

## Early and Middle Pleistocene elk (*Alcinae* JERDON, 1874, *Cervidae*, *Mammalia*) from Poland

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**Abstract.** Three alcine species: *Cervalces carnutorum* (LAUGEL, 1862), *Cervalces latifrons* (JOHNSON, 1874) and *Alces alces* LINNAEUS, 1758, were found in Early and Middle Pleistocene sites in Poland. The morphology of the teeth and limb bone fragments of the Early Pleistocene *C. carnutorum* from Żabia Cave and the Middle Pleistocene *C. latifrons* from the Kozi Grzbiet are described in relation to Eurasian representatives of the *Alcinae*. The size of *C. carnutorum* was larger than typical forms of the species from localities in W. Europe. *C. carnutorum* differed from the other elk in its feeding adaptations and diet, and was similar to other cervids, though it was fully adapted to living in wetlands. A single tooth from Kozi Grzbiet has a size and structure typical of *C. latifrons* which was widespread in Holarctic in the Middle Pleistocene.

**Key words:** *Alcinae*, morphometry, palaeoecology, Lower and Middle Pleistocene, Poland.

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### I. INTRODUCTION

This paper contains descriptions of elk remains from the Early Pleistocene deposits of Żabia Cave and Middle Pleistocene deposits of the Kozi Grzbiet. Two species of *Alcinae* were found in these localities: *Cervalces carnutorum* and *Cervalces latifrons*.

Żabia Cave is located north-west of the village of Podlesice and is developed in Oxfordian limestones on the northern slope of mount Sulmów (50°35'N; 19°31'E). The mountain, being a part of the so called Podlesice rocks, belongs to the Zborowsko-Ogrodzienieckie range which is part of the Częstochowa Upland (KONDRACKI 1994; SZELEREWICZ-GÓRNY 1986). It was discovered in 1944 by spar prospectors (KOWALSKI 1951) and in 1978 rediscovered by cavers from the AKSiA club who, after digging through a slump, found previously inaccessible cave corridors with bone remains (MAZIK & LOREK 1979). Since 1979 excavations in Żabia Cave have been conducted by the staff of the Palaeontology Department and the Institute of Geology, Wrocław University.

The cave is a large karstic well (over 18 m deep), with corridors and crevices filled by deposits and its total length is 60 m. It is located at 406.3 m a.s.l. The profile of the deposits is presented in papers of BOSÁK et al. (1982), IVANOV (1997); LINDNER (1992) and SZYNKIEWICZ (1992). Twenty one horizons have been distinguished, mostly with bone remains. Cervid remains were found in horizon 15, composed of brown cave clay with numerous fragments of eroded limestone and bones.

The sediments in Żabia Cave represent eight climatic cycles over the period of their deposition (BOSÁK et al. 1982; SZYNKIEWICZ 1992). Deposits from horizons 14 and 15, with cervid remains, and probably 16, separated by an erosion gap, testify to a period of cooling and increasing humidity of the climate (cycle VI). Hitherto studies indicate a Lower Biharian age of the horizons 6-19a (cycles III-VII), the terminal part of Otwock (Eburon) glaciation and Celestynów Interglacial (Waal). Vertebrate remains clearly indicate that horizons 12 and 15 were deposited in conditions of a cooler climate (the end of Otwock glaciation or the beginning of Celestynów interglacial), with the dominance of temperate climate species. Horizon 17 shows a distinct warming of the climate (Celestynów Interglacial) with increasing proportion of more thermophilous species. The remains include snails, amphibians, reptiles, a few birds, and among the mammals insectivores, bats, lagomorphs, rodents, carnivores, cervids and bovids. The results of studies and descriptions of the bone remains have been published in the papers of: BOSÁK et al. (1982); CROITOR & STEFANIAK (in prep); CZYŻEWSKA (1987, 1989); IVANOV (1997); KOWALSKI (1989); LINDNER (1992); MŁYNARSKI & SZYNDLAR (1989); NADACHOWSKI (1989, 1990); NADACHOWSKI et al. (1989); RZEBIK-KOWALSKA (1989, 1994); STEFANIAK (2001, 2004, in prep.); SZYNDLAR (1984) and SZYNKIEWICZ (1992).

The locality Kozi Grzbiet is located in a deposit-filled karstic crevice formed in Devonian limestones in the Świętokrzyskie Mts, ca. 20 km west of Kielce (50°5'N; 20°21'E). The profile of the deposits includes five horizons. Remains of fauna were contained in the complex of deposits forming horizon 2, deposited during Małopolska interglacial (Cromer II or III Interglacial). Thermoluminescence dating indicates an age of 685-615 thousand years BP, and fluoro-chlorapatite dating – 700-555 thousand years BP (LINDNER 1991, 1992; LINDNER et al. 1995).

The faunal remains indicate a late Biharian age. The fauna includes snails, amphibians, reptiles, birds and mammals including insectivores, bats, lagomorphs, numerous rodents, much diversified carnivores and ungulates. The analysis of the species composition of the animal remains indicates deposition in a woodland environment with a warm, humid climate, although steppe and cool-climate components were also present (BOCHEŃSKI 1989, 1991, 1993; KOWALSKI 1989; LINDNER 1992; MŁYNARSKI & SZYNDLAR 1989; NADACHOWSKI 1989, 1990; NADACHOWSKI et al. 1989; RZEBIK-KOWALSKA 1994; STWORZEWICZ 1981, 1989; WISZNIOWSKA 1989).

The bone material obtained from the two localities includes teeth, or their fragments, and fragmented limb bones.

The tooth structure terminology follows HEINTZ (1970) and OBERGFELL (1957), the limb bone terminology – HEINTZ (1970); KÖHLER 1993, KRYSIAK (1975); POPLEWSKI (1948) and VISLOBOKOVA (1990). The length of maxillary teeth was measured on the labial margin and on the lingual side of the occlusal surface of mandibular teeth. Molar width measurements were based on the first cusp of the tooth, while in premolars the greatest height was measured.

Measurements of jaws and limb bones followed the commonly accepted standards (DRIESCH 1976; DUERST 1930; HEINTZ 1970). Teeth and limb bones were measured with slide caliper to the nearest 0.1 mm. All measurements are given in millimetres. Ranges of variation of measurements are given in tables and in the text where Min and Max denote the range of values, M – the arithmetic mean, N – the number of specimens.

An attempt was made at reconstructing the structure, habitat and mode of locomotion based on the analysis of limb bone and tooth structure, using KÖHLER's (1993) method and FLEROV's (1962) divisions.

