliński *et al.*, 1998) and then were conducted by M. Urbanowski until 2001. The complex profile of the cave deposits (16 layers) and the terrace in front of the cave (11 layers) was composed of loams, limestone rubble, sands, silts and humus. The terrace layers were built of eolian sands, limestone rubble, loams, silts and humus. The deposits contained numerous animal remains and artefacts of the Middle (2 phases) and Upper Palaeolithic (several settlement phases), the Neolithic and the Middle Ages. Descriptions of the stratigraphy, fauna and palaeoecology are contained in Gierliński *et al.* (1998), Ochman (2003), Tomek and Bocheński (2005), Rzebik-Kowalska (2006), and Wojtal (2007), and Nadachowski *et al.* (2009) provided details of the taphonomy of the bone remains.

Raj Cave (Jaskinia Raj; 50°49´N/20°30´E) (Late Pleistocene – Holocene, Middle Vistulian – Holocene, MIS 3 – ?MIS 1). It is situated in the valley of the Bobrzyczka strem, near Kielce in the Holy Cross Mountins. It was discovered in 1963/64. The excavations by J. K. Kozłowski revealed 11 strata, composed of cave loams with rubble and sand, silts, sands, humus and dripstones. Two cultural levels (Mousterian) were distinguished in the profile. In addition to the archaeological artefacts, the deposits contained numerous animal remains (Kowalski, 1951; Czyżewska and Usnarska, 1980; Madeyska and Cyrek, 2002; Lorenc, 2008).

Północna Duża Cave (Jaskinia Północna Duża; 50°57´N/19°55´E) (Late Pleistocene – Holocene, Late Vistulian – Holocene, MIS ?3 – MIS 1). It is located in the Kaczawa Mountains, on the north-western slope of Mt. Połom (Góra Połom), in the vicinity of the city of Wojcieszów.

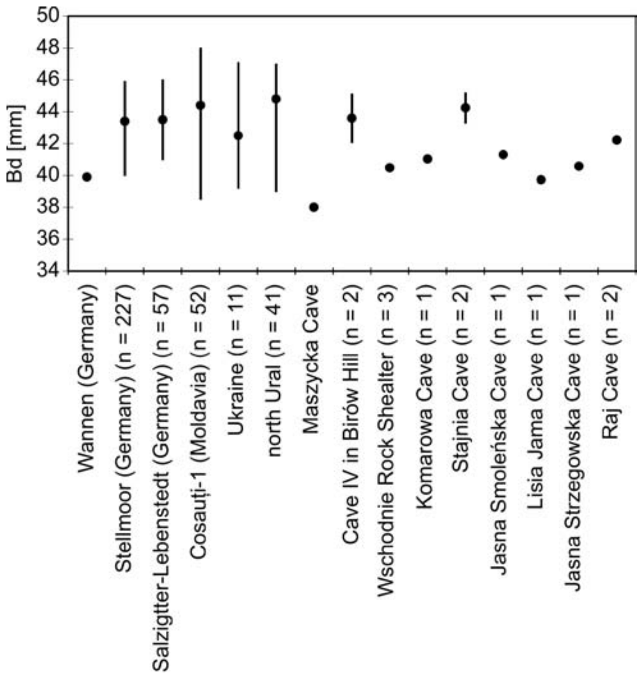

Fig. 8. Width of distal epiphysis of radius in reindeer from Pleistocene localities of Poland, Germany, Ukraine, Moldova and Russia

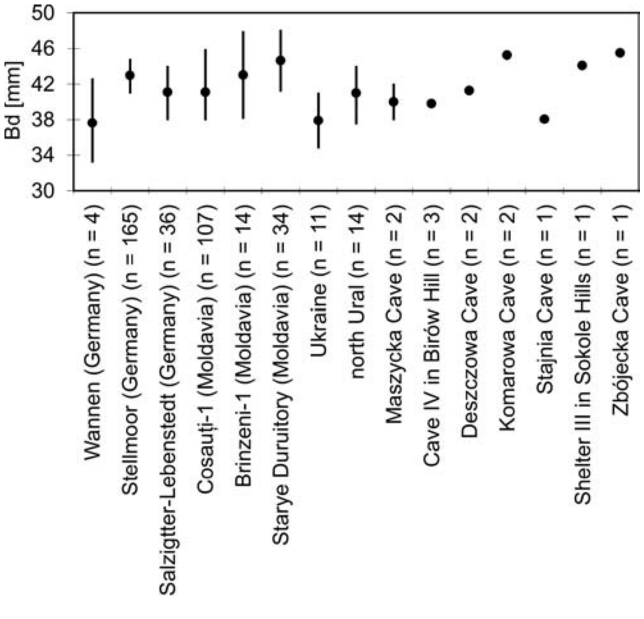

Fig. 9. Width of distal epiphysis of metacarpus in reindeer from Pleistocene localities of Poland, Germany, Ukraine, Moldova and Russia

It was excavated in 1924. The excavations were conducted by L. Zotz (in 1935). The cave deposits (cave loams) contained a few animal remains (Zotz, 1937, 1939; Bieroński *et al.*, 2007; Wiśniewski *et al.*, 2009).

