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MIDDLE AND LATE PLEISTOCENE ELKS (*CERVALCES* SCOTT, 1855 AND *ALCES* GRAY, 1821) FROM POLAND: PALAEOENVIRONMENTAL AND PALAEOGEOGRAPHIC IMPLICATIONS

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Abstract: The paper deals with remains of the elks *Cervalces latifrons*, *Cervalces* sp. and *Alces alces* from Middle and Late Pleistocene sites in Poland. A form of the genus *Cervalces* occurred in Poland from the early (Kozi Grzbiet, MIS 19–17) to the late Middle Pleistocene (Biśnik Cave, MIS 6 or MIS 5e). The genus *Alces* appeared in Poland in the Eemian Interglacial (Dziadowa Skała Cave). Compared to the other cervids, elk remains from Poland are very few, but they mark important faunal changes. Kozi Grzbiet and Sitkówka are virtually the only Polish localities from the lower part of the Middle Pleistocene with the remains of large mammals, and the only records of *Cervalces latifrons*. The specimens from Biśnik Cave are among the last records of the occurrence of *Cervalces* in Europe. During the Last Glacial Maximum, elks were absent. Though the elks were the least abundant cervids, they were present at sites from milder climatic regimes (interglacials and interstadials) till the Holocene. Elk remains of that period are single teeth and postcranial skeletal bones from the beginning of glaciation in the deposits of Łokietka Cave (MIS 5a–d), Interplenivistulian (MIS 3): caves Biśnik and Obłazowa) and Borsuka Cave (MIS 3–2). In the Late Vistulian (MIS 1, Allerød and Younger Dryas), the elk recolonized the area occupied by Poland.

Key words: Alceini, caves, Pleistocene, Poland

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INTRODUCTION

Despite the extensive literature, the question of the origin of the Recent elk is still open. According to Heintz and Poplin (1981), *Alces alces* (Linnaeus, 1758) came into existence in the Late Pleistocene and its direct ancestor was *Cervalces latifrons postremus* (Vangengeim and Flerov, 1965). Vislobokova (1986, 1990), Churcher and Pinsof (1987) and Kahlke (1990) maintain that the contemporary elk arose probably at the end of the Middle Pleistocene in Eurasia or even, as suggested by Azzaroli (1981, 1985), in Europe. Some authors (Vörös, 1985; Kahlke, 1990) regard *Alces brevirostris* (Kretzoi, 1944) as intermediate between *Cervalces latifrons* (Johnson, 1874) and *Alces alces*. Unfortunately, this taxon is only known from the isolated remains of antlers, a skull fragment and a post-cranial skeleton. Russian authors mention *Alces americanus* (Clinton, 1822) from eastern Eurasia (Boeskorov, 2001; Nikolskiy, 2010; Vasiliev, 2011). In their opinion, it is the form leading to the Recent *Alces alces*. Boeskorov (2001) regards *Cervalces postremus* as a distinct species. According to Nikolskiy (2010), *Alces americanus* is a synonym of some forms of

Cervalces latifrons postremus and could occur in Europe at the end of the Middle Pleistocene and in the Eemian Interglacial (Taubach, Weimar-Ehringsdorf). Alekseeva (1980) and Vasiliev (2011) propose the names *Alces* sp. and *Alces* cf. *alces* for the early forms of the genus *Alces* from the end of the Middle Pleistocene and the Eemian. Alekseeva (1980) refers to late forms of the genus *Cervalces* as *Alces* cf. *latifrons*. It follows from these data that the origins of the extant genus *Alces* can be placed at the end of the Middle Pleistocene. Unfortunately, the fragmentary character of the fossil record precludes the possibility of any ultimate explanation of the occurrence and systematics of the genus *Cervalces* and its relationship to *Alces*.

On the basis of genetic data (Lister and Piljen, 1990; Hundertmark *et al*., 2002; Udina *et al*., 2002), the place of origin of the extant species *Alces alces* was Western Siberia and Far East, and it came into existence in the period between the end of the Middle and the beginning of the Late Pleistocene.

Though the localities with fossil elk remains are numerous in Eurasia and North America, the evolution and systematics of fossil elks remain controversial. Authors differ in their opinions on the generic assignment of the specimens and, consequently, on the trends of elk evolution. Three genera have been distinguished within the Alceini: *Alces* Gray, 1821, *Cervalces* Scott, 1885 and *Libralces* Azzaroli, 1952. Another two genera have been described from the Ciscaucasia: *Tamanalces* Verestchagin, 1957 and *Pseudalces* Flerov, 1962 (Flerov, 1952; Flerov and Shevryeva, 1963); their status and systematic position have been questioned in numerous papers (Baigusheva, 1971; Azzaroli, 1981, 1985; Heintz and Poplin, 1981; Vislobokova, 1986, 1990; Kahlke, 1990; Croitor, 2005; Van der Made *et al.,* 2014). Most authors agree that four species of elk occurred in Europe during the Pliocene and the Quarternary: *Cervalces* (*Alces*) *gallicus* (Azzaroli, 1952), *Alces* (*Cervalces*) *carnutorum* (Laugel, 1862), *Alces* (*Cervalces*) *latifrons* and *Alces alces* Linnaeus, 1758, but their generic assignment is still under debate.

In his papers mentioned above, Azzaroli (1981, 1985) maintained that only two genera of elks were valid: *Alces* and *Cervalces*. He regarded the earlier described *Libralces* as a synonym of *Cervalces*. The view was shared by Heintz (1970); Vislobokova (1986, 1990); Czyżewska (1987); Sher (1987); Mäuser (1990); Pfeiffer (1999a); Boeskorov (2001, 2002), Breda (2001a, 2005, 2008), Breda and Marchetti (2005); Stefaniak (2007); Nikolskiy (2010) and Vasiliev (2011).

Other authors included all the above species in the genus *Alces* (Kurtén and Anderson, 1980; Heintz and Poplin, 1981; Kahlke, 1990; Lister, 1993b; Kahlke, 1999; Pfeiffer, 1999a, b; Foronova, 2001; Van der Made *et al.,* 2014).

A new concept of elk evolution was presented by Nikolskiy (2010). On the basis of an analysis of various structural characteristics of the skull, antlers, teeth and post-cranial skeleton, as well as occurrence and stratigraphic position, he distinguished 9 species and 4 unspecified taxa.

The occurrence of fossil elks in Poland was considered by Niezabitowski-Lubicz (1932), Kowalski (1959), Szymczyk (1973a–c), Czyżewska (1989) and Wyrost (1989, 1994). Remains of *Cervalces carnutorum* (Laugel, 1862) from the Lower Pleistocene locality, the Żabia Cave (upper Villafranchian, lower Biharian, Q1; MIS 58–40). The cave yielded more than 30 bones of minimum two individuals. A single premolar tooth (P^3) of the largest fossil elk

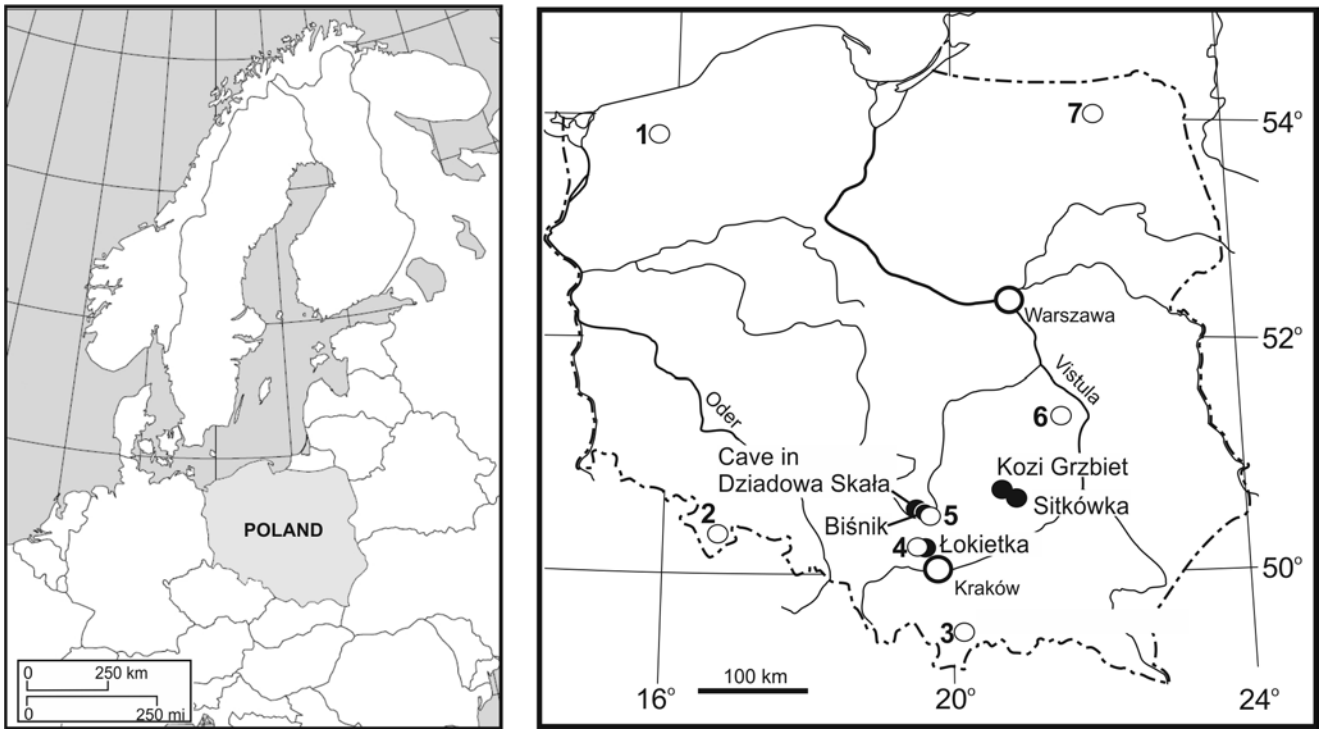


Fig. 1. Pleistocene sites in Poland where remains of elk (*Alces alces*) were found. Source sites of materials studied are indicated as solid circles. Hollow circles – sites mentioned in the text: 1 – Rusinowo; 2 – Radochowska Cave; 3 – Obłazowa Cave, 4 – Borsuka Cave, 5 – Jasna Strzegowska Cave and Mroczna Cave, 6 – Zwoleń, 7 – Dudka.

Table 1

Stratigraphy of Biśnik Cave, according to various sources.