The bone remains from the Żabia Cave are stored at the Palaeozoology Department, Wrocław University (collection ZPALUWr/JŻ), the material from Kozi Grzbiet comes from the collection of the Institute of Systematic and Evolution of Animals (MF/KG) and is deposited at the Palaeozoology Department, Wrocław University. The material described in this paper was compared with literature data on fossil elks from Eurasian and North American localities dated as Pliocene, Pleistocene and Holocene, and with bones of recent *Alces alces* LINNAEUS, 1758, from the collection of the Palaeozoology Department and the Natural History Museum, Wrocław University.

## II. SYSTEMATIC PART

Subfamily **Alcinae** JERDON, 1874Genus **Cervalces** SCOTT, 1885***Cervalces carnutorum*** (LAUGEL, 1862)

(Tables I-III; Figs. 1-1F, 2-9)

Locality – Żabia Cave.

Horizon – 15.

**M a t e r i a l.** 37 specimens (ZPALUWr/JŻ/62 - 102) from two individuals: left mandible fragment with P<sub>4</sub>-M<sub>3</sub>; left P<sub>2</sub>, left P<sub>3</sub>, left M<sub>1</sub>, left M<sub>2</sub>; fragment of left M<sub>3</sub>, two I<sub>1</sub> (left and right), two I<sub>2</sub> (left and right), two I<sub>3</sub> (left and right), left canine, right P<sup>2</sup>, right P<sup>3</sup>, right P<sup>4</sup>, right M<sup>2</sup>, right M<sup>3</sup>; left radius (distal epiphysis of a juvenile), right radius (distal epiphysis of a juvenile); a fragment of distal epiphysis of metacarpal; scaphoid; fragment of lunate; fragment of triquetrum; triquetrum; pisiform; fragment of shaft and distal epiphysis of right tibia; two fragments of proximal base of phalanx I; phalanx I; three fragments of distal base of phalanx I (pathological); two fragments of distal base of phalanx II; fragment of phalanx II of a juvenile.

Measurements are given in Tables I-III and in the descriptions.

**D e s c r i p t i o n.** The crown of P<sub>2</sub> is little worn. As a result of partial fusion of the parastylid with the paraconid, valley 1 is very shallow. The anterior wing of the protoconid is small. The metaconid is lower than the protoconid. The endostylid is fused with the entoconid as a result of which valley 4 is closed (Fig. 1A).

The P<sub>3</sub> is slightly worn. The paraconid tubercle is displaced towards the metaconid tubercle and fuses with it at half the height of the crown, resulting in a rather well molarized tooth (initially molarization degree III, then IV). Valley 1 is larger compared to P<sub>2</sub>. The posterior metaconid wing is close to the entoconid.

The P<sub>4</sub> is much worn, with the anterior part of the preserved crown. The tooth is strongly molarized (degree V). The paraconid is fused with the parastylid and the metaconid, and the entoconid with the endostylid (Fig. 1B).

The molars have low crowns. The lingual walls of these teeth are strongly inclined towards the labial walls. M<sub>1</sub> has a well-developed cingulum on the anterior wing of the protoconid. On the posterior wing of the hypoconid a small cingulum is present. On the lingual side a pronounced metastylid (3.9 mm thick) and a smaller entostylid (2.7 mm thick) reaching up to 1/2 of the crown height. The metaconid and entoconid tubercles are less developed (ca. 2 mm thick). Nearly all stylids and cusp tubercles except the entostylid reach up to 2/3 of the crown height. In the less worn specimen (ZPALUWr/JŻ/65), on the internal side of the protoconid, from its apex to the base, united with the ectostylid tubercle, there is an oblique enamel convexity which may be interpreted as a remain of paleomeryx fold (Fig. 1E). Such a structure of the M<sub>1</sub> is visible in illustrations of elk teeth from East Runton (AZZAROLI 1953).

The structure of M<sub>2</sub> is similar to the M<sub>1</sub>. The metaconid, entoconid and metastylid are ca. 3 mm thick, the thickness of entostylid being 2.1 mm. On the inner side of the protoconid a poorly developed enamel convexity is visible.

In the M<sub>3</sub>, on the internal side of the protoconid, no enamel convexity is marked which could be the remains of a paleomeryx fold (Fig. 1F).

A fragment of left mandibular bone of an adult with greatly worn teeth includes the posterior part of the mandible body with P<sub>4</sub>-M<sub>3</sub> (crowns of P<sub>4</sub> and M<sub>3</sub> are damaged). The mandibular ramus has no angular process, and somewhat damaged condylar and coronoid processes. The mandible shaft and the mandible ramus form a more acute angle (96°) compared to that in the recent elk (110°). The mandible ramus is relatively high, like that in the elk (Fig. 2). The mandible width behind the M<sub>1</sub> is 35 mm, the height 58 mm, behind the M<sub>2</sub> the width is 35.3 mm and behind the M<sub>3</sub> it is 30.7 mm.