Naciekowa Cave (Jaskinia Naciekowa; 50°56´N/ 15°54´E) (Late Pleistocene – Holocene, Middle Vistulian – Holocene, MIS 3 – MIS 1). The cave, at present no longer in existence, was discovered in 1957 during marble exploitation on Mt. Połom, in the Kaczawa River valley near Wojcieszów. Before it was destroyed, M. Pulina, Z. Ryziewicz and T. Czyżewska removed the bone remains of Pleistocene animals, to this day not analysed in detail (Bieroński *et al.*, 2007).

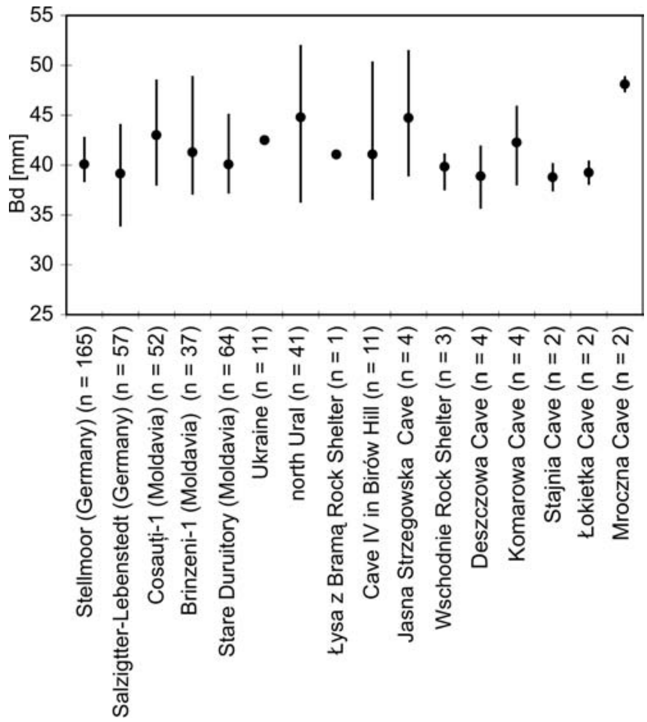

Fig. 10. Width of distal epiphysis of tibia in reindeer from Pleistocene localities of Poland, Germany, Ukraine, Moldova and Russia

MATERIAL AND METHODS

The material included remains obtained in the period from the 1940s to the present. It came from the collections of the Palaeozoology Department, Zoological Institute, Wrocław University (ZPALUWr) and the Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Kraków (MF). A total of 2,704 specimens of bones, antlers and teeth were examined (Table 1). The material included both entire bones and bone fragments, as well as whole or incomplete teeth and antler fragments. Some of the remains show traces of human activities, as well as gnawing by carnivores and rodents; some bones and teeth show traces of digestion. The measurements of the bones, teeth and antlers followed Driesch (1976). The number of bones, teeth and antlers from individual sites is presented in Table 1; the table includes both complete remains and fragments. The measurements of components of the post-cranial skeleton were compared with literature data from selected European sites.

Characteristics of the material

The material was in diverse states of preservation. Most of the bone remains were damaged to different extents. The measurements were taken only from well preserved bones

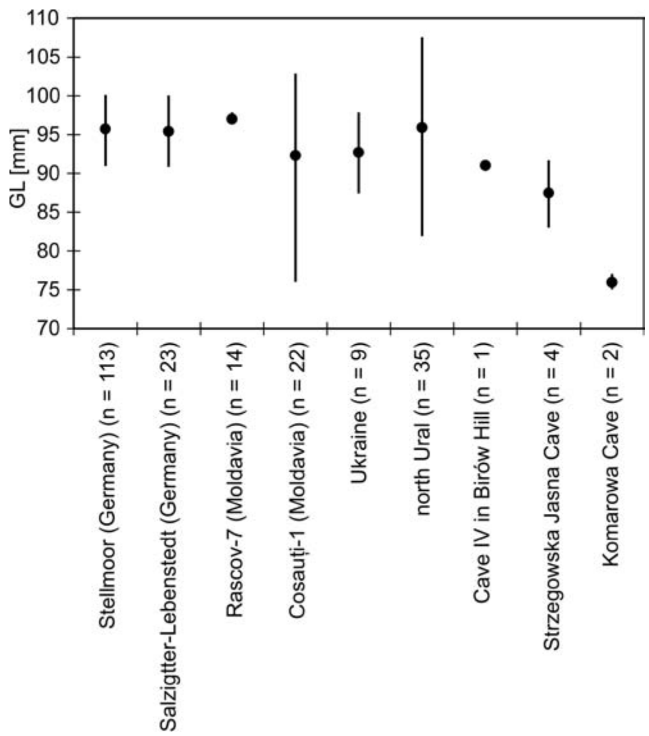

Fig. 11. Length of calcaneus in reindeer from Pleistocene localities of Poland, Germany, Ukraine, Moldova and Russia