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

Cervalces latifrons (Johnson, 1874) was found in the Middle Pleistocene site Kozi Grzbiet (upper Biharian/Galerian, Q2/Q3; Podlasian Interglacial; Cromerian II–Cromerian III; MIS 19–17; Stefaniak, 2007; Stefaniak *et al.,* 2009a). Also, Holocene remains from the environs of Chodzież (Szymczyk, 1973b, c), have been studied in detail. However, information on the remains from the Middle and Late Pleistocene is still inssufficient and limited to the records mentioned in the descriptions of individual localities, or in comprehensive studies (Wojtal, 2003, 2007; Stefaniak and Marciszak, 2009; Stefaniak *et al.,* 2009b, Nadachowski *et al.,* 2011). According to Nikolskiy's (2010) system, the systematic position of the Polish taxa of Alceini was the following. The elk from the Żabia Cave represented *Cervalces* (*Libralces*) sp. (1.5–1.1 myr), which was intermediate between *Cervalces* (*Libralces*) *gallicus* (2.1–1.5 myr) and *Cervalces* (*Libralces*) *carnutorum* (1.1–0.9 myr). The form from Kozi Grzbiet would probably represent *Cervalces amplicontus* or *Cervalces alaskensis*. His concept, though interesting, would require a detailed presentation of the characteristics which he adopted as criteria for distinguishing new taxa.

Van der Made *et al.,* (2014) described the occurrence of *Cervalces* (*Alces*) *gallicus* in Poland, but placed it in the genus *Alces*. In their opinion, the fossil elk which survived for the longest time was *Cervalces* (*Alces*) *latifrons*; in Europe, it occurred till about 200 thousand years ago. The form represented in the Eemian Interglacial was *Alces* sp., conspecific with *Alces brevirostris*, and the Recent elk appeared at the beginning of the last glaciation. These authors mentioned a metacarpal bone from the Biśnik Cave, layer 7 (MIS 4/3), which had been earlier assigned to *Megaloceros giganteus* Blumenbach, 1797, and then identified by them as representing a large elk, possibly *Cervalces*. On the basis of data from Pleistocene and Holocene localities, they compared the size of M_3 and phalanges of fossil elks through time and documented the trend of decreasing size in elks from the Middle Pleistocene to the Holocene.

The purpose of this study is to describe new remains and reconsider the earlier-described remains of the genera *Cervalces* and *Alces* from the Polish Middle and Upper Pleistocene cave deposits.

GEOLOGICAL SETTING

The osteological material described in this paper was collected in the caves Biśnik, Dziadowa Skała and Łokietka in the Kraków-Częstochowa Upland, the Obłazowa Cave in the Orawa-Nowy Targ Basin, the cave Kozi Grzbiet, and a karst doline in the Sitkówka Quarry, near Chęciny, in the Holy Cross Mts (Fig. 1). For the stratigraphy of the localities studied, see Tables 1 and 2.

Kozi Grzbiet (50°51′N, 20°11′E; Early-Middle Pleistocene, Late Biharian/Galerian, Q2/Q3; Podlasian Interglacial; Cromerian II–Cromerian III; MIS 19–17). Kozi Grzbiet is a deposit-filled karst crevice in Devonian limestones in the Świętokrzyskie Mts, about 20 km west of Kielce. It was described in detail by Głazek *et al.* (1977), Lindner (1991, 1992), Lindner *et al.* (2013); the fauna was dealt with in an array of papers (Stworzewicz, 1981; Szyndlar, 1981; Nadachowski,

Table 2

Stratigraphy of the other localities, described in the paper.

	Western Europe		**Poland**		Kozi Grzbiet Lindner *et al.,* 2013	Dziadowa Skała Cave Wojtal, 2007; Lorenc, 2013	Łokietka Cave Wojtal, 2007	Obłazowa Cave Valde-Nowak *et al.,* 2003	Obłazowa Cave Valde-Nowak and Nadachowski, 2014
MIS 1	Holocene		Holocene			9	1	I	I
MIS 2	Weichselian	Late Weichselian	Vistulian	Main Stadial LGM		8–7	?2	V–II	V–II
MIS 3/2								VII	VII
MIS 3		Interpleniglacial		Grudziądz Interstadial		6		XI–VIII	XIX–VIII
MIS 4		Older Pleniglacial		Świecie Stadial				XII	
MIS 5a				Gniew Interstadial				XIX–XIII	
MIS 5b		Early Weichselian					5–3		
MIS 5c				Toruń Stadial					
MIS 5d									
MIS 5e	Eemian		Eemian			4–3c–a	6		
MIS 6	Drenthe (+ Warthe)		Odranian (+ Wartanian)						
MIS 7	Röpersdorf – Schöningen		Lublinian						
MIS 8	?Saalian		Krznian						
MIS 9	Dömnitz – Reinsdorf		Zbójnian						
MIS 10	Fuhne		Liwecian						
MIS 11	Holsteinian		Mazovian						
MIS 12	Elsterian		Sanian 2						
MIS 13									
MIS 14	Cromerian IV		Ferdynandovian						
MIS 15									
MIS 16	Glacial C		Sanian 1						
MIS 17	Cromerian III								
MIS 18	Glacial B				2c–a				
MIS 19	Cromerian II		Podlasian						
MIS 20	Glacial A								
MIS 21	Cromerian I								
MIS 22	Dorst		Nidanian						

1985; Czyżewska, 1989; Kowalski, 1989; Nadachowski *et al.,* 1989; Wiszniowska, 1989; Stefaniak, 2007). They represented four species: *Cervus elaphus* Linnaeus, 1758*, Praemegaceros verticornis* (Dawkins, 1872)*, Capreolus suessenbornensis* Kahlke, 1956 and *Cervalces latifrons*. Because of the earlier (Stefaniak, 2007) misidentification as P^3, a revised description of the premolar from Kozi Grzbiet is also given.

Sitkówka, near Chęciny (50°48′N, 20°33′E; Early Middle Pleistocene – Late Pleistocene). The site, located within a quarry on Mt. Jaźwica, near Chęciny, in the Świętokrzyskie Mts., was described by Czarnocki (1935; see also Woroncowa-Marcinowska *et al.,* 2013). Vertebrate remains (i.e. cave bear) were found in a karst doline at the depth of 8–10 m, in sands and clayey sands. In the opinion of Woroncowa-Marcinowska *et al.* (2013), the fauna originated from the South-Polish Glaciation and was deposited in the doline during the interglacial period. The fauna has been only partially analysed; for the rest was also done assessment (Pawłowska, unpublished data). Among the identified ungulates, *Cervalces latifrons* and *Rangifer tarandus* (Linnaeus, 1758) were found (Woroncowa-Marcinowska *et al.,* 2013). The remains are a part of the J. Czarnocki collection, Geological Museum of the Polish Geological Institute, National Research Institute (PIG-PIB), Warsaw.

Biśnik Cave (50°23′N, 19°40′E; Middle Pleistocene – Holocene, end of Q3 – Holocene, Röpersdorf-Schöningen (Lublinian) Interglacial and Saalian Glacial (Krzna Glacial; MIS 7/8 – Holocene, MIS 1). The stratigraphy of Biśnik Cave, located in the Biśnik Crag in the Wodąca Valley, near the village of Smoleń in the Częstochowa Upland, is still debatable (Table 1). For detailed description of the site see Cyrek (2002), Cyrek *et al.* (2009, 2010), Stefaniak *et al.* (2009a). Here the present authors adopt the view of Gąsiorowski *et al.* (2014), Krajcarz *et al.,* (2014) and Marciszak and Socha (2014) and postulate a Middle Pleistocene age for layer 15. The remains of more than 160 animal taxa, included cervids which were present in all the levels: *Cervus elaphus, Megaloceros giganteus, Capreolus priscus* Soergel, 1914, *Capreolus capreolus* (Linnaeus, 1758)*, Rangifer tarandus*, *Cervalces* and *Alces alces* (Wiszniowska *et al.*, 2002; Socha, 2009, 2014; Stefaniak and Marciszak, 2009; Cyrek *et al.*, 2010; Socha *et al.,* 2010; Van Asperen and Stefaniak, 2011; Tomek *et al.*, 2012; Croitor *et al.,* 2014; Marciszak, 2014; Piskorska and Stefaniak, 2014; Van der Made *et al.*, 2014). The elk remains in the Biśnik Cave occurred in

layers 19 (MIS 7), 16 (MIS 6) and 15 (MIS 6 or 5e), dated as the end of the Middle Pleistocene, and in layer 1 a–b of the Holocene deposits.

Dziadowa Skała Cave (50°32´N, 19°31´E; Late Pleistocene–Holocene, Eemian–Holocene, Q2 – Holocene, MIS 5 – MIS 1). Cave in Dziadowa Skała is located in the Podlesice Rocks, near the village of Skarżyce. It is a horizontal cave with nine layers of deposits (Chmielewski, 1958, 1975; Kowalski, 1958; Madeyska, 1981; Lorenc, 2006a, b, 2007, 2008; Wojtal, 2007; Cyrek, 2009; Stefaniak *et al.,* 2009b). Numerous bird and mammal remains were found in the cave (Chmielewski, 1958; Kowalski, 1958; Madeyska, 1981; Bocheński, 1990; Wojtal, 2007). Remains of the *Capreolus capreolus* and *Alces alces* were found in the interglacial (Eemian) layer. The reindeer, present in almost all the layers, was the most abundantly represented species.

Łokietka Cave (50°13´N, 19°48´E); Late Pleistocene – Holocene, Early Vistulian–Holocene, MIS 5d – MIS 1). The Łokietka Cave is situated on Mt. Chełmowa in the Prądnik Valley, in the Ojców National Park. The first studies in the cave were conducted by J. Zawisza in 1872 and S. Czarnocki in 1896 and 1899 (Zawisza, 1873; Kowalski, 1951). The excavations were resumed in 1998. From eight to five layers of cave loams, loesses 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 (Lipecki *et al*., 2001; Sobczyk and Sitlivy, 2001a, b; Wojtal, 2007). The few cervid remains were identified as *Rangifer tarandus*, *Cervus elaphus* and *Alces alces*. The elk remains were found in the early Vistulian layer 5.

Obłazowa Cave (49°25´N, 20°09´E; Late Pleistocene – Holocene, middle Vistulian – Holocene, MIS 5 – MIS 1). The Obłazowa Cave is located in the rock Obłazowa, in its south-western part, on the Białka River in the Pieniny Mts. The excavations started in 1985 and continued till present. The excavations yielded numerous mollusc and vertebrate remains. The studies resulted in an array of publications, the most important being Nadachowski *et al.* (1993), Madeyska and Cyrek (2002), Valde-Nowak *et al.* (2003), Wojtal (2003), Wojtal *et al.* (2004) and Valde-Nowak and Nadachowski (2014). The dominant cervid was *Rangifer tarandus*; its remains were found in all the layers. A few remains of the *Cervus elaphus* and a two *Alces alces* tooth were also found.