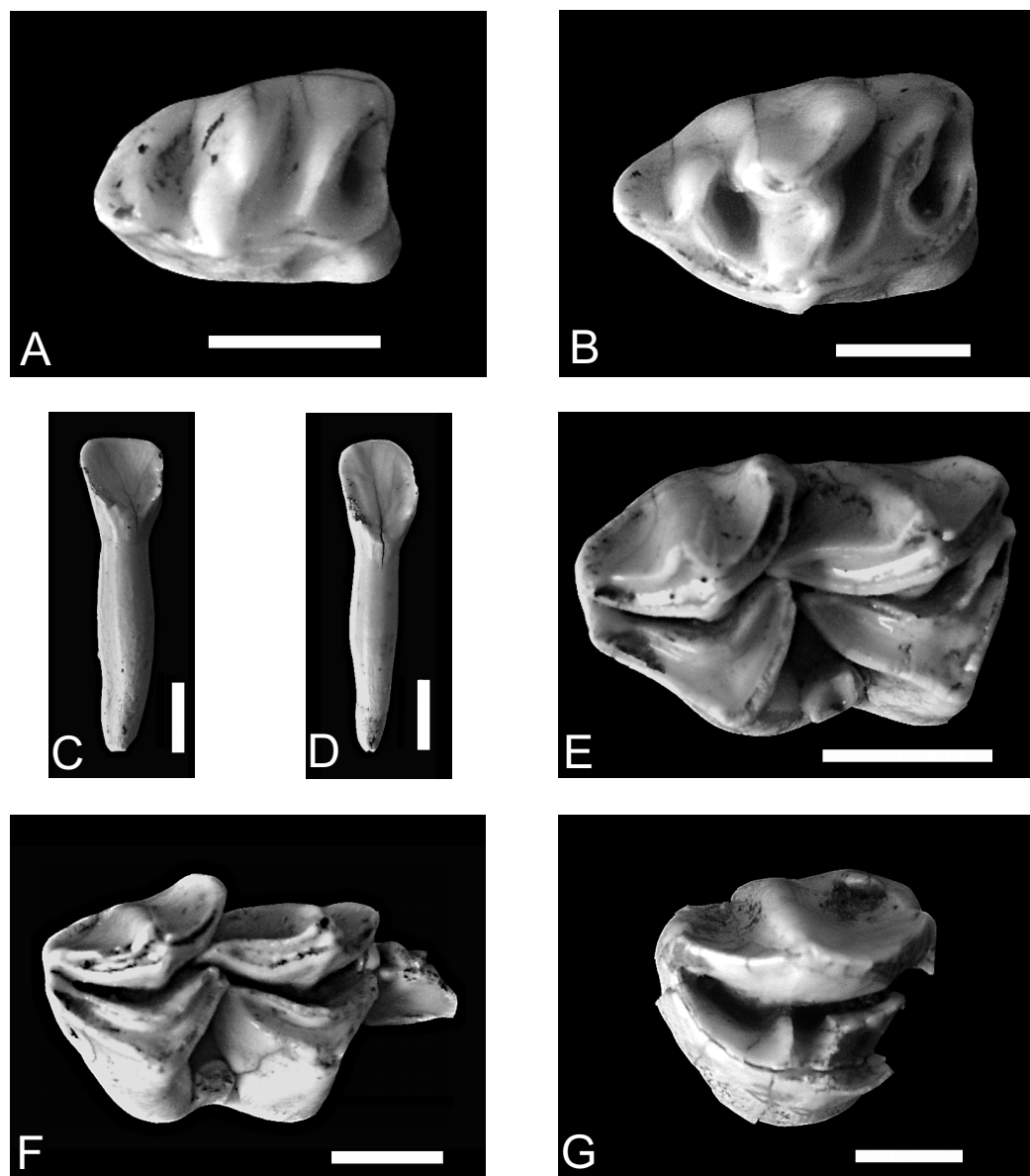


Fig. 1. A – Żabia Cave, left  $P_2$  (ZPALUWr/JŻ/63) in occlusal view of *Cervalces carnutorum*; B – Żabia Cave, left  $P_4$  (ZPALUWr/JŻ/64) in occlusal view of *Cervalces carnutorum*; C – Żabia Cave, left  $I_1$  (ZPALUWr/JŻ/70) in occlusal view of *Cervalces carnutorum*; D – Żabia Cave, left  $I_2$  (ZPALUWr/JŻ/71) in occlusal view of *Cervalces carnutorum*; E – Żabia Cave, left  $M_1$  (ZPALUWr/JŻ/65) in occlusal view of *Cervalces carnutorum*; F – Żabia Cave, left  $M_3$  (ZPALUWr/JŻ/66) in occlusal view of *Cervalces carnutorum*; G – Kozi Grzbiet, right  $P^3$  (MF/KG/20) in occlusal view of *Cervalces carnutorum*. The scale bar is 10 mm and applies to all figures.



Fig. 2A. Żabia Cave. Left mandible (ZPALUWr/JŻ/62) with  $P_4 - M_3$  in labial view of *Cervalces carnutorum*. The scale bar is 10 mm.

Table I

Measurements of premolar teeth of *Cervalces carnutorum* from the Żabia Cave

Tooth	N	L	W
$P_2$	1	19.1	14.2
$P_3$	1	23.9	15.6
$P_4$	1	27.5	20.4
$P^2$	1	20.6	21.9
$P^3$	1	22	25.9
$P^4$	1	22.3	27.6

The crown of  $I_1$  is slightly asymmetrical and chisel-shaped. The internal wall in contact with  $I_2$ , is somewhat bent (Fig. 1C). Crown length 12-12.1 mm; crown length at its base 8.9-9.1 mm; crown height 10.6-11.3 mm.

The  $I_2$  is chisel-shaped and slightly bent towards the  $I_3$  (Fig. 1D). Its length at the top of the crown is 11.6-11.8 mm; the length at the crown base is 7.9-8.4 mm; the crown height is 13.1-13.4 mm.

The shape of the  $I_3$  is similar to the  $I_2$ , but it is smaller. The tooth length at the top of the crown is 8.1-8.2 mm; the length at the base of crown is 6.3-6.4 mm; the crown height is 12 mm.

The lower canine is small and similar to the incisors. Its length at the crown edge is 6.1 mm; the length at the base of crown is 5.7 mm.

The lingual wall of the upper premolars is strongly inclined towards the labial wall. The  $P^2$  has on its lingual wall a slight concavity dividing the tooth crown in two cusps. At the base of the crown there is a small cingulum. The labial side bears a thick parastylid and a slightly smaller paracone tubercle. The mesostyle is poorly marked. The styles and tubercles are fused at the base of the crown. The paracone is displaced towards the parastyle, making the tooth crown asymmetrical.

The  $P^3$  has its crown worn on the entire surface. On the labial side there is a groove, deeper than in the  $P^2$ , dividing the crown in two parts. At the base of the metastyle a tubercle of enamel is present. The remaining elements of the tooth are developed similarly to those in  $P^2$  (Fig. 3A).

In the  $P^4$ , contrary to the remaining premolars, the paracone tubercle is located almost in the middle of the lingual wall making the crown symmetrical. On the lingual side there is a deep groove, separating the protocone and the hypocone. Like in the  $P^3$ , at the base of metastyle an enamel tubercle is present, while between the paracone and the parastyle a smaller enamel tubercle is present (Fig. 3B).

The crown of the  $M^2$  is worn on the entire occlusal surface. Like in the premolars, the lingual wall is strongly inclined towards the labial wall, which in turn is slightly inclined to the middle of the tooth. On the labial side there is an entostyle reaching to a 1/3 of the crown height. The protocone fold is strongly developed. On the hypocone a large spur is present. Both these structures fuse, as a result of crown wear, with the posterior protocone wing and posterior hypocone wing. At the base of crown a poorly marked cingulum is visible. On the lingual side the thickest stylid is the parastyle (3.2 mm), the mesostyle thickness is 2.8 mm and the paracone tubercle diameter is 2.9 mm. The metacone tubercle thickness is 2.1 mm. The mesostyle is poorly developed. The tubercles and stylids are fused at the base of the crown and reach almost to its top (Fig. 3C).

The  $M^3$  is slightly worn. The large entostyle reaches up to 1/2 of the crown height. The tooth structure on the lingual side is like that of the  $M^2$ . At the base of the crown, on the labial side, a characteristic enamel collar is developed which connects the metastyle with the mesostyle, and is provided with a small tubercle at the height of metacone. The metacone tubercle is well developed (Fig. 3D).