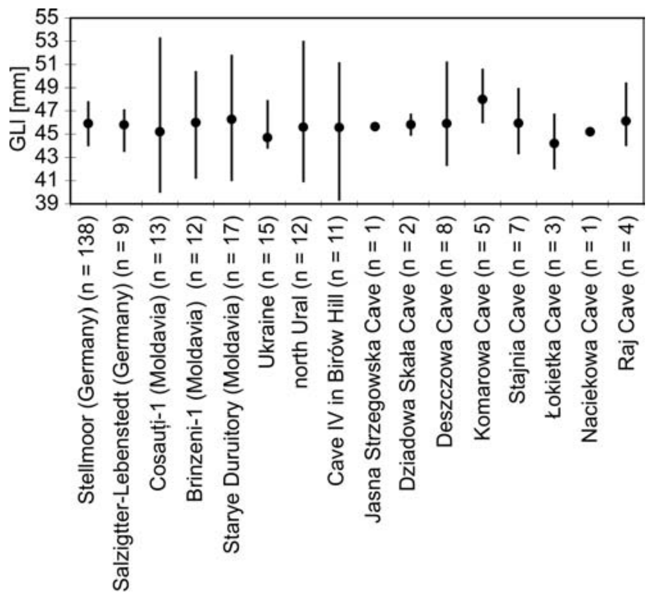

Fig. 12. Length of astragalus in reindeer from Pleistocene localities of Poland, Germany, Ukraine, Moldova and Russia

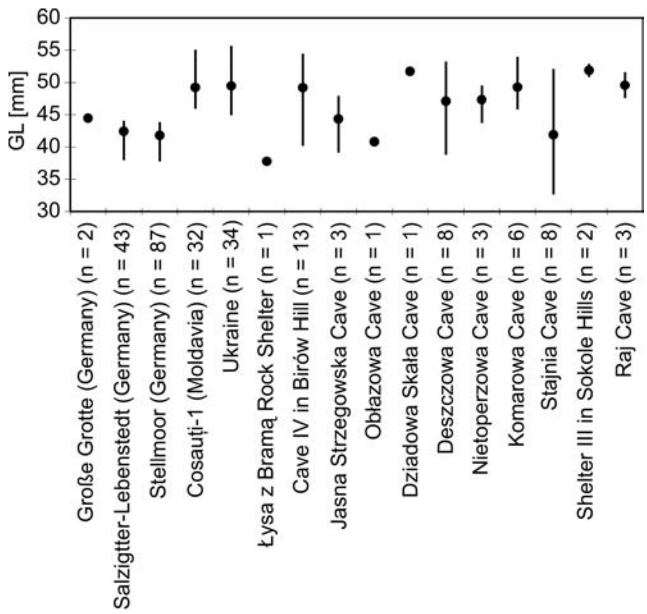

Fig. 13. Length (GL) of phalanx I in reindeer from Pleistocene localities of Poland, Germany, Ukraine, Moldova and Russia

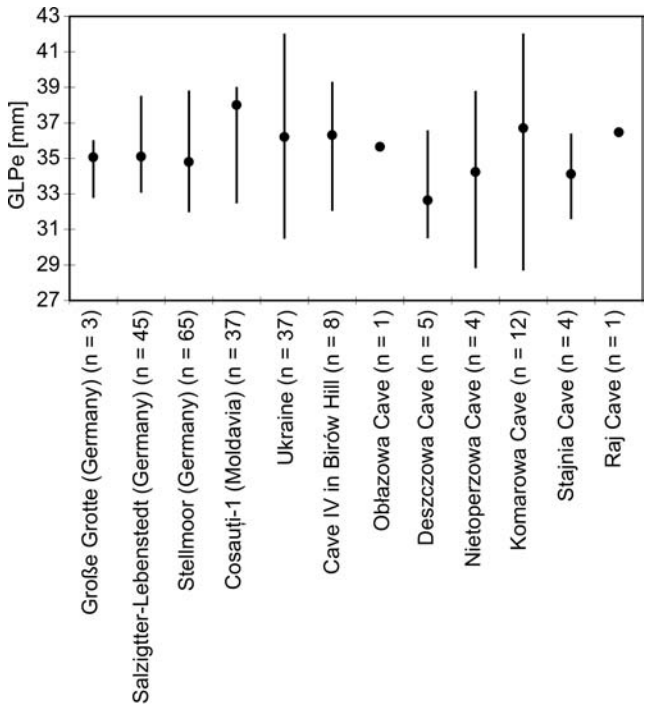

Fig. 14. Length (GLpe) of phalanx II in reindeer from Pleistocene localities of Poland, Germany, Ukraine, Moldova and Russia

and they constitute the basis of this paper. Most frequently phalanx I and phalanx II were well preserved, which made complete measurements possible. Also upper and lower teeth, which were well preserved, were used in the analysis.