MATERIAL AND METHODS

The material studied is stored in the collections of the Department of Palaeozoology, Wrocław University (ZPALU-Wr, Biśnik Cave), the Institute of Systematics and Evolution of Animals, PAS, Kraków (MF, Kozi Grzbiet, Dziadowa Skała Cave, Łokietka, Obłazowa Cave) and the Geological Museum of the Polish Geological Institute, National Research Institute (PIG-PIB), Warsaw (Sitkówka, near Chęciny). The material comprises 8 isolated upper- and lower-cheek teeth, as well as a fragment of a mandible and a metatarsal bone. The fragments are well-preserved, except for the specimen from the Obłazowa Cave, which is only partly preserved.

The nomenclature of tooth structure (Fig. 2) follows the cervid nomenclature proposed by Obergfell (1957) and Heintz (1970). Individual age of the animals, to which the teeth belonged, was estimated on the basis of the tooth wear (Lochman *et al*., 1987).

Taxa identification: The skull structure characteristics, especially those of the jaw and mandible region, and the antlers are crucial in identification of fossil elk remains.

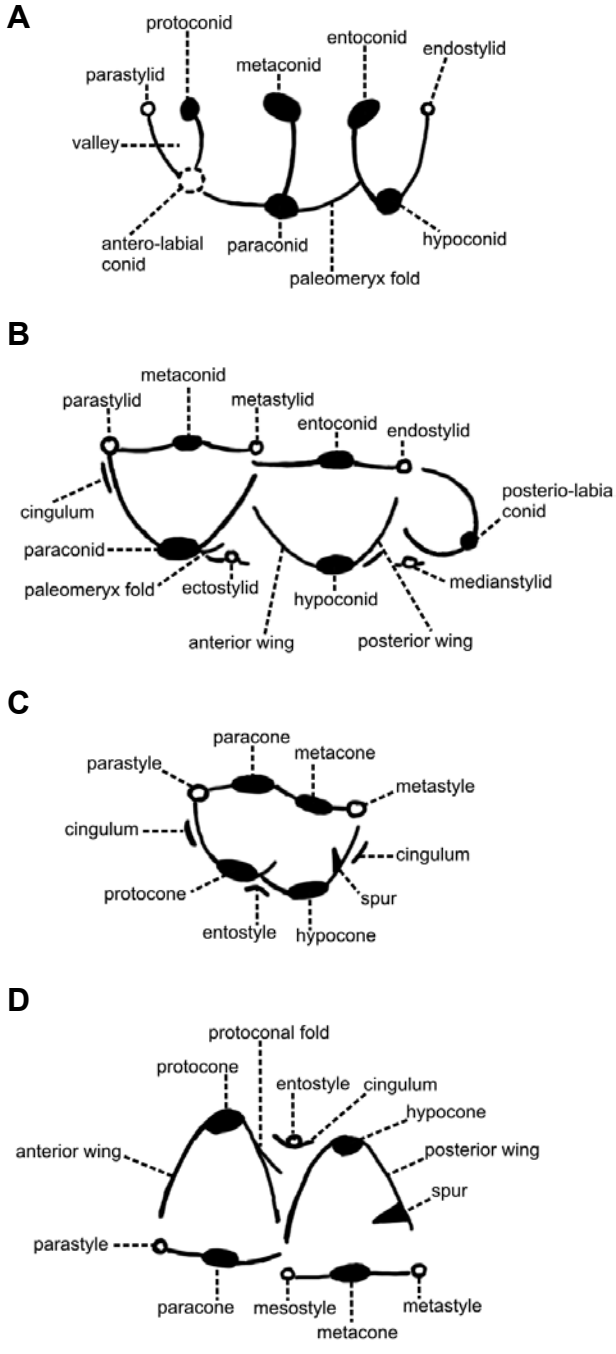


Fig. 2. Schematic structure of cervid teeth after Heintz (1970) and Obergfell (1957). **A.** Lower premolar. **B.** M_3. **C.** Upper milk tooth. **D.** Upper molar.

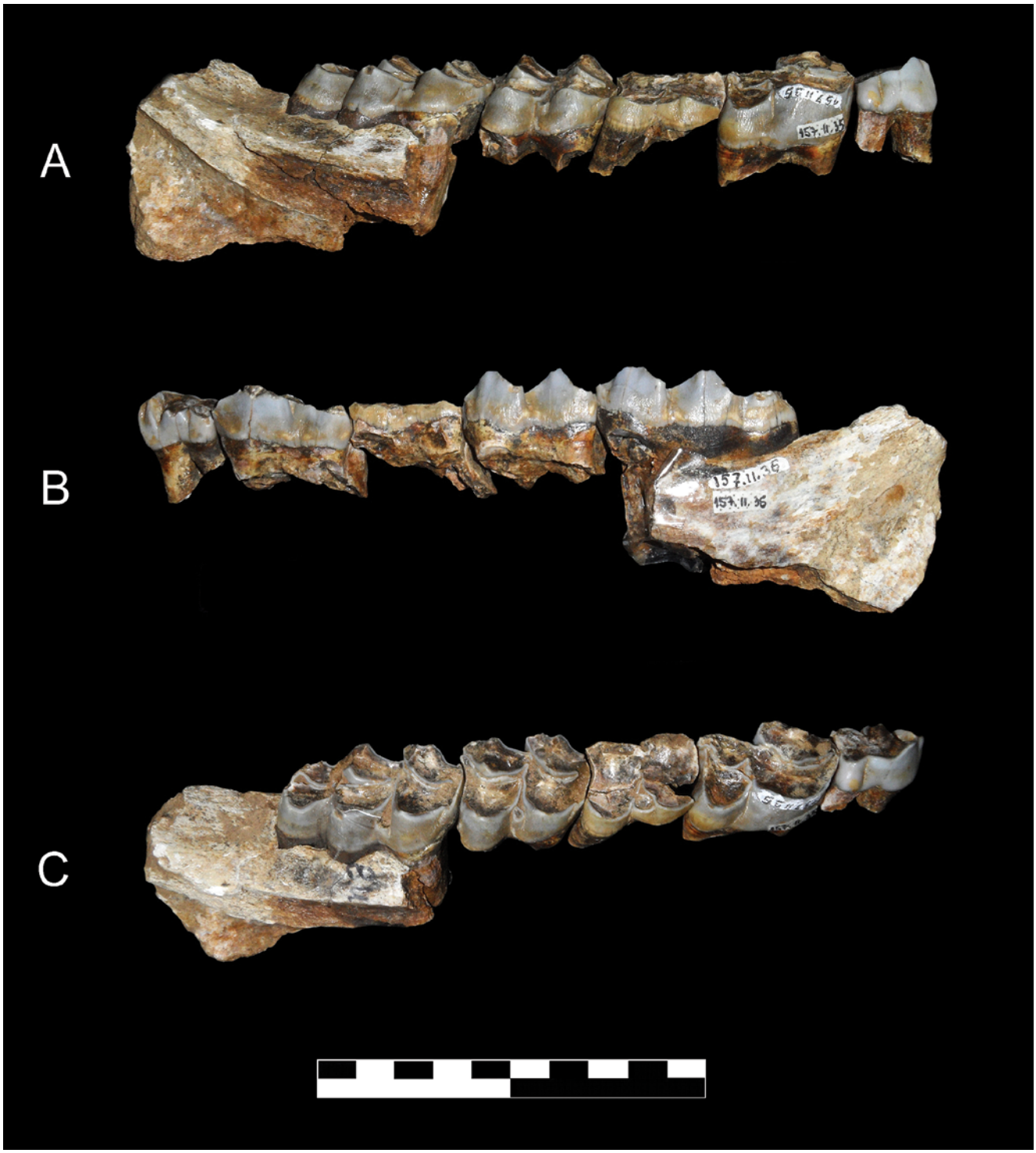


Fig. 3. *Cervalces latifrons* (Johnson, 1874). Sitkówka quarry near Chęciny. Right mandible with P_3–M_3 (MUZ PIG 157.II.35, 36, 41–43). Scale bar 10 cm. **A.** View from the labial side. **B.** View from the lingual side. **C.** View from the occlusal side.

Fig. 4. *Cervalces* sp. Scale bars in A–D 2 cm. **A.** Biśnik Cave. Right P^3 (ZPALUWr/JB/03/W-2414); A.1 – view from the posterior side; A.2 – view from the lingual side; A.3 – view from the anterior side; A.4 – view from the labial side; A.5. – view from the occlusal side. **B.** Biśnik Cave. Left P^3 (ZPALUWr/JB/99/118/10); B.1 – view from the posterior side; B.2 – view from the lingual side; B.3 – view from the anterior side; B.4 – view from the labial side; B.5 – view from the occlusal side. **C.** Biśnik Cave. Left M^3 (ZPALUWr/JB/06/W-5099); C.1. – view from the posterior side; C.2 – view from the lingual side; C.3 – view from the anterior side; C.4 – view from the labial side; C.5 – view from the occlusal side. **D.** Biśnik Cave. Left P^4 (ZPALUWr/JB/04/W-2950); D.1 – view from the posterior side; D.2 – view from the lingual side; D.3 – view from the anterior side; D.4 – view from the labial side; D.5 – view from the occlusal side.