Table II

Measurements of molar teeth in *Cervalces carnutorum* from the Żabia Cave

Tooth	N	L	M	W <sub>ant.</sub>	M	W <sub>post.</sub>	M
$M_1$	2	25.3-25.9	25.6	18.1-18.3	18.2	20-20.4	20.2
$M_2$	2	27.6-28.8	28.2	20.3-20.5	20.4	21.2-21.9	21.55
$M_3$	2	37.7-40.2	38.95	20	—	21.2	20.4
$M^2$	1	30.8	—	28.9	—	27.4	—
$M^3$	1	29.1	—	28.8	—	27.5	—

Greatly damaged distal epiphyses of right and left radii come from the same juvenile individual. Both epiphyses are large, with strongly developed, deep surfaces for carpal bones, in the shape of obliquely running trochleae (Fig. 3E). The widths of the distal bases are 69 and 70.4 mm, their antero-posterior lengths are 36 and 37.5 mm.

Among the material only bones of the carpal proximal row are represented, probably coming from one individual. All the carpal bones have a structure characteristic of elk, are relatively high and not flattened. The length of the scaphoid is 47.5 mm and its height is 37.5 mm. The width of the lunate is 30 mm and the height is 35.7 mm.

Of the metacarpal bones, only a fragment of the distal part of a bone is preserved. This fragment of shaft has well-developed inferior median orifices, anterior and posterior, that are visible as well



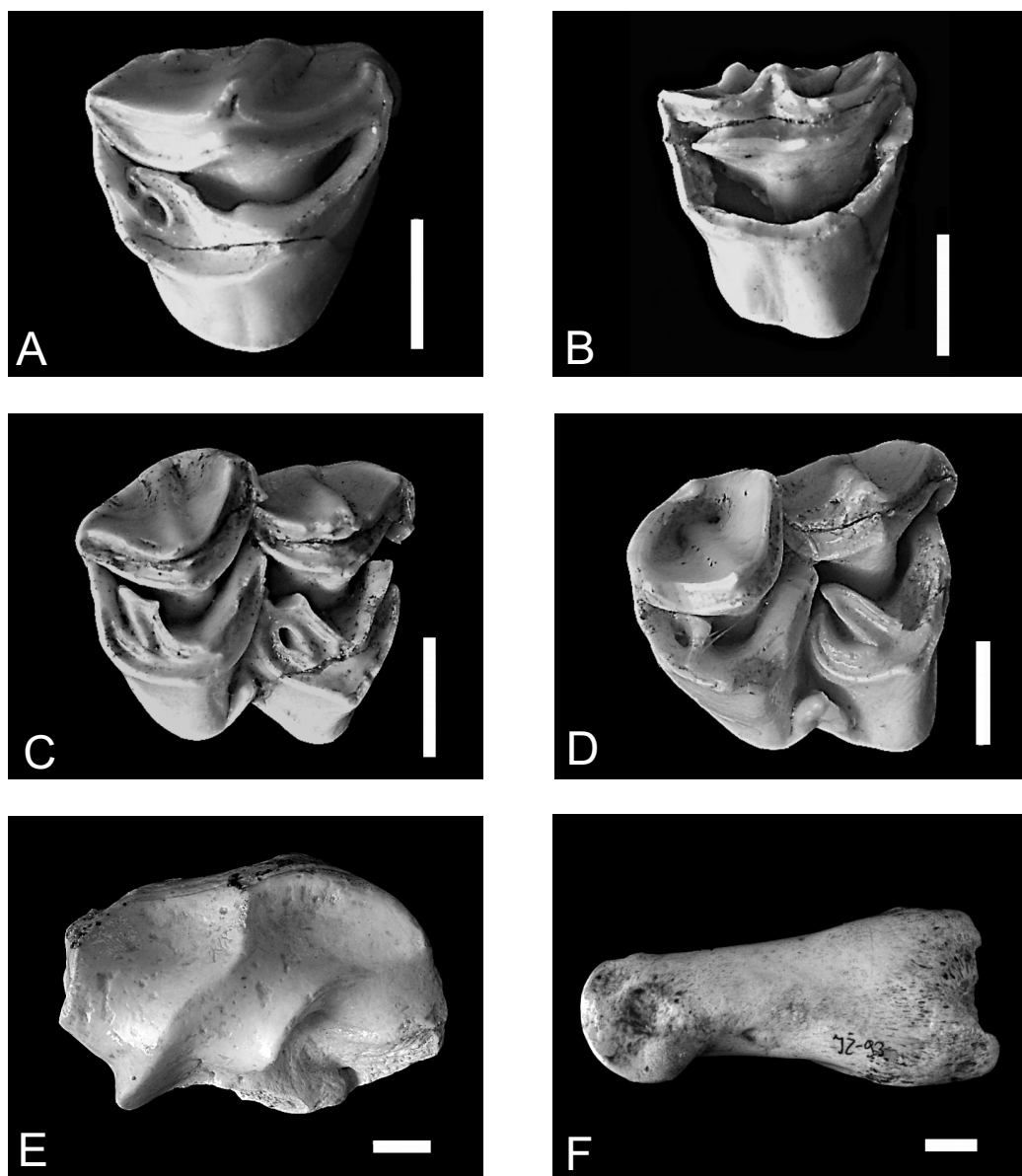


Fig. 3. Żabia Cave. A – right P<sup>3</sup> (ZPALUWr/JŻ/77) in occlusal view of *Cervalces carnutorum*; B – right P<sup>4</sup> (ZPALUWr/JŻ/79) in occlusal view of *Cervalces carnutorum*; C – right M<sup>2</sup> (ZPALUWr/JŻ/80) in occlusal view of *Cervalces carnutorum*; D – right M<sup>3</sup> (ZPALUWr/JŻ/81) in occlusal view of *Cervalces carnutorum*; E – distal end of the left radius (ZPALUWr/JŻ/83) young specimen of *Cervalces carnutorum*; F – phalanx I (ZPALUWr/JŻ/93) in lateral side of *Cervalces carnutorum*. The scale bar is 10 mm and applies to all figures.

as the one of trochleae. The median anterior orifice is deep. The saggital crest of the trochlea is strongly developed.

The fragment of right tibia includes a part of the shaft with the crest. On the posterior surface of the shaft muscle ridges are visible. The distal shaft has a preserved lateral surface and an articular surface for the lateral bones.