Skeleton measurements

Bone and teeth measurements followed Driesch (1976). They were taken by electronic calliper to the nearest 0.01 mm. The bone circumference was measured to the nearest 0.1 mm. All measurements are given in millimetres.

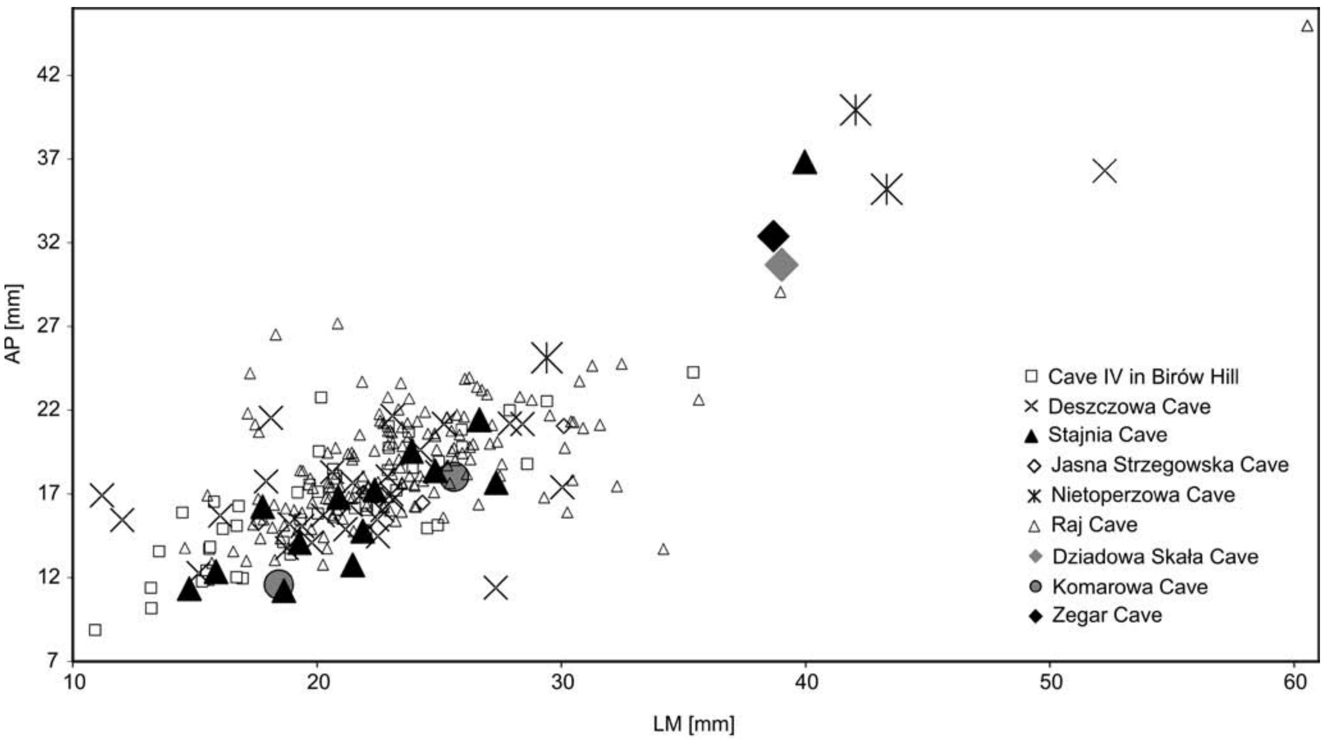

Fig. 15. Antler stem width (AP) to thickness (LM) ratio

Determining ecotype of reindeer from the Upper Pleistocene localities of Poland

Flattening of the antler stem above the coronet makes identification of the ecoform of the reindeer possible. The degree of flattening of the stem is expressed as the ratio of its thickness to width (AP/LM, where AP is the antero-posterior diameter of the stem above the coronet and LM is the latero-central diameter of the stem above the coronet (perpendicular to AP). The closer the LM value is to the AP value, the more rounded is the stem cross-section, which places the reindeer in the tundra group (Bouchud, 1959). When the LM value departs considerably from the AP value, the cross-section shape is more flattened, characteristic of the forest reindeer group.