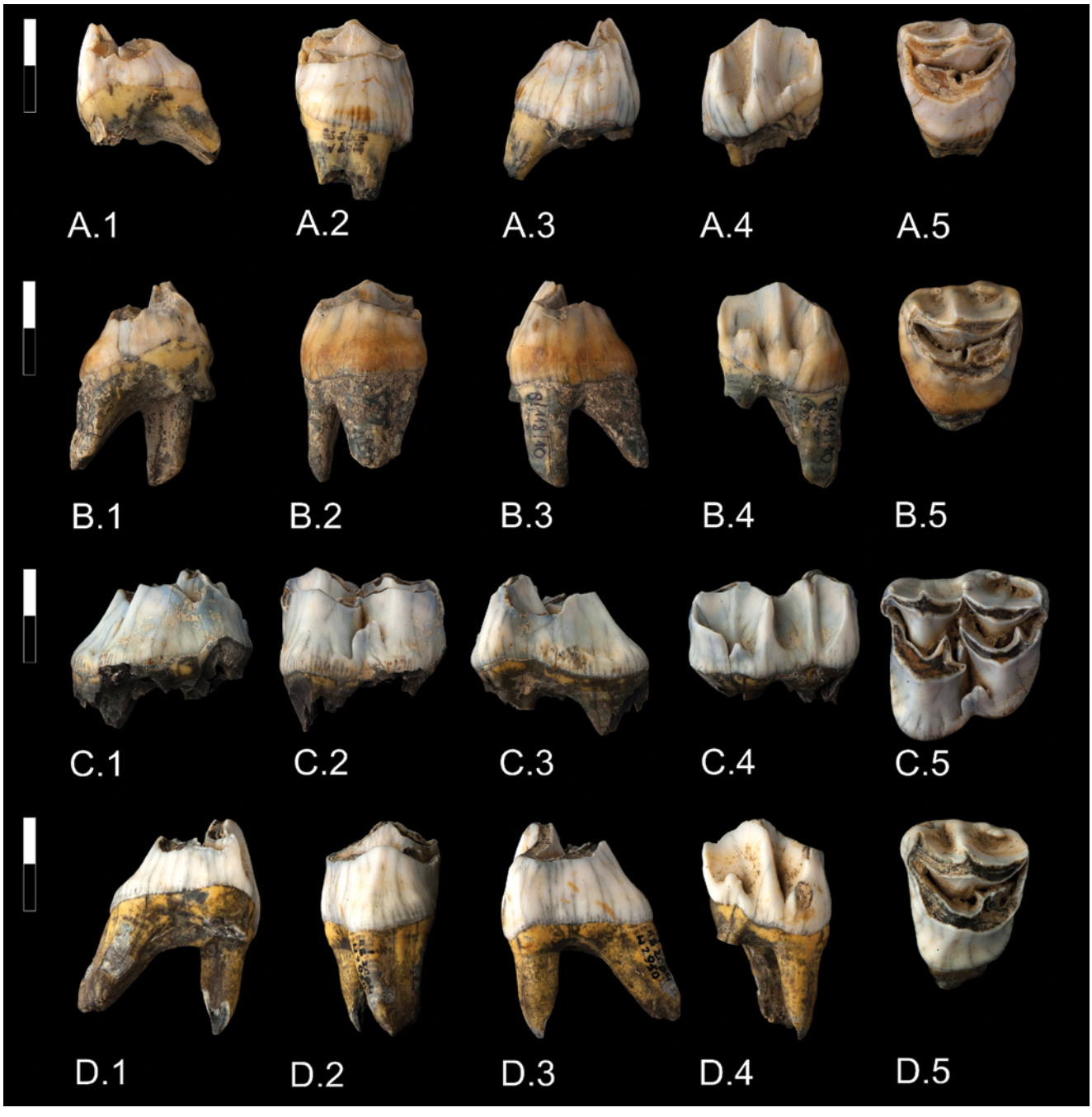
Unfortunately, the material from Poland includes only isolated teeth, mandibles and single fragments of post-cranial, skeletal bones. Consequently, the authors used osteometric differences and structural characters of teeth in order to compare and identify the taxa. The size of teeth, degree of development of stylids, tubercle cusps and additional ridges, cingulum and tubercles were adopted as identification criteria. The most characteristic differences involve the measurements of teeth, which are larger in *Cervalces latifrons* than in *Alces alces*.

Measurements: The measurement methods followed Dürst (1926), Kahlke, 1958, 1960), Heintz (1970) and von den Driesch (1976). The length (GL) of upper teeth was measured on the labial edge near the occlusal surface, of lower teeth – on the lingual side. Width measurements of molars were taken at the base of the first and second lobe of the tooth, the corresponding abbreviations being W_1 (DTa), W_2; the greatest width was measured for premolars – W. Metacarpal bone: GL – greatest length; Bp – breadth of proximal end; Dp – depth of proximal end; SD – smallest breadth of diaphysis; DD – smallest depth of diaphysis; Bd – breadth of distal end; Dd – depth of distal end.

The teeth, mandibles and metacarpal bone measured to the nearest 0.01 mm with electronic caliper. All the measurements are given in mm.

Some authors measure the tooth length at the base of the crown, but in the case of elks, the measurement mode does not affect the identification.

The measurements were compared with literature data on fossil and extant elk and shown in Appendix Tables 1–6.



Unpublished data from localities, referable to the last glaciation and the Holocene in the Czech Republic and Poland, were also used.

RESULTS

The measurements of fossil and extant elks are shown in Appendix Tables 1–6.

Systematic palaeontology

Family CERVIDAE Goldfuss, 1820
Subfamily CAPREOLINAE Brookes, 1828
Tribe ALCEINI Brookes, 1828
Genus Cervalces Scott, 1885
Cervalces latifrons (Johnson, 1874)
Figs 3, 7; Appendix Tables 1–4

Locality: Kozi Grzbiet; layer 2c; (Podlasian Intergalcial; Cromerian II–Cromerian III; MIS 19–17): fragment of P^2 (MF/KG/19); Sitkówka quarry near Chęciny (Middle Pleistocene): right mandible with P_3–M_3 (MUZ PIG 157. II.35, 36, 41–43).

Description and discussion: The description, measurements and detailed analysis of the specimens from Kozi Grzbiet were presented by Stefaniak (2007; see also Appendix Table 4; Fig. 1G). As mentioned above, the tooth was previously identified as P^3, but its re-examination, as well as the comparison of morphology and measurements, indicate that it is P^2. The characteristic features of P^2 are: the greater length of the labial wall between the paracone and the metastyle, compared to P^3, and the more convex shape of the lingual part, which is more compressed in P^3. The crown of P^2 was not worn; it belonged to an individual during teeth replacement and its age, based on comparison with the extant elk, can be estimated as being about 17–20 months (Lochman *et al.,* 1987).

The specimen from Sitkówka is a much damaged fragment of a right mandible with isolated P_3–M_3 (Fig. 3). Only M_3 is still in the mandible fragment. The crowns are much worn and low, indicating individual age of more than 10 years. Valley 2 in P_3 is open. In P_4 the protocone has fused with the entoconid, the entostylid of molars is much worn. M_1 is much damaged, while in the crowns of M_2 and M_3 the posterior wing of protoconid has fused with the anterior wing of entoconid. The third lobe of M_3 is also much worn. The structure of cheek teeth is characteristic of elk with well-developed metaconid, entoconid, metastylid and entostylid cusps of molar teeth, strongly molarised P_4 (5 degree of molarisation according to Heintz, 1970), on P_3 anterior and posterior wing of antero-labial tubercle are developed; parastylid and paraconid are not developed. All measurements are shown in Appendix Tables 1–3 .

Cervalces sp.
Figs 4, 8–10; Appendix Tables 4–5

Locality: Biśnik Cave; layer 19 (Krznian or Krznian/Lublinian; ?Saalian or ?Saalian/Intra–Saalian Interglacial; MIS 8 or 8/7): right P^3 (ZPALUWr/JB/03/W-2414). Layer 16 (Odra Glaciation; Saalian; MIS 6): left P^3 (ZPALUWr/JB/99/118/10). Layer 15 (Odranian or Eemian; Drenthe or Eemian; MIS 6 or MIS 5e): left M^3 (ZPALUWr/JB/06/W-5099); left P^4 (ZPALUWr/JB/04/W-2950).

Description: All measurements are shown in Appendix Tables 4. P^3 is worn on all the crown surface (Fig. 4.A). The hypocone fold has fused with the occlusal surface; the individual age of the specimen can be estimated as about 5–6 years. On the labial side, on the cingulum connecting the paracone cusp with the metastyle, there is no cusp. The left P^3 indicates an age of about 5 years at the moment of death. The anterior wing of the protocone is slightly worn. The hypocone fold has not fused with the occlusal surface. On the labial surface the parastyle and metacone cusps are well-developed, and the metastyle has the form of a small ridge. The base of the tooth on the labial side bears a well-developed cingulum in the form of a collar, connecting the parastyle, metacone and metastyle. A well-developed cusp is visible between the metacone and metastyle; its height reaches nearly half the height of the crown (Fig. 4.B). The left M^3 is worn on all the crown surface. The endotstyle cusp is well-developed, thick and reaches half crown height. A cusp is located between the protocone fold and the wall of the anterior wing of the hypocone. The hypocone spur is well-developed. A characteristic feature of elk cheek teeth, in the form of a well-developed cingulum, forming a collar with developed cusp, especially between the mesostyle and metastyle, is visible on the labial side. The metacone cusp is present (Fig. 4.C). The individual's age is about 5 years. The crown of P^4 is worn on all its occlusal surface, the hypocone fold is nearly completely fused with the hypocone. The degree of wear indicates an individual age of about 5–6 years. The parastyle cusp is well-developed on the labial side of the tooth. The cingulum connecting the paracone cusp with the metastyle bears a small cusp, reaching nearly 1/3 crown height (Fig. 4.D).

Genus Alces Gray, 1821
Alces alces (Linnaeus, 1758)
Figs 5, 7, 11; Appendix Tables 2–3, 5–6

Locality: Dziadowa Skała Cave; layer 14 (Eemian Interglacial; MIS 5e): right M_3;

Description: The whole occlusal surface is worn. The first lobe is not connected with the second lobe. The posterior wing of hypocone is connected with the entostylid and the third lobe. The apex of entostylid is worn to about half its original height (Fig. 5.A). The measurements are shown in Appendix Table 2. The individual's age, based on the tooth, is estimated as about 10.5–11.5 years.

Locality: Łokietka Cave; layer 5 (early Vistulian, MIS 5a–d): right M_3 (MF/6578)

Description: The tooth has its anterior and posterior metaconid wing damaged, its crown is much worn, as is the ectostylid (Fig. 5.B); the probable age is about 10.5–12.5 years. The measurements are shown in Appendix Table 2.

Locality: Biśnik Cave: layer 7 (Middle Plenivistulian, Świecie Stadial/Grudziądz Interstadial, MIS 4/3): left adult