The first phalanges are large and strongly elongated. The saggital pit is deep, the internal articular surface is high and saggitally elongated, with a nearly rectangular sesamoid articular surface on the posterior margin. On the dorsal surface of the internal side of the shaft a clear protuberance is developed. On the posterior (sole) surface of the shaft, at it base, strong tubercles are developed: one smaller, externally located and reaching to a 1/3 of the phalanx length, another larger, reaching nearly a 1/2 of the phalanx length. The lateral sole tubercles are poorly developed. The internal ligamental pit on the distal surface is strongly developed. Phalanx no ZPALUWr/JŻ/93 has well-developed, flattened and widened sole surfaces of articular trochlea of the distal base (Fig. 3F). Compared to the previously preceding phalanx, it is longer and more massive which may indicate its origin from a hind leg skeleton. The articular trochleae of two specimens (ZPALUWr/JŻ/98-99) have deformities visible which may result from pathological changes. Measurements and variation of phalanx I of the elk from the Żabia Cave and Eurasian Pleistocene and Holocene are given in Table III.

Table III

Measurements of phalanx I of *Cervalces carnutorum* from the Żabia Cave

Measurement	Min-Max	M	N
DAP <sub>ant.</sub>	37-40.8	38.37	4
DT <sub>ant.</sub>	29.3-33.2	31.5	4
DAP <sub>post.</sub>	25.2-27.5	26.68	6
DT <sub>post.</sub>	25.5-27.5	26.62	6

The articular surface of phalanx II has a concavity divided in two pits, a smaller internal one and a larger external pit. The extensor process is poorly developed. The ligamental tubercles protrude little. The measurements are: DAP<sub>ant.</sub> – 37 mm; DT<sub>ant.</sub> – 28.9 mm.

**R e m a r k s.** The structure of the teeth and limb bones of the elk from the Żabia Cave is in agreement with the description of fossil remains of the elk *Cervalces gallicus*, *Cervalces carnutorum* and *Cervalces latifrons* (AZZAROLI 1979, 1981, 1985, 1994; CHURCHER & PINOFS 1987; HEINTZ 1970; HEINTZ & POPLIN 1981; KAHLKE H. D. 1960, 1965, 1969, 1990, 1997, 2001; MÄUSER 1990; PFEIFFER 1999 b; VISLOBOKOVA 1992). The analysed material also resembles that of recent *A. alces*. All teeth have relatively low crowns and their wear pattern is characteristic of fossil and recent elk. The structure of lower premolars with a high degree of molarization, especially in the P<sub>3</sub> and P<sub>4</sub>, is close to that in the teeth of fossil elk from the Forest Bed Formation. The crowns of the upper teeth have strongly inclined labial and lingual walls, characteristically developed tubercles, styles and cingula. Also, the upper molars have a strongly developed protocone fold, forming an island characteristic of elk teeth. The lower molars of the elk from Żabia Cave, especially the protoconid of the M<sub>1</sub>, have an enamel ridge. The ridge is interpreted by some authors as a trace of a paleomeryx fold (AZZAROLI 1952, 1953, 1979, 1981, 1985, 1994; CHURCHER & PINOFS 1987; HEINTZ 1970; VISLOBOKOVA 1992) or as an enamel ridge formed as a result of compressing components of the tooth crown (HEINTZ & POPLIN 1981). The presence of the remains of a paleomeryx



fold is by many authors regarded as a diagnostic feature of *C. gallicus* (AZZAROLI 1952, 1953, 1981, 1994; CHURCHER & PINSON 1987; HEINTZ 1970; HEINTZ & POPLIN 1981; KAHLKE H. D. 1956, 1958, 1971a, b, 1990; MÄUSER 1990; VISLOBOKOVA 1990). The same is true of the degree of molarization of the premolars. The importance of this character in the evolution of elk (and deer in general) was stressed, among others, by HEINTZ 1970; MÄUSER 1990 and VISLOBOKOVA (1990). BREDA (2001), BREDA et al. (2005) and PFEIFFER (1999a) suggest that, because of a wide variation among cervids in the degree of molarization of their premolars, the character is of no particular importance. However, in my opinion structural characters of teeth should be considered, and their variation is smaller than that of antlers which are a very important identification criterion; compared to antlers they vary less individually, with age and due to the effects of hormonal and environmental factors.

The size of teeth, stressed by all the authors mentioned, is an important criterion of species identification. Besides this, antler size and proportions are an important criterion in identification of fossil elk, as shown by BREDA & MARCHETTI (2005). Comparison of the size of teeth of the fossil elk from the Żabia Cave with the size of teeth of fossil and Holocene elk reveals that they are close to the teeth of *C. gallicus* from Senèze and localities in England (AZZAROLI 1953; HEINTZ 1970), but smaller than those of *C. latifrons* from Eurasian localities (KAHLKE H. D. 1956, 1958, 1960, 1965, 1969, 1971, 1972, 1997, 2001). They are similar in size to the teeth of Holocene and recent elk (SZYM CZYK 1973c), and to molars of *C. carnutorum* from Saint-Prest, and smaller than teeth of this species from Untermassfeld (HEINTZ & POPLIN 1981; KAHLKE H. D. 1997, 2001) (Figs 4-8; Tables I-II).

The differences in the structure of teeth and mandible include a sharper angle between the mandible shaft and ramus in the elk from the Żabia Cave, compared to recent elk, and a different (the shape of an asymmetrical spade) structure of the first incisor. According to FLEROV (1962) recent *A. alces* has an I<sub>1</sub> with symmetrical walls as an adaptation to feeding on bark, leaves and twigs. In their structure, the incisors of *C. gallicus* resemble the teeth of cervids that feed on a mixed diet, including both the leaves of trees and shrubs as well as herbaceous plants. This may suggest a differ-

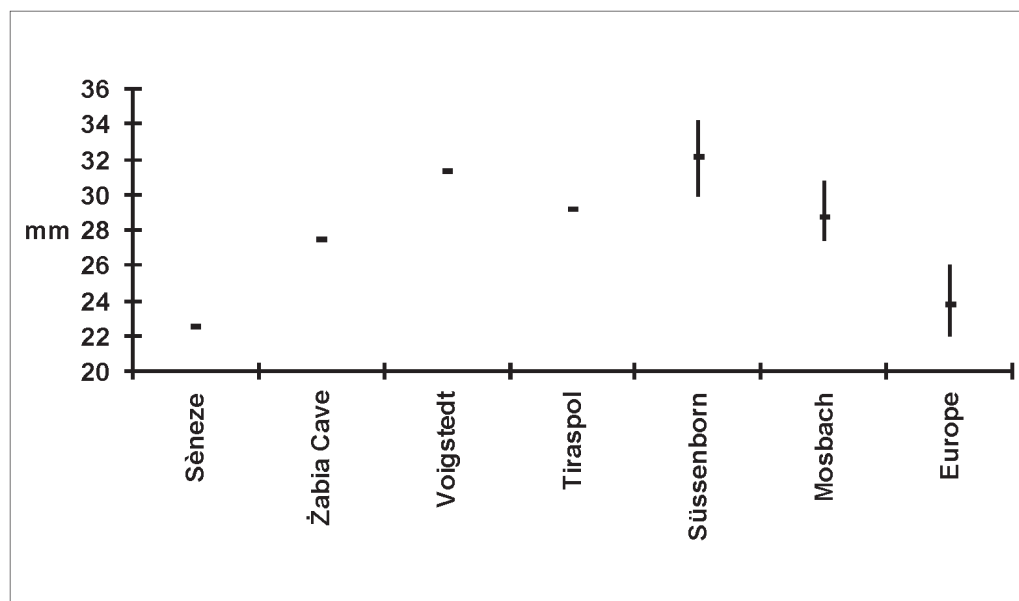


Fig. 4. Variation of length of tooth P<sub>4</sub> in elks of the Eurasian Pleistocene genus *Cervalces* SCOTT, 1885 and the Central European Holocene *Alces alces*.