Teeth measurements

Age determinations, based on measurements of crown height of M_1, are as follows. The height of the tooth crown, measured on the buccal side, was obtained for M_1 teeth from the sites of the Pleistocene reindeer in Poland analysed, and then compared with the corresponding values from control samples, collected by the Canadian Wildlife Service (Morrison and Whitridge, 1997). The control samples of more than 70 left mandibles come from a much larger sample of 1000 mandibles and their associated skulls, collected by the Canadian Wildlife Service (CWS) in the late 1960s. They were taken during extensive studies on a herd of *Rangifer tarandus groenlandicus* and are now kept in the collection of the Canadian Natural History Museum. Age classes were distinguished from the literature and then the measured teeth were assigned to them, on the basis of mean values of M_1 height. All the Pleistocene sites in Poland are presented in graphs.

Comparative analysis included Pleistocene localities in Europe, Asia and North America.

RESULTS

All the measurements of teeth and bones are presented in Appendix Tables 1–18 in the electronic version of the paper.

Length (L) and width (W) measurements of upper teeth of *Rangifer tarandus* from the Polish sites

The values of length and width of tooth crowns from the Late Pleistocene localities in Poland analysed are presented as scatter diagrams.

The graph in Fig. 2 presents the measurements of P^4 from the fossil material, found in the Upper Pleistocene strata of the Polish sites. Most of the specimens of P^4 teeth from the cave localities of Poland analysed are similar and fit within the length range of 12.86–16.37 mm, except for the left P^4 from Stajnia Cave. The longest crowns were those of the left P^4 from Cave IV in Birów Hill and the left P^4 from Dziadowa Skała Cave, which were also very narrow. The specimens from Stajnia Cave and Dziadowa Skała Cave were the widest.

The graph in Fig. 3 shows the measurements of M^3 from the fossil material found in the Upper Pleistocene strata of the Polish sites. The measurements of tooth M^3 did not vary in any significant way. Some of the teeth from

Komarowa Cave had the longest crowns; some other teeth from Komarowa Cave and those from Stajnia Cave, the shortest. One of the teeth from Stajnia Cave had the smallest crown width. Also two teeth from Cave IV in Birów Hill were outside the rather consistent arrangement of points.

Length (L) and width (W) measurements of lower teeth of *Rangifer tarandus* from the Polish sites

The values of length and width of tooth crowns from the Late Pleistocene localities in Poland analysed are presented as scatter diagrams.

The graph in Fig. 4 shows measurements of P_4 from fossil material, found in the Upper Pleistocene strata of the Polish sites. The measurements of tooth P_4 from different localities, like those of the preceding tooth, are similar. The longest crown, found in the tooth from an Upper Pleistocene layer in Dziadowa Skała Cave, distinctly differs in its length from the remaining teeth. The left P_4 from Obłazowa Cave have the second longest crown among all the measured P_4. The tooth from Cave IV in Birów Hill, and the teeth from Stajnia Cave have the shortest crowns. The range in variation of the crown length is 12.93–20.12 mm.

The graph in Fig. 5 shows measurements of M_3 from the fossil material found in the Upper Pleistocene strata of the Polish sites. Also the measurements of tooth M_3 from different localities are similar. Only one of the teeth from Komarowa Cave departs distinctly from the remaining specimens. The left M_3 from Cave IV in Birów Hill and from Obłazowa Cave have the longest crowns. The crowns from the former and two teeth from Stajnia Cave are among the widest. The range in variation of the crown length was 18.04–26.31 mm.

On the basis of these results and literature analysis, it can be said that the teeth of the reindeer from different localities in Poland were similar with respect to crown measurements. No changes, associated with the different geological ages of the localities, were observed.

Age determinations, based on crown length of M_1

An attempt was also made to determine the individual ages of the reindeer, on the basis of the crown height of the lower first molars, measured on the labial side (Table 2). The crown length was measured on the buccal side. In reindeer, the age can be determined by the number of dentine layers in teeth M_1. The crown height of the buccal side of tooth M_1 decreased with age in all of the populations analysed. The measurements were compared with the literature data from two sites situated in the Western Canadian Arctic, at Pokiak and Barry (Morisson and Whitridge, 1997).

The data indicate the occurrence of reindeer aged 2 to 13 years at the localities studied; most of the remains came from animals, which died between 5 and 8 years of age.

It is clear from the graph in Fig. 6 that the youngest individuals (H = 13.41 mm in an individual, aged less than 2 years; tooth from Deszczowa Cave, Upper Pleistocene layer) have the greatest height of M_1 crown on the buccal side. With age, the tooth enamel becomes worn (H = 9.39 mm for 5.5 years; H = 7.9 mm for 7 years; H = 5.6 mm for 10 years). The most worn crown (H = 2.37 mm) was assigned to an individual aged 13 years; the tooth came from a mixed Holocene layer. The smallest crown height in a reindeer from the Upper Pleistocene was H = 3.73 mm. The tooth was found in Cave IV in Birów Hill.