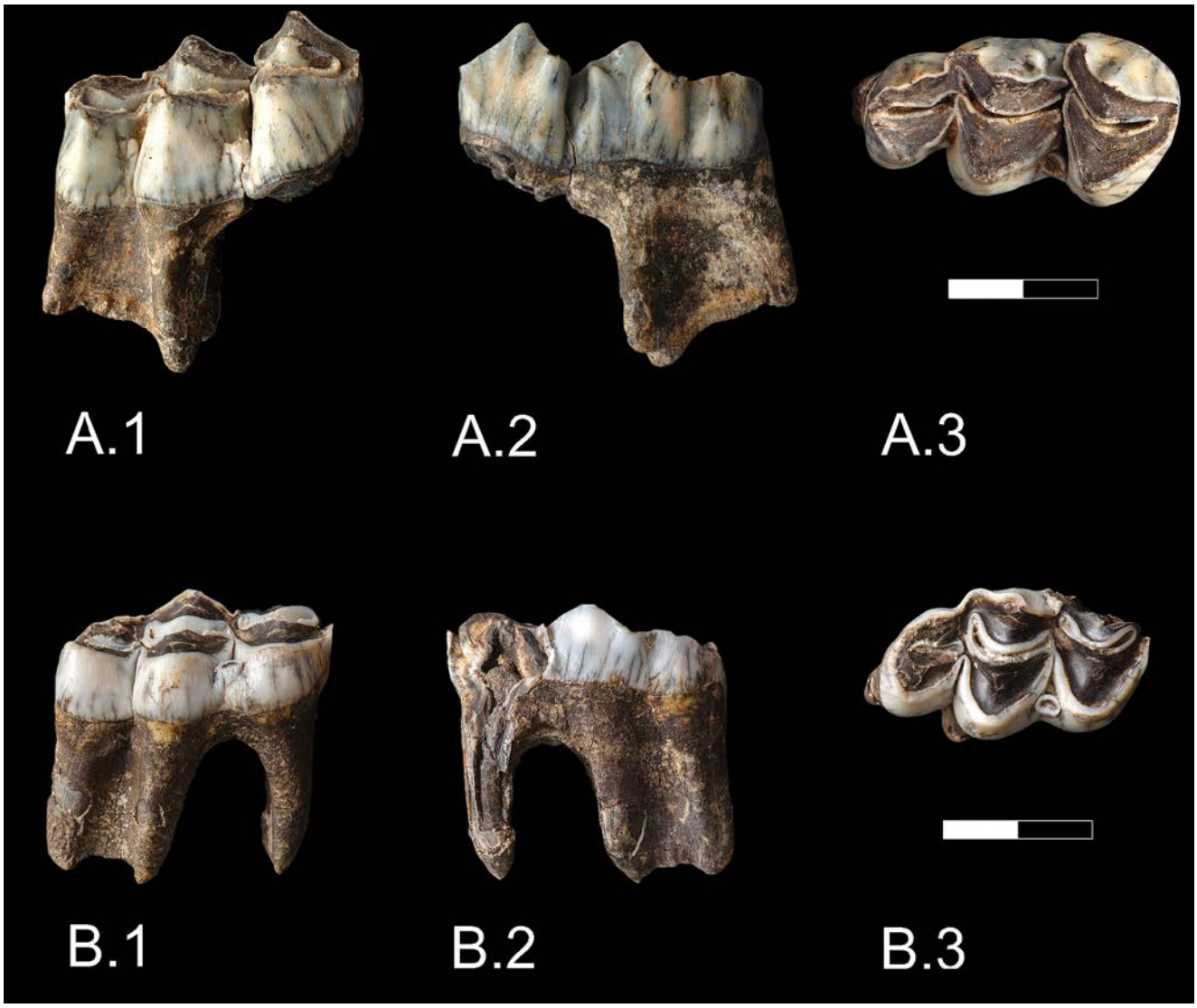


Fig. 5. *Alces alces* (Linnaeus, 1758). Scale bars 2 cm. **A.** Cave in Dziadowa Skała. Right M_3 (MF/5560); A.1 – view from the labial side; A.2 – view from the lingual side; A.3 – view from the occlusal side. **B.** Łokietka Cave. Right M_3 (MF/6578); B.1 – view from the labial side; B.2 – view from the lingual side; B.3 – view from the occlusal side.

metacarpus (ZPALUWr/1690). The measurements are shown in Appendix Table 6.

Locality: Obłazowa Cave: layer XIX (Grudziądz Interstadial, Interplenivistulian, MIS 3); right M^3; individual age ca. 12–14 years.

Decsription: The fragment of the M^3 from layer XIX includes the complete posterior lobe and a fragment of lingual wall of the anterior lobe; the crown is much worn. The characteristic structure of the labial wall of the posterior lobe, which is strongly concave, and the asymmetry in the size of the anterior and posterior lobes unequivocally point to M^3. The measurements are shown in Appendix Table 5.

DISCUSSION

Cervalces vs Alces

This paper contributes new information about Middle and Late Pleistocene elks remains from Poland. Unfortunately, the osteological material includes no antlers and anterior parts of skull, which are mainly diagnostic for the genera *Cervalces* and *Alces*. However, it should be noted that the structure of all the studied teeth is characteristic for elks.

It has been pointed out in the literature (Mäuser, 1990; Breda, 2008; Nikolskiy, 2010) that cheek teeth in the genera *Cervalces* and *Alces* differ in the development of ectostylid and medianstylid (lower teeth) and entostylid (upper teeth). In the genus *Cervalces*, they are massive and often as high as the crown on the side, on which they are situated. They wear along with the crown. In *Alces*, the stylids are less massive, often poorly developed, and their height often does not reach the occlusal surface (Mäuser, 1990; Breda, 2008; Nikolskiy, 2010). Also the remaining stylids and tubercle cusps on the labial side in species of *Cervalces* are significantly thicker, and also the additional enamel ridges, cingulum and cusps at the base of upper molars are larger in *Cervalces*. The characteristic is present already in the

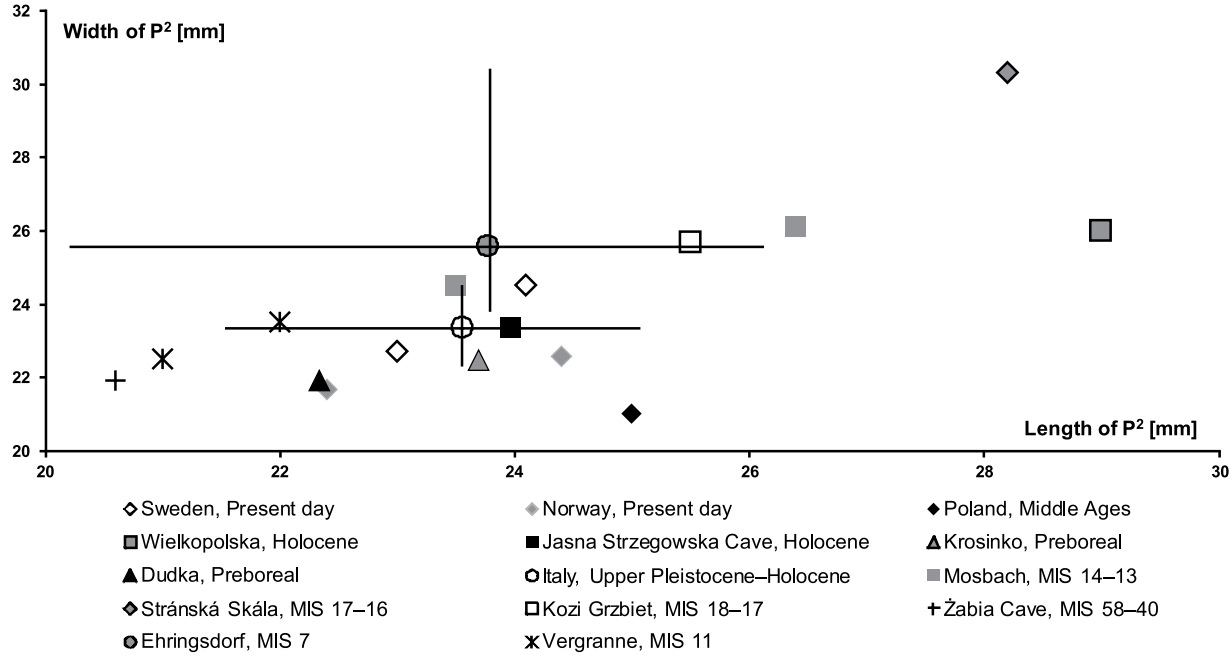


Fig. 6. Length-to-width ratio of P^2 of fossil elks from Polish and Eurasian Quaternary localities. Based on data from Appendix Table 4.

primitive *Cervalces carnutorum* from the Żabia Cave (Stefaniak, 2007). Nikolskiy (1996, 2010) and Nikolskiy and Boeskorov (2011) indicated the importance of the degree of molarisation of P_3 in the evolution of elks (see also Mäuser, 1990). According to all the above-mentioned authors, the degree of molarisation of the tooth increases in the elk evolution. In Recent forms, the tooth is molarised, and valley 2 is usually closed. Nikolskiy (2010) and Nikolskiy and Boeskorov (2011) noted also that in the fossil and extant Asian *Alces* teeth with archaic features were found more frequently than in the European *Alces alces*. Besides the difference in the number of chromosomes, this characteristic, according to these authors, indicates that the two populations evolved independently. Pfeiffer (1999a) and Breda (2001a, 2005) are of the opinion that the characteristic varies in elks and that valley 2 is closed in the holotype of *C. gallicus*. The tooth from Kozi Grzbiet was identified as *C. latifrons*, on the basis of its structure and measurements, which were within the range of variation of P^2 of *C. latifrons* from other European localities (Kahlke, 1956, 1960, 1965, 1966, 1971a, b, 1995a, b, 1997), and were larger than P^2 and lower teeth of *C. gallicus, C. carnutorum* and the extant *A. alces* (Fig. 6; Appendix Table 4).

The elk remains from Sitkówka were identified as *Cervalces latifrons*, on the basis of the plesiomorphic structure of P_3, the development of entostylid in molars and the measurements which are typical of the Middle Pleistocene individuals of the species from European localities. Both the measurements of isolated teeth and the molar length of the specimen from Sitkówka (Fig. 7; Appendix Tables 1–3) are within the range of variation of large *C. latifrons* from the period between MIS 17 and MIS 13 (Kahlke, 1960, 1965, 1966, 1971a, 1995a, b; Mäuser, 1990; Van der Made *et al.,* 2014).

Elk evolution involved size increase from the oldest species (*C. gallicus*, *C. carnutorum*) to *C. latifrons*, which is expressed as an increase in length of molar rows. In the specimen from Sitkówka, the length of the mandibular molar row is typical of large representatives of the species. Late forms of *Cervalces* are smaller (dated as the period Holstein Interglacial); also the evolution of the genus *Alces* involved a gradual decrease in size from the Middle Pleistocene forms to the extant representatives (Appendix Table 3). The presence of *C. latifrons* indicates a Middle Pleistocene age of at least some of the layers.

The upper teeth (P^3, P^4, M^3; Figs 8–10; Appendix Tables 3–4) from the Biśnik Cave have also a much more developed cingulum on the labial side, with a characteristic cusp, which is larger than in the extant *Alces alces*; in their structure they resemble teeth of primitive elks of the genus *Cervalces* (see Kahlke, 1960, 1965, 1969). Also, M^3 (Fig. 4.C) has ancestral, structural characteristics: large endostyle and pronounced metacone cusp (Kahlke, 1960, 1965, 1966; Mäuser, 1990; Nikolskiy, 1996, 2010; Vasiliev, 2005; Nikolskiy and Boeskorov, 2011). The size of the upper teeth from the Middle Pleistocene layers (19–15) of the Biśnik Cave (Figs 8–10), which are larger than in the extant *Alces alces* from the Pleistocene and Holocene localities of Europe, indicate appurtenance to older forms of the species. At the same time, their measurements are smaller than in the typical *Cervalces latifrons* from Süssenborn, Voigstedt, Stranska Skala, Kozi Grzbiet, and *Alces alces* from Siberia (Figs 8–10; Appendix Tables 3–4). The measurements of P^3 and P^4 from the Biśnik Cave are comparable to those of *C. postremus* from the Saalian locality Weimar-Ehringsdorf (MIS 7) (Kahlke, 1968, 1975). The above characters made us assign the teeth from Biśnik Cave to *Cervalces* sp.