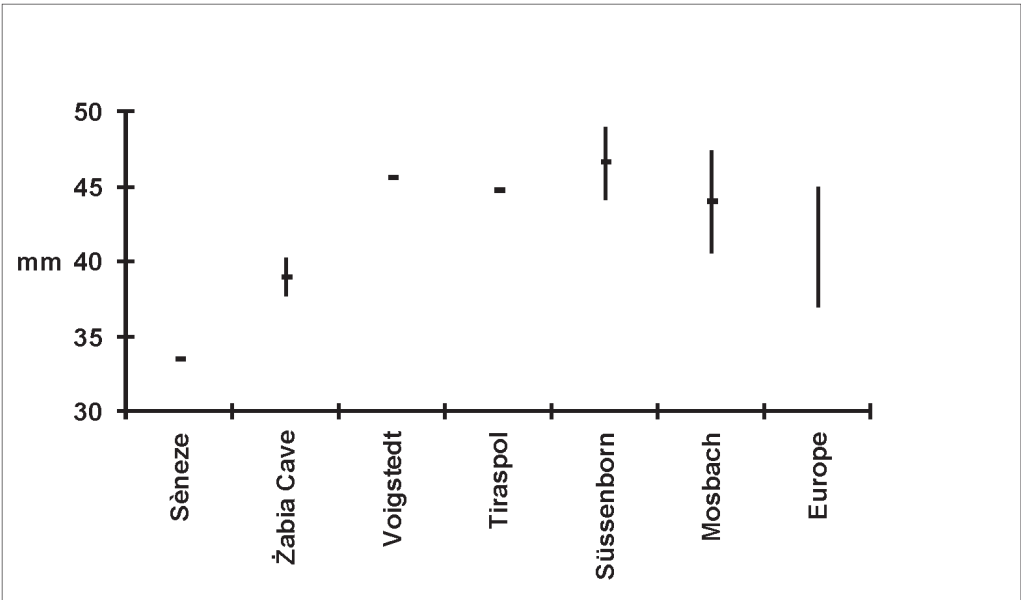


Fig. 5. Variation of length of tooth  $M_3$  in elks of the Eurasian Pleistocene genus *Cervalces* SCOTT, 1885 and the Central European Holocene *Alces alces*.

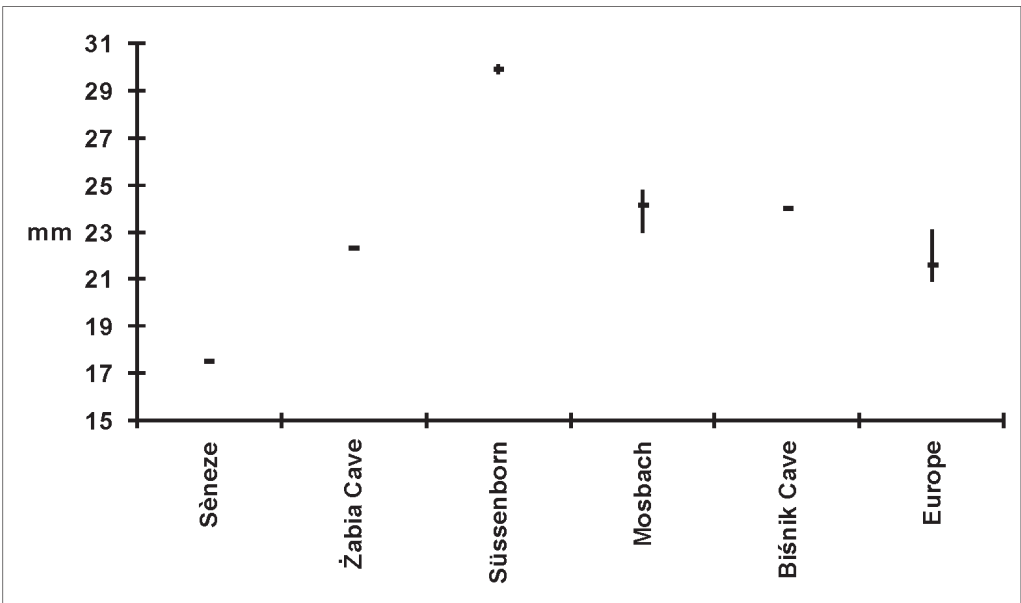


Fig. 6. Variation of length of tooth  $P^4$  in elks of the Eurasian Pleistocene genus *Cervalces* SCOTT, 1885 and the Central European Holocene *Alces alces*.

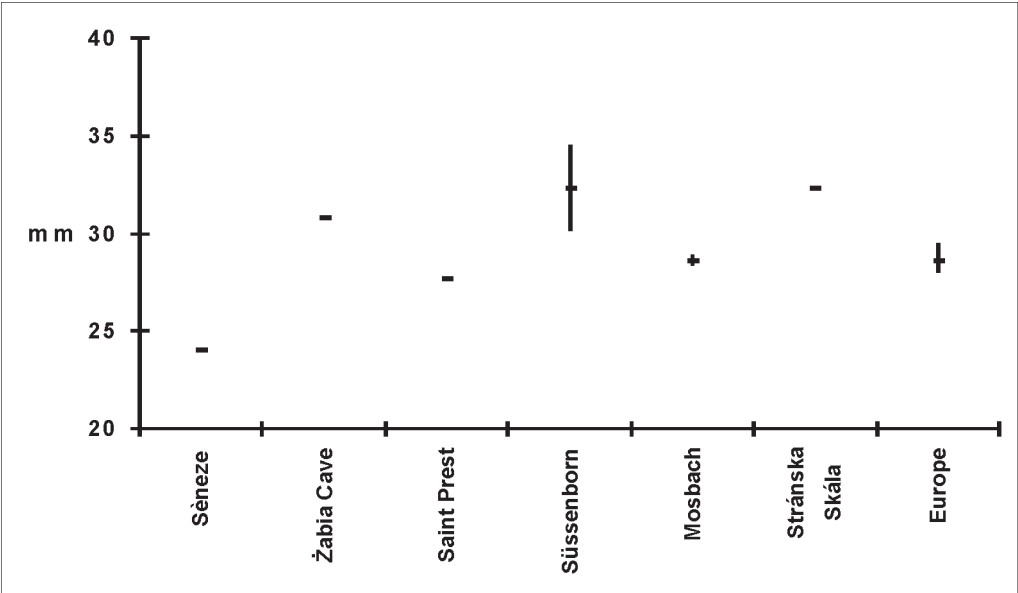


Fig. 7. Variation of length of tooth  $M^2$  in elks of the Eurasian Pleistocene genus *Cervalces* SCOTT, 1885 and the Central European Holocene *Alces alces*.