The degree of wear of the M_1 crown increases linearly with age (Dauphiné, 1976). The highest crown corresponds to the youngest age. The enamel wears with age. Digestion in ruminants, including the reindeer, depends on effective mastication, using large areas of the teeth. The wear of the teeth has an essential effect on survival and reproduction. The fossil record suggests that the increase in crown height of molar teeth is an adaptation to feeding under conditions of dry ecosystems with sparse vegetation.

Measurements of the post-cranial skeleton

As in the case of cheek teeth, in order to analyse the differences between the measurements of the postcranial, skeletal bones of the fossil reindeer, the measurements of selected bones from the Upper Pleistocene cave localities from Poland and other localities in Eurasia were compared.

Humerus

The mean measurements of the width of the distal epiphysis of the humeral bone from all the sites were similar. Individual measurements from the sites in Poland were within the ranges of variation of the measurements from Germany or Moldova. The maximum values from the Stellmoor (52.7 mm), Cosauţi-1 (52 mm) and the northern Urals (51.2 mm) localities (Fig. 7) were very similar to each other.

Radius

All the measured radius bones at the Polish sites come from Upper Pleistocene sediments. The greatest width of the distal epiphysis of the radius was recorded from Stajnia Cave. The number of remains from most caves of Poland was so small that it could not be assumed to fully reflect Bd means, and the measurements from such sites were below the minima of ranges in variation from Cave IV in Birów Hill and Stajnia Cave, but fit within the ranges in variation from the more distant localities. The only exception was the single measurement from Maszycka Cave, with the smallest value (Fig. 8).

Metacarpus

The greatest values of the width of the distal epiphysis of metacarpal bone among the Polish localities were recorded from Zbójecka and Komarowa caves. The smallest Bd was that for the bone from Stajnia Cave, but the value was still within the ranges in variation for the sites in Ukraine and Russia, and also at the Wannen locality. The maxima of the ranges in variation were distinctly greater at the sites in Moldova and Russia. Also the mean Bd for these sites were among the highest for all the analysed localities, and the range in variation was 41.1–44.65 mm. The mean value for the distal epiphysis from Cave IV in Birów Hill was among the smallest for the sites compared and was within the lower range in variation from the sites in Moldova. The mean from Komarowa Cave was the highest value (the Stare Duruitory locality in Moldova had a similar mean value), but because of the small number of preserved bones (n = 2), the mean value was not very informative (Fig. 9).

Tibia

All the tibiae from the localities in Poland analysed came from strata, dated as Upper Pleistocene. The greatest values of the width of the distal epiphysis were recorded for Jasna Strzegowska Cave. The range in variation of the mean values of the width of the distal epiphysis was 38.79–48.1. The mean values were similar for nearly all of the sites. The remains from Mroczna Cave (the greatest mean values) were an exception, but were still within the range in variation of the parameter for Cave IV in Birów Hill, Jasna Strzegowska Cave and the localities in the northern Urals (Fig. 10). The distribution of maximum and minimum values of the range in variation showed that smaller individuals were found in the west of Europe and the size became larger eastward.

Calcaneus

The length of the calcaneus from the Polish sites was distinctly smaller, compared to the localities in Germany, Moldova, Ukraine or Russia, and the values were within the lower limit of the ranges in variation. The bones from Mroczna Cave were exceptional in being wider. The mean values from the German sites were close to those from Moldova and Russia. The maxima of the ranges in variation showed that large individuals were characteristic for the eastern areas (Fig. 11).

Talus

The mean length of the talus from the Polish sites was close to the mean values from Germany, Ukraine, Moldova and Russia. The greatest values were recorded for the Cosauți-1 (Moldova) locality and the site in the northern Urals (Russia). As in the case of other components of the post-cranial skeleton, the length of the tarsi showed that individuals from eastern areas were larger than those from western Europe (Fig. 12).

Phalanx I

The mean values of length of the phalanx I for sites in Germany were distinctly smaller and close to the mean from Stajnia Cave. The means from Cave IV in Birów Hill, Deszczowa, Nietoperzowa, Komarowa and Jasna Strzegowa caves, as well as Raj Cave, corresponded to the mean values from eastern sites, namely Cosauți-1 (Moldova). The graph shows a distinct difference between the ranges in variation for the western and eastern sites. The phalanx I from Germany is decidedly smaller than those from Moldova and Ukraine (Fig. 13).

Phalanx II

The mean lengths of the phalanx II were similar for nearly all the localities, the exceptions being the distinctly smaller length of the phalanx II from Deszczowa Cave and the largest value among all the sites, from the Cosauți-1 locality. The greatest maximum values came from the locality in Ukraine and from Komarowa Cave. The maximum GLpe values from the western sites were distinctly smaller, compared to the eastern sites (Fig. 14).