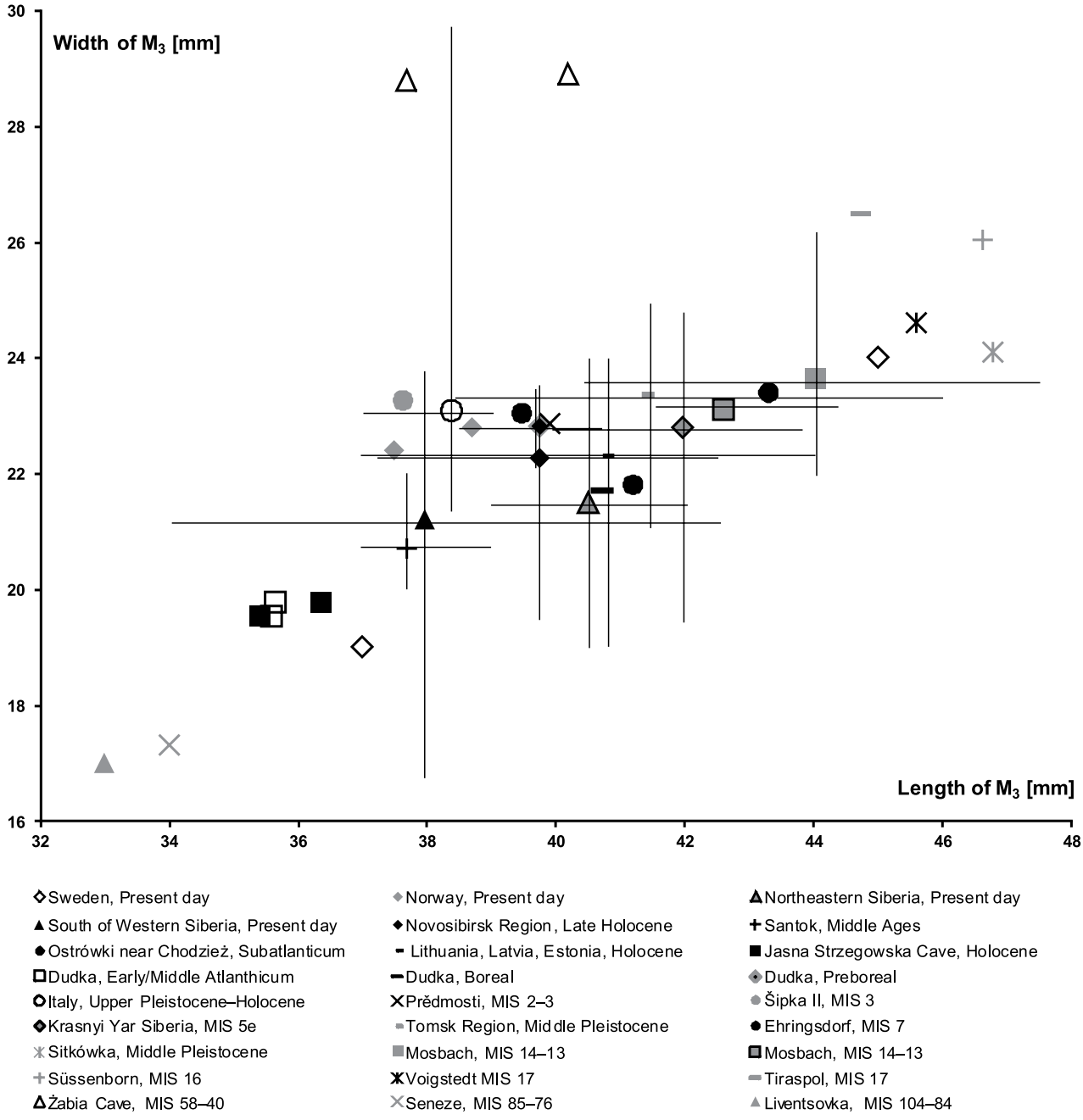


Fig. 7. Length-to-width ratio of anterior lobe (DTa) of M_3 of fossil elks from Polish and Eurasian Quaternary localities. Based on data from Appendix Table 2.

The measurements of M_3 from the Dziadowa Skała Cave and the Łokietka Cave are smaller than those of *C. postremus* from Weimar-Ehringsdorf (MIS 7) and of *Cervalces latifrons* from the Middle Pleistocene localities. The dimensions of the tooth from the Dziadowa Skała Cave are also close to those of specimens of *Alces* cf. *alces* from the Eemian deposits in Krasnyi Yar and the Middle Pleistocene *Alces* sp. from Western Siberia (Fig. 7; Table 2) and the recent elk, hence the authors propose to classify the Eemian remains from the Dziadowa Skała Cave and those from the Upper Pleistocene deposits of the Łokietka Cave as *Alces alces* (Kahlke, 1960, 1965, 1966, 1975; Alekseeva, 1980; Mäuser, 1990; Foronova, 2001; Vasiliev, 2005, 2011).

The measurements of the preserved fragment of M^3 from the Obłazowa Cave are within the range of variation for fossil elks of the genera *Cervalces* and *Alces* (Appendix Table 5). Its morphology is typical of the genus *Alces*.

The measurements of the metacarpus from the Biśnik Cave are large, compared to the other fossil and extant elks, and the bone is massive, as indicated by its considerable width (after Van der Made *et al*., 2014; see also Fig. 4).

Its measurements are comparable to those of such bones of large representatives of *Cervalces latifrons* from the Middle Pleistocene (Moldova) and the Eemian Interglacial (Eich). They are larger than in *Alces alces* (Fig. 11; Appendix Table 6). Archaeological and stratigraphic data (Cyrek *et al.,* 2014;

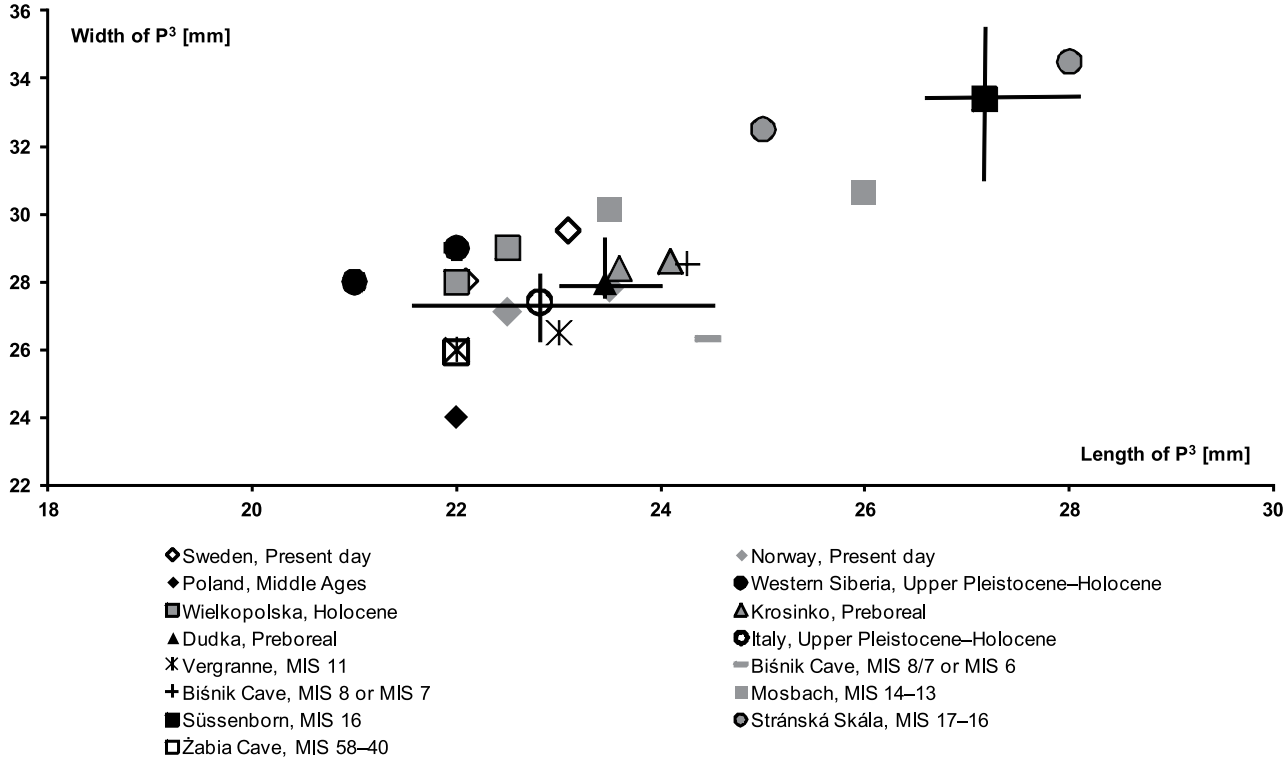


Fig. 8. Length-to-width ratio of P^3 of fossil elks from Polish and Eurasian Quaternary localities. Based on data from Appendix Table 4.

Gąsiorowski *et al.,* 2014; Krajcarz *et al.,* 2014; Marciszak and Socha, 2014; Socha, 2014) indicate its probable age as the end of the Świecie Stadial (Middle Plenivistulian, MIS 4) and the Grudziądz Interstadial (Interplenivistulian, MIS 3). Barring redeposition or stratigraphic error, it may, as suggested by Van der Made *et al.* (2014), represent a large, relic form of *Cervalces latifrons*, which survived till the Vistulian Glaciation, with the simultaneous occurrence of smaller forms of the extant *Alces*. As mentioned above, the layers of the Biśnik Cave, dated as the Middle Pleistocene, contained the remains of representatives of *Cervalces*, but their size was smaller and typical of later forms of *Cervalces latifrons*.

Palaeoenvironmental implications

C. latifrons is the largest fossil elk species. It was larger than *A. alces,* living today. Compared to *C. gallicus* and *C. carnutorum*, it was characterised by a greater shoulder height, larger and more massive teeth, combined with a reduction of some crown components, as well as changes in the skull proportions and structure. These features may indicate adaptation to the colder and more changeable climate of the Middle Pleistocene, the environment of the steppe and cold steppe, taiga and mixed forests (Bubenik, 1986; Czyżewska, 1987; Kahlke, 1990; Lister, 1993b; Azzaroli, 1994; Breda *et al.,* 2005; Breda, 2005, 2008; Stefaniak, 2007; Nikolskiy, 2010). The presence of remains of this species at Kozi Grzbiet and Sitkówka indicates that during the Podlasian Interglacial (MIS 19–17) the locality was within the area covered by boreal forests, with some water bodies and open areas.