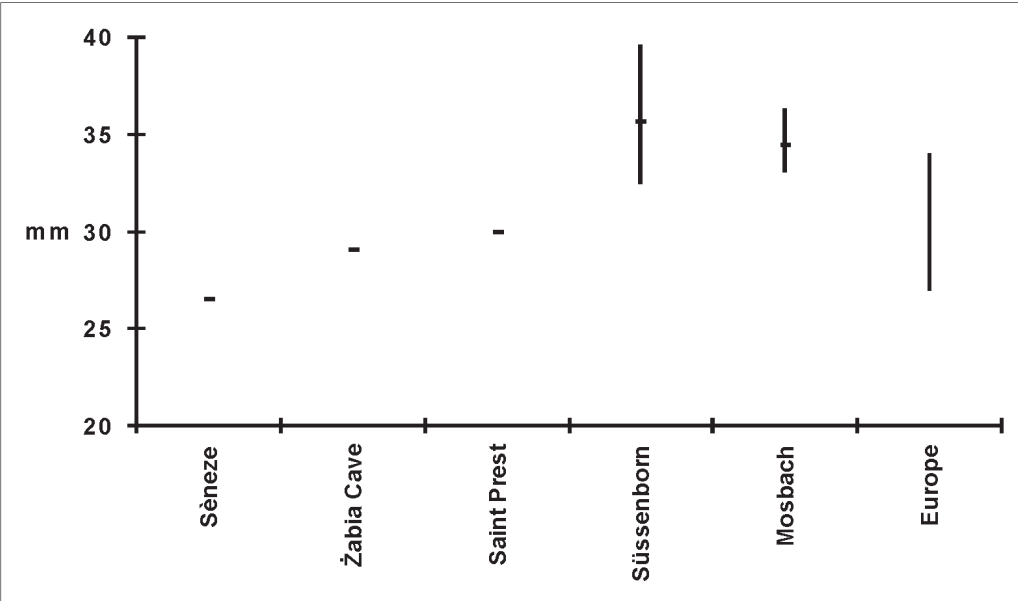


Fig. 8. Variation of length of tooth  $M^3$  in elks of the Eurasian Pleistocene genus *Cervalces* SCOTT, 1885 and the Central European Holocene *Alces alces*.

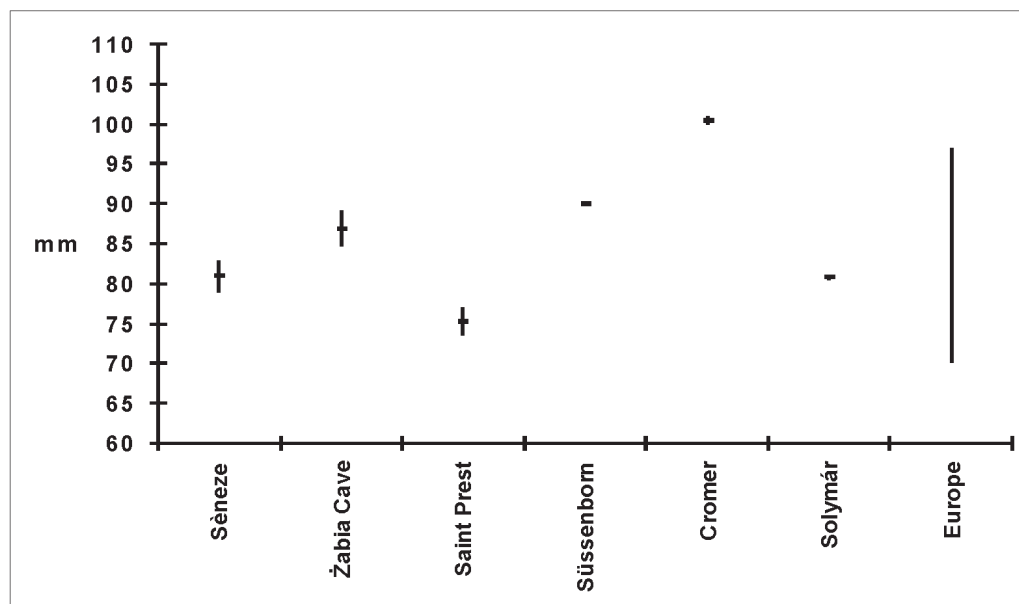


Fig. 9. Variation of length of phalanx I in elks of the Eurasian Pleistocene genus *Cervalces* SCOTT, 1885 and the Central European Holocene *Alces alces*.

ent feeding behaviour and manner of mastication, and also a different food composition compared to *A. alces*. This is in agreement with observations of AZZAROLI (1994), who, based on differences in the structure of the viscerocranium between representatives of the genera *Cervalces* and *Alces*, suggested a different habitat and feeding mode in the two groups. On the other hand, according to BREDA et al. (2005) the genera were adapted to similar habitats and fed on a similar kind of vegetation.

The size of the few preserved remains of limb bones, like the size of the teeth and mandible, is close to those of *C. gallicus* from Senèze, smaller than that of *C. latifrons* and *C. carnutorum*, and similar to the size of bones of the Holocene and recent elk (Fig. 9; Table III). The structure of skeletal parts described here does not differ from the limb bone structure in recent elk and other fossil elk. All carpal bones have a structure characteristic of elk, are high and not flattened which is associated with the characteristic locomotion of elk (VISLOBOKOVA 1990). This is in agreement with CZYŻEWSKA's (1987) suggestion of a similar mode of locomotion in representatives of the genus *Cervalces* and recent elk. Long limbs facilitated movement among thick vegetation, tree trunks and overcome aquatic obstacles.