Antler measurements

Measurements of AP (stem width above coronet) and LM (stem thickness above coronet) were taken from the reindeer antler fragments and shown as a graph.

The graph shows dependence between the stem width (AP) and stem thickness (LM). The points, departing from the consistent arrangement, may indicate the presence of a representative of the forest reindeer group in the fossil record. Such specimens were found in Deszczowa Cave and a single specimen – in Cave IV in Birów Hill. The graph shows also that the greatest circumference of the coronet was recorded from Deszczowa Cave and Cave IV in Birów Hill (Fig. 15).

DISCUSSION

The earliest reindeer remains were found in Germany at Süßenborn and were identified as *Rangifer arcticus stadelmanni* (Kahlke, 1969). According to Bouchud (1967), the reindeer from Süßenborn is related to the extant *Rangifer tarandus groenlandicus* from North America. *Rangifer tarandus groenlandicus* is regarded as the ancestor of the extant subspecies of the reindeer in Eurasia (Geist, 1998). The refugium, from which *Rangifer tarandus guettardi* originated, was located in the west, that of *Rangifer tarandus constantini* was associated with Beringia. During the Last Glacial Maximum, *Rangifer tarandus constantini* replaced *Rangifer tarandus* cf. *guettardi* in Moldova and continued its westward expansion. At the end of the Vistulian Glaciation, *Rangifer tarandus constantini* invaded the area of present-day France. Its distribution at that time extended from eastern Siberia to western Europe. Rankama and Ukkonen (2001) suggest that western Europe is the area of origin of the extant tundra subspecies. It is likely that the reindeer from Villestofte is an intermediate form between the large-toothed reindeers of the Upper Pleistocene and the modern *Rangifer tarandus tarandus*. According to Rankama and Ukkonen (2001), the origins of the forest subspecies may be associated with the forest refugia east of Fennoscandia. Considering Røed's (2005) suggestion of a diphyletic origin for the modern reindeer subspecies of Eurasia, both *R. tarandus constantini* and *R. tarandus guettardi* may have contributed to the origin of the Recent *R. tarandus fennicus* and *R. tarandus tarandus*. Among the consequences of the change of living conditions after the invasion of northern areas was the development of many adaptations, which made life in the tundra and forest-tundra possible, including breathing cold and dry air or selecting soft and nutritious food (Flerov, 1952; Sokolov, 1995).

The limited number of Polish reindeer remains examined, which could be measured, provides only a partial picture of the variation, compared with the sites outside Poland, where the number of complete bones was much greater. Despite the generally large number of the examined remains from the Polish sites, in some cases only one or two measurements were possible. The reason was the poor state of preservation of the bones (broken epiphysis was the most frequent damage). The greatest number of bones came from Raj Cave and Cave IV in Birów Hill; Komarowa, Deszczowa and Stajnia caves were equally rich (Table 2). During the study, the authors found no morphometric differences in the dimensions of the teeth and bones of the post-cranial skeleton between individuals from different parts of the Late Pleistocene. The reason could be that as mentioned above, most data come from localities representing MIS 3 and MIS 2 time, and there is a lack of a clear stratigraphy for the majority of the localities.

Osteometric analyses of Late Pleistocene reindeer remains from the sites in western, central and eastern Europe indicate that the body size underwent geographical variation (Weinstock, 2000; Croitor, 2010).

The Late Pleistocene localities of western and central Europe show differences in the mean size of the reindeer from higher latitudes (northern Germany), compared to its conspecifics from the south (Moldova), as well as differences in the mean size between the reindeer from western and central Europe and the eastern representatives of the species (Ukraine, Russia) (Weinstock, 2000).

The graphs of post-cranial skeleton measurements show that the reindeer from Poland were similar in size to those from the German localities, whereas representatives of the eastern populations were decidedly larger.

Reindeer antler remains were found in most of the strata in the Polish localities examined. They are characterised by slender stems with round cross-sections, which is typical of tundra reindeer. In favourable conditions with an abundant food supply, the tundra reindeer grow spectacular antlers, and the number of prongs increases, resulting in different degrees of flattening of the stem. However, the antler still preserves its slender form (Bouchud, 1967).

Banfield (1961) distinguished two forms within Recent reindeer: the tundra form (group *Cylindricornis*) and the forest form (group *Compressicornis*). They were distinguished on the basis of antler form, body size and skull morphology. The antlers in the first form (tundra reindeer) are usually long and slender. The stem is cylindrical, the trez is palmate, while the brow tine and prongs are digitiform. The posterior tine is usually present, well-developed and located far from the coronet. The second form (forest reindeer) usually has short and heavy antlers. The stem is somewhat flattened, often striated. The trez and brow tines and terminal tines are usually palmate, and the terminal tines may be poorly developed. The posterior tine as a rule is located close to the trez tine (Bouchud, 1959). It is clear from the graph in Fig. 15 that the stem width/thickness ratio in the great majority of cases corresponds to that of the tundra reindeer, which only confirms Kowalski's (1959), opinion that the reindeer remains, most frequently found in Poland, represent *Rangifer tarandus*, living at present in the north of Europe, and they are remains of the former distribution range, which shrank, when the climate became warmer.