Climatic requirements and habitat were probably similar for *Cervalces* and *Alces*, despite the structural differences in their skulls, antlers and post-cranial skeletons (Kahlke, 1990; Lister, 1993b; Boeskorov, 2001; Breda and Marchetti, 2005; Breda *et al.*, 2005; Breda, 2008). The occurrence of their remains in the cave deposits of the Kraków-Częstochowa Upland indicates the presence in the environs of the sites, at least for some period, of large water bodies, wetlands and boreal forests during the Odra Glaciation, Lublin Interglacial, Eemian, and the beginnings of the Vistulian. The studies in the Biśnik Cave confirm this view. In the Middle Pleistocene, a lake and river surrounded by forests and open areas occurred in the Wodąca Valley, where the caves are located. In the Holocene, the lake dried periodically and now the valley is dry (Cyrek, 2002; Mirosław-Grabowska, 2002; Stefaniak *et al.*, 2009b; Cyrek *et al.,* 2010). As shown by Socha (2014) in his palaeoclimatic reconstruction of the Biśnik Cave, the climate during the deposition of layers 19 and 16 (MIS 6–7) was boreal, while a distinct warming took place during the deposition of layer 15 (end of MIS 6 and/or Eemian Interglacial MIS 5e).

In the Eemian and at the beginning of Vistulian Glaciation, similar conditions must have prevailed in the region of Podlesice and Ojców, where the caves Dziadowa Skała and Łokietka are situated (Wojtal, 2007; Stefaniak *et al.*, 2009b).

Owing to the climate amelioration during the Interplenivistulian, it was possible for the elk to occur for a brief period in Poland (Kraków-Wieluń Upland: Biśnik Cave, Borsuka Cave, and Nowy Targ Basin: Obłazowa Cave; Wilczyński *et al.,* 2012; Valde-Nowak and Nadachowski, 2014).

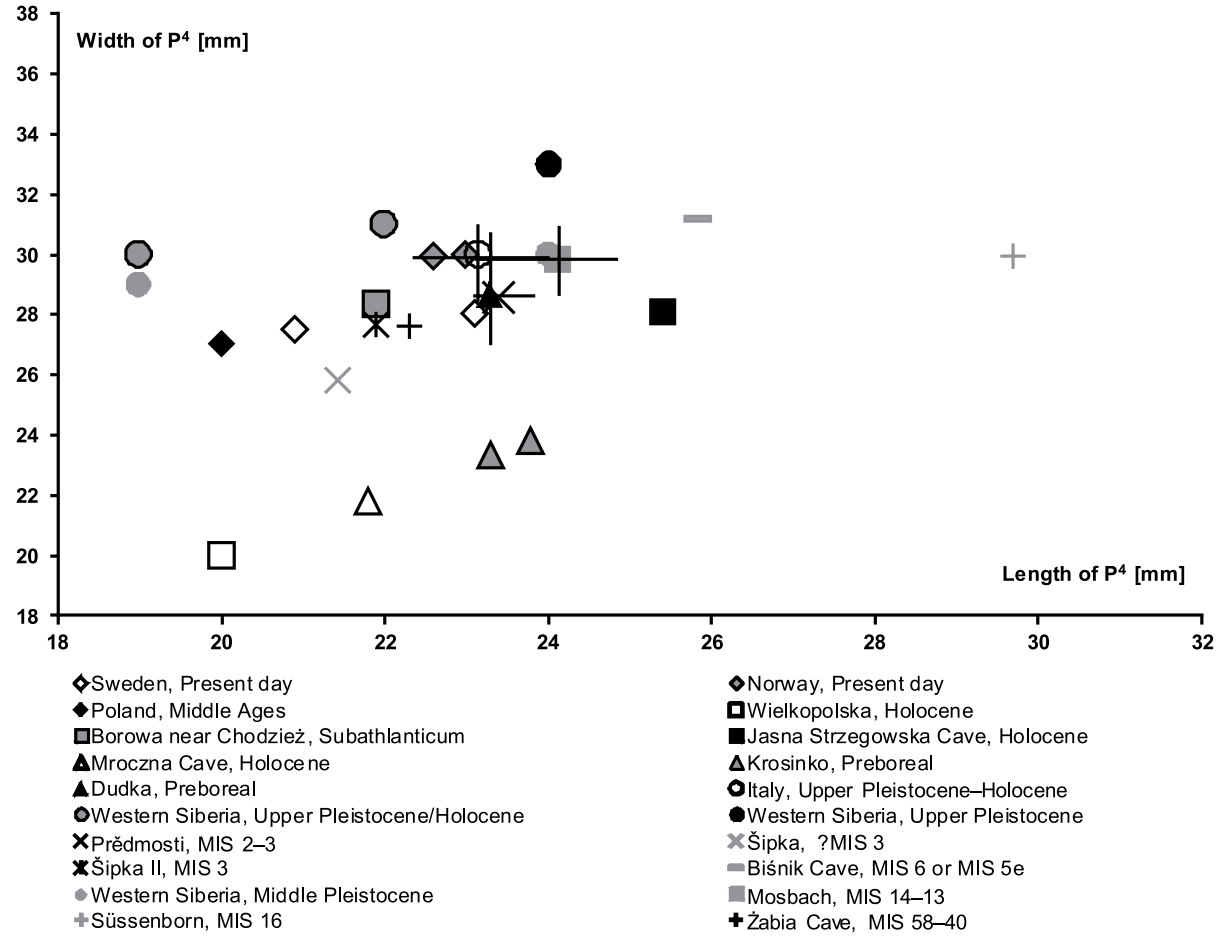


Fig. 9. Length-to-width ratio of P^4 of fossil elks from Polish and Eurasian Quaternary localities. Based on data from Appendix Table 4.

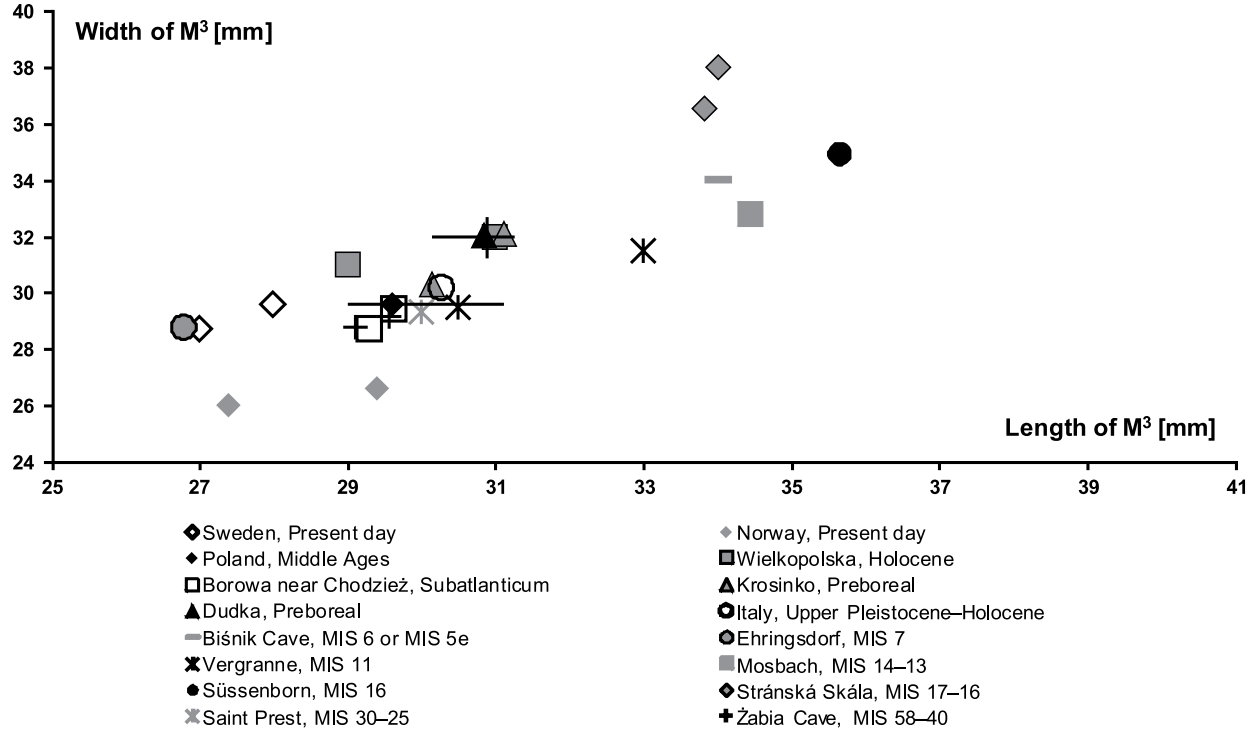


Fig. 10. Length-to-width ratio of M^3 of fossil elks from Polish and Eurasian Quaternary localities. Based on data from Appendix Table 5.

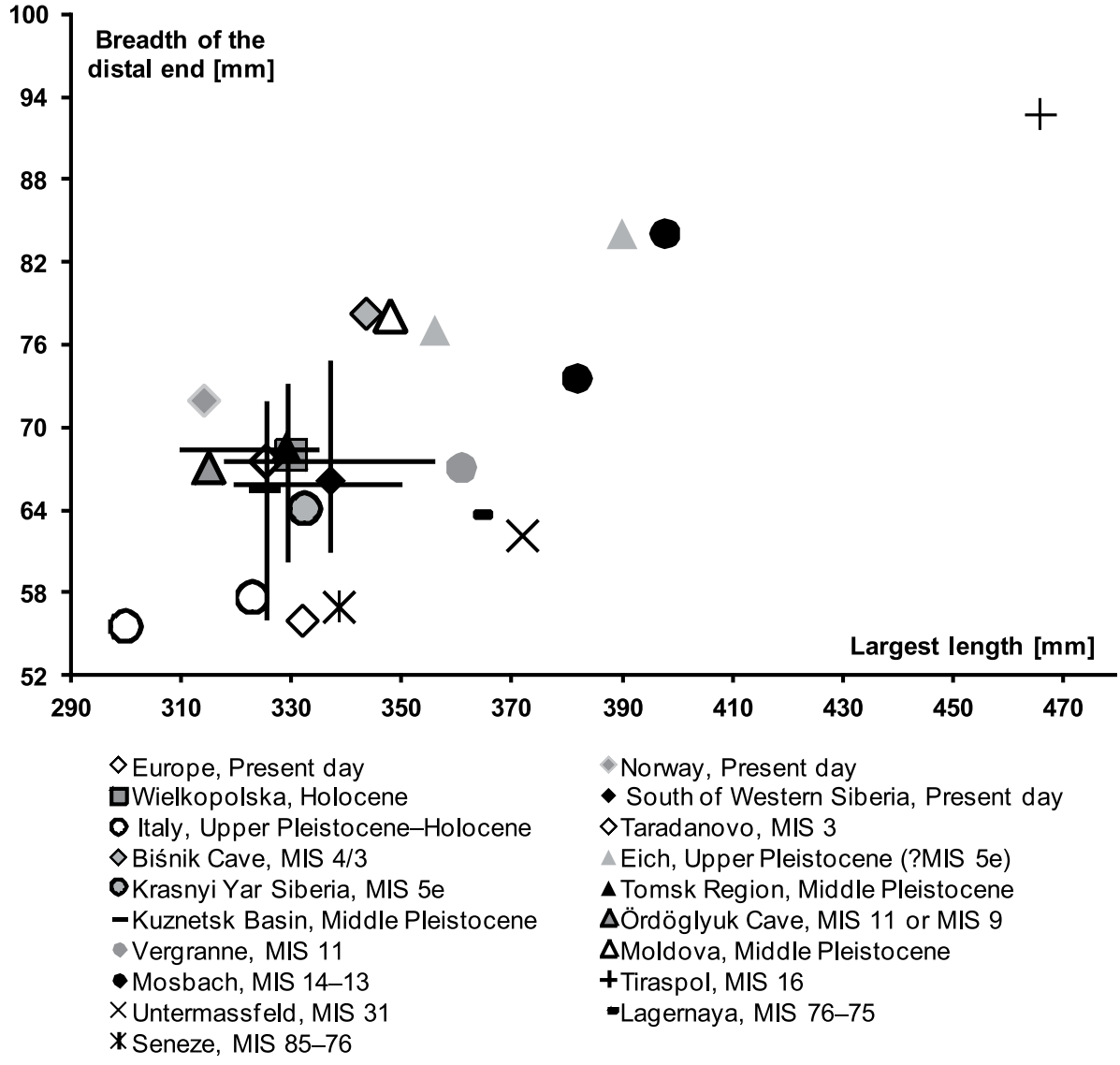


Fig. 11. Greatest length (GL) to breadth ratio of the distal end (Bd) of metacarpus of fossil elks from Polish and Eurasian Quaternary localities. Based on data from Appendix Table 6.

Palaeogeographic implications

In Eurasia, *C. latifrons* was abundant from the Middle Pleistocene (Galerian) till the Upper Pleistocene (Aurelian). It occurred also in North America from the Middle Pleistocene until the Pleistocene/Holocene boundary (Azzaroli, 1952, 1953, 1979, 1981, 1996; Sher, 1971, 1986; Alekseeva, 1977; Bubenik, 1986; Lister, 1986, 1993a, 1996; Vislobokova, 1986, 1990; Churcher and Pinsof, 1987; Azzaroli *et al.,* 1988; Czyżewska, 1989; Kahlke, 1990; Musil, 1995; Franzen *et al.,* 2000; Breda and Marchetti, 2005; Breda *et al.,* 2005; Stefaniak, 2007; Nikolskiy, 2010). Previously, remains of *C. latifrons* were only known in Poland from Kozi Grzbiet. The studies by the authors show that the species was also present at another site – Sitkówka near Chęciny, with an age similar to that of Kozi Grzbiet.

The appearance of the Recent *Alces alces* in Europe, dated as Eemian Interglacial, is confirmed by its occurrence in the deposits of the Dziadowa Skała Cave, dated as MIS 5e. The elk occurred in Poland also at the beginning of the Vistulian Glaciation, as indicated by the presence of its remains in the deposits of the Łokietka Cave, and retreated during the Plenivistulian (MIS 4). It returned for a brief period in the Interplenivistulian, as demonstrated by the few localities in southern Poland, and recolonized the area of Poland at the end of the Pleistocene.

Among sites from the Vistulian Glaciation, a few elk remains were found at the lower cultural levels (the beginning of the glaciation) of the Neanderthal hunters site in Zwoleń (Gautier, 2005) and in stratigraphically unassigned deposits at the Raj Cave (Kowalski, 1972; Patou-Mathis, 2004).

At the beginning of the Vistulian Glaciation, the distribution range of *Alces alces* extended to Italy and the Balkan Peninsula. During the coldest periods of the Vistulian, the

range in Europe became limited to southern and south-western Europe (Musil, 1986, 2010; Czyżewska, 1987). It can be assumed that the species was absent from the territory of Poland during a larger part of the Vistulian. The presence of elk remains in layer XIX of Obłazowa cave, dated as the Grudziądz Interstadial (MIS 3; Valde-Nowak and Nadachowski, 2014) confirms the occurrence of elk in Poland during periods of climate amelioration. Isolated elk remains were found in the late Pleistocene sediments of Borsuka Cave (Wilczyński *et al.,* 2012): a few dozen pendants, made of incisors of this species, and a fragment of a phalanx. One of the pendants was radiocarbon-dated at about 27000 years BP. Remains of a few other taxa clearly indicate warmer conditions and forest environment, e.g. snails, badger, lynx, and beaver, showing that during some periods of the Late Vistulian the environment in southern Poland was suitable also for the elk. Elk records from that period come also from localities in Moravia: Švédův stůl, the Kůlna Cave, Šipka and Prědmostí (Musil, 1961, 1965, 1986, 2008, 2010). At that time, the range of the Recent elk in Europe reached its maximum, extending in the west to central and southern France, northern Italy, Switzerland, the former Yugoslavia, southern Germany, Moldova, Ukraine and the Caucasus. Its distribution was similar to that of the genus *Cervalces* (David, 1980; Musil, 1986; Döppes and Rabeder, 1997; Kahlke, 2000; Breda, 2001b; Breda and Gallini, 2001; Breda and Marchetti, 2005).

At the end of the last glaciation, the elk expanded its range again, as a result of the climate warming in Eurasia (Guthrie, 1995; Schmölcke and Zachos, 2005). At the end of the Pleistocene, with the expansion of boreal forests, it was among the first representatives of forest fauna to recolonize Central Europe, probably from the east and north (Schmölcke and Zachos, 2005). The oldest remains of the species in Central Europe are dated as Allerød and Younger Dryas (locality Dudka; Hundertmark *et al.,* 2002; Gumiński, 2003; Schmölcke and Zachos, 2005; Płonka *et al.,* 2011). In Poland, the oldest elk remains, from the Pleistocene/Holocene boundary, come from south-eastern part of the country and are dated at about 12,000 years BP (Nadachowski, pers. com.). The presence of elk remains in northern Poland should also be mentioned; they are represented by a unique ritual object from Rusinowo in Pomerania, made of antler, dated as 10,700 ± 60 BP (Płonka *et al.,* 2011).

Elk remains were found in the Holocene sediments of different caves of southern and western Poland (Fig. 1): in the Kraków-Częstochowa Upland (Biśnik and Jasna Strzegowska caves, Wschodnie Rock Shelter), Sudety Mts (Radochowska Cave) and Nowy Targ Basin (Obłazowa Cave), as well as in open sites across Poland (Niezabitowski-Lubicz, 1929, 1932; Kowalski, 1959; Szymczyk, 1973a–c; Wyrost, 1989, 1994; Valde-Nowak *et al.,* 2003; Wojtal, 2003, 2007; Wojtal *et al.,* 2004; Socha and Stefaniak, 2006; Bieroński *et al.*, 2007, 2009; Stefaniak *et al.*, 2009b).

At the beginning of the Holocene, *Alces alces* reached its maximum distribution range; then, from the end of the Boreal period, its range began to shrink gradually. With the expansion of deciduous forests and the warming of the climate in the Atlantic period, the species became extinct in south-western Europe, persisting only in Central Europe. The expansion of agricultural tribes and climatic changes in the later part of the Holocene caused the elk to become extinct in most of its earlier range at the end of the Middle Ages. At present, a slow westward expansion of the species is observed, and the western edge of its distribution runs across Poland (Szymczyk, 1973a; Schmölcke and Zachos, 2005).

Stratigraphic implications

The occurrence of *Cervalces latifrons* in Kozi Grzbiet and Sitkówka confirms their Middle Pleistocene age. The accompanying fauna, including the large form of *Cervus elaphus* (Van der Made *et al.,* 2014), as well as stratigraphic data, place Kozi Grzbiet in the Podlasian Interglacial (Cromerian II – Cromerian III; MIS 19–17). The presence of a large form of *Cervalces latifrons* at Sitkówka indicates an age similar to that of Kozi Grzbiet for some of the layers, or younger than Glacial C (San 1 Glacial) – Elsterian (San 2 Glacial); MIS 16–12. As mentioned above, the period from the Holsteinian Interglacial to the Mazovian Interglacial (MIS 11) witnessed a significant decrease in the size of *Cervalces latifrons*.

The presence of *Cervalces* sp. indicates a Middle Pleistocene age of levels 19, 16 and 15 from the Biśnik Cave. Stratigraphic information, isotopic and archaeological dating (Cyrek *et al.*, 2010; Gąsiorowski *et al.*, 2014; Krajcarz *et al.*, 2014; Socha, 2014), as well as the occurrence of the elk all point to MIS 7 as the period of deposition of layer 19. Layers 16 and 15 are similar in age to layer 19 (MIS 7, Röpersdorf-Schöningen Interglacial) or perhaps can be dated as the Odra Glaciation (MIS 6, Drenthe Glacial).

CONCLUSIONS

Elks, the largest extant cervids, came into existence at the end of the Pliocene. In the Lower Pleistocene, their representatives (*Cervalces gallicus*) reached Europe with other cold-adapted mammals. The elks live in a cool, boreal climate and are associated with wetlands, river valleys and various types of forests. The habitat of the extinct Pleistocene elks was similar. Their remains are never numerous in palaeontological material. Representatives of all their evolutionary lineages, including the largest species *Cervalces latifrons*, occurred in the Middle Pleistocene of Poland. The paper describes elk remains from several cave localities, dated as Middle Pleistocene, Eemian interglacial and Vistulian. The extant *Alces alces* came into existence at that time (Eemian Interglacial). The few described remains include teeth, fragments of mandibles and metacarpal bones of *Cervalces* sp. and *Alces alces*. In the Middle Pleistocene and the Eemian Interglacial, the elks occurred in Poland during periods of boreal climate. The presence of the remains of *Cervalces* sp. confirms the Middle Pleistocene age of strata 19–15 in the Biśnik Cave. The only elk locality from the beginning of the Vistulian (MIS 5a–d) in Poland is the Łokietka Cave. Elks were absent from the territory of Poland during a larger part of the Vistulian. Their

isolated remains were found in the late Pleistocene deposits of the Biśnik Cave, the Obłazowa Cave (MIS 3) and the Borsuka Cave (beginning of MIS 2). The elks recolonised the area at the end of the Vistulian Glaciation, during the Allerød and Younger Dryas. In the early Holocene they were rather abundant. As a result of climatic changes and increasing anthropopressure, starting with the Subatlantic period, the elks' distribution range shrank. At present, the western limit of the distributon of the elk crosses Poland. The presence of elk remains at the localities studied indicates the presence of elk-friendly habitats in the environs of the sites. At the sites studied, the elk remains were found in cultural layers associated with human occupancy from the end of the Middle Pleistocene and the beginning of the Vistulian, but probably because of the scarcity of the material, no direct evidence of hunting was found.

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