The age of the Recent reindeer from Canada was determined on the basis of wear of the M_1 crown (Morrison and Whitridge, 1997). Most of the remains were assigned to the age classes, 5–6 years and 6–7 years. The absence of individuals of less than two years in the fossil record may result from the poor fossilization potential of such remains. Several factors contribute to the high mortality in these age classes. The huge mortality in the youngest age class is mainly due to predators; in most wild reindeer populations, half of the young do not reach the age of six months. The increased mortality among adult males starts at the age of 3–4 years and increases with age (Bergerud, 1980). The reason is the higher reproductive cost, compared to females (gradual loss of fat and decrease in body mass). The annual loss of body mass starts in the autumn, with the beginning of the mating season, and is associated with insufficient feeding of the males that take part in the courtship. They enter the winter season with much poorer fat reserves, accumulated before the start of the adverse period. Even the strongest adult males die of starvation during early winters (Leader-Williams, 1988; Kojola, 1991).

According to Jacobi (1934) most of the reindeer remains from the last glaciation in Europe correspond to the type "arcticus", and only a few specimens of "tarandus" were found. With the end of the glaciation, "tarandus" replaced "arcticus" (Bouchud, 1959, 1967). The discovery of the appearance of both forest and tundara reindeer forms at the end of the Pleistocene in Europe and North America suggests that the ecological split between the two developing forms took place before the last glaciation (Bouchud, 1967). The fossil material from the sites in Poland represents a much later stage in the history of the genus *Rangifer*, when the two forms were already separated. This is indicated by the presence in the material of antlers with an oval stem cross-section. The presence of a single antler with a flattened cross-section of the stem may indicate that the individual concerned had immigrated into the Kraków–Częstochowa Upland during one of the far-ranging migrations from forested areas. The small number of antlers with flattened stems may indicate difficult feeding conditions for the reindeer herds in the area (Bouchud, 1967). An alternative explanation is that humans brought the remains of the forest form antlers to the area and abandoned them there.

Populations of the tundra reindeer, herds of which spread throughout Europe in the Late Pleistocene, were not homogeneous and they showed a regional (geographical) variation in body size and antler shape, though the antlers were always well-developed (Bouchud, 1967). With respect to slenderness of the stem, most of the reindeer from the sites in Poland resemble the reindeer from the eastern areas of Europe and from France.

Medium-sized teeth predominate in the fossil teeth of adults. Only in Komarowa Cave, larger teeth are prevalent. Bouchud (1967) found a dependence between the mean size of the fossil reindeer and the climate. The variation among the reindeer is small and becomes more pronounced, especially in cool periods, between the animals living in western Europe from the end of the Odra Glaciation to the beginning of late Vistulian Glaciation. The remains from the sites examined are those of medium-sized individuals, which were probably weaker and worse fed than their conspecifics from the south and east of Europe. The presence of small-sized animals is much more likely in big herds, compared to small herds. In the stadial periods, competition for food was especially intensive in large herds.

The dentition of the reindeer from the sites in Poland is characterised by medium-sized premolars and relatively long and wide molars. Small teeth are found among the reindeer, feeding on large quantities of lichens and small quantities of bark and branches. The tooth structure in the reindeer from the caves analysed indicates adaptations to life in a steppe-tundra; the wide molars made it possible for the animals to masticate hard food (e.g., shrub twigs and tree bark). Such food probably originated from shrubor tree-rich tundra areas. During their migration, the reindeer herds probably reached the steppe-tundra zone, where the climate and environmental conditions probably made wintering possible. During the last glaciation, the zone extended from ca. 45°N to ca. 50°N. Considering the fact that humans collected the antlers and hunted the reindeer, it can be supposed that Cave IV in Birów Hill and Deszczowa Cave were inhabited by humans from early spring until the beginning of summer, as suggested earlier by Czyżewska and Usnarska (1980).

CONCLUSIONS

The body size of fossil reindeer from the Late Pleistocene of the sites analysed in Poland indicates a form, intermediate between the slender and smaller north-western European reindeer and the larger forms from southern and eastern Europe. The reindeer remains from the sites analysed in Poland represent mainly the tundra form of *Rangifer tarandus*.

Single specimens of antlers of the forest form may have been brought into the area by humans, or single individuals of the forest ecotype may have wandered into the area during their seasonal migrations. On the basis of these studies, there is no evidence of morphometric differences between populations of reindeer from different parts of the Late Pleistocene of Poland.

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