The structure of metacarpal and metatarsal bones as well as phalanges of the elk from the Żabia Cave, and the structure of such bones in other representatives of the genus *Cervalces* (AZZAROLI 1952; KAHLKE 1965, 1969; PFEIFFER 1999; VISLOBOKOVA 1988; VÖRÖS 1985) may suggest that the elk of this genus were adapted to living in woodlands with waterbodies (wetlands). The metapodia are of type A<sub>2</sub>, phalanges of type A. Proportions between particular sections in most elk are the following: Radius>Metacarpus<Humerus; Tibia>Femur>Metatarsus, except *C. gallicus*, in which Radius>Metacarpus=Humerus; Tibia>Metatarsus. In ruminants of wetland habitats limb bones become shortened and the proportions are roughly equal: Radius=Metacarpus>=Humerus; Tibia>=Femur>Metatarsus (KÖHLER 1993). The existing differences in the proportions of limb

bones, compared to other ruminants living in wetlands, may be explained by the specific life style of elk which, besides living in wetlands and feeding on aquatic vegetation, also eat leaves, bark and twigs of trees at higher levels.

The structure of the above-described premolars and molars does not depart from such structure in recent elk (*A<sub>4</sub>*), which suggests feeding on a similar diet.

The length of limbs of ancestral elk facilitates movement in water. Such forms could also live in forest edges, among shrubs. Their large size facilitated obtaining food – leaves and young twigs – from higher vegetation which is difficult of access for smaller deer. They can also utilize low-growing herbaceous vegetation, which is indicated by the structure of incisors of the elk from the Żabia Cave, with slightly asymmetrical crowns. It is possible that elk of the genus *Cervalces* lived in shrubland in river valleys, among water bodies, in woodland near water bodies or in open areas (Breda et al. 2005).

The deposits from the Żabia Cave, where the elk remains were found, based on geological data and accompanying fauna (including the deer *Metacervoceros rhenanus* (DUBOIS, 1904) (STEFANIAK in press), have been dated as lower Biharian – 1.4–1.2 M years BP, which corresponds with the occurrence of *C. carnutorum* (1.8–ca 1.05 M years BP) (Breda et al. 2005; LISTER 1993a, 1996).

The analysis of the material and literature data indicates that the remains of this elk from Żabia Cave probably represent *C. carnutorum*. The above-mentioned characters of the teeth, mandible and limb bones of *C. carnutorum* suggest that during deposition of horizon 15 in Żabia Cave, woodland, open habitats and water courses were present in the area.

**G e o g r a p h i c a l a n d t e m p o r a l d i s t r i b u t i o n.** Remains of *C. carnutorum* are known from over 10 localities in Europe and Central Asia from the Lower Pleistocene (ALEKSEEVA 1977; AZZAROLI 1952, 1979, 1981, 1994; AZZAROLI et al. 1988; BAJGUSHEVA 1971; Breda et al. 2005; CZYŻEWSKA 1989; HEINTZ 1970; HEINTZ & POPLIN 1981; HEINTZ et al. 1971; KAHLKE H. D. 1990; KAHLKE R. D. 1994; LISTER 1996; MALEZ 1986; VISLOBOKOVA 1986, 1988, 1990). The locality of Żabia Cave is the only locality with this elk in Poland.

### *Cervalces latifrons* (JOHNSON, 1874)

(Fig. 1G)

Locality – Kozi Grzbiet.

Horizon – 2c.

**M a t e r i a l.** Fragment of left P<sup>3</sup> (MF/KG/19)

**D e s c r i p t i o n.** The crown of the P<sup>3</sup> has a damaged lingual wall (Fig. 1G). The tooth length is 25.5 mm and its width is 25.7 mm. There is no groove separating the protocone and the hypocone. On the labial side of the tooth there is a thick parastyle (the thickness at the base of the crown is 7.5 mm) and the paracone tubercle (the thickness at the base is 6.5 mm). Near the metastyle there is a cingulum ridge characteristic of elk teeth which is 7.1 mm high and 4.5 mm thick.

**R e m a r k s.** The morphology of the above-described tooth is typical of teeth of fossil species *C. gallicus*, *C. carnutorum*, *C. latifrons* and recent *A. alces*. The most important diagnostic characters are: the structure of labial wall of the tooth, strong cingulum, and also characteristic, strongly inclined and low walls of the tooth. The assignment to *C. latifrons* is also supported by the large size of the premolar, within the range of variation of P<sup>2</sup> of *C. latifrons* from European localities (KAHLKE H. D. 1956–1959, 1958, 1960, 1965, 1969), larger than P<sup>2</sup> of *C. gallicus*, *C. carnutorum* and recent *A. alces*.

*C. latifrons*, the largest fossil elk, was larger than *A. alces*. Compared to *C. gallicus* and *C. carnutorum* it was larger at the shoulder, possesses higher crowned and more massive teeth, combined with reduction of some components of the crown, as well as changes in proportions and structure of the skull. These characters may suggest an adaptation to a colder and more variable climate of the Middle Pleistocene, with steppe and cold steppe habitats, as well as taiga and mixed woodlands

(AZZAROLI 1981, 1994; BUBENIK 1986; CHURCHER & PINSOFF 1987; CZYŻEWSKA 1987; KAHLKE H. D. 1990; KAHLKE R. D. 1994; KURTÉN 1968; HEINTZ & POPLIN 1981; LISTER 1984, 1993b; VISLOBOKOVA 1990). The presence of remains of this species in Kozi Grzbiet indicates that during the Małopolska Interglacial (Cromer II or III Interglacial) the locality was situated in an area covered by a boreal forest, with water bodies and open areas.

**D i s t r i b u t i o n.** *C. latifrons* was common in Eurasia from the Middle Pleistocene (Galerian) to the Upper Pleistocene (Aurelian). From the Middle Pleistocene to the Pleistocene/Holocene boundary it occurred in North America (ALEKSEEVA 1977; AZZAROLI 1952, 1981, 1994, 1996; AZZAROLI et al. 1988; BREDÁ & MARCHETTI 2005; BREDÁ et al. 2005; BUBENIK 1986; CHURCHER & PINSOFF 1987; CZYŻEWSKA 1989; DAVID 1980; GLIOZZI et al. 1997; HEINTZ 1970; KAHLKE H. D. 1971 a, b, 1990, 1995; KAHLKE R. D. 1994; LISTER 1986, 1993a, 1994, 1996; MALEZ 1986; MUSIL 1995; TSOUKALA 1992; SARDELLA et al. 1998; VISLOBOKOVA 1986, 1990). Kozi Grzbiet is the only locality with *C. latifrons* in Poland.

### III. DISCUSSION

The phylogeny and systematics of elk, in spite of the fact that it attracted attention of many authors (AZZAROLI 1979, 1981, 1985, 1994; BREDÁ & MARCHETTI 2005; BUBENIK 1986; CHURCHER & PINSOFF 1987; CZYŻEWSKA 1987; HEINTZ & POPLIN 1981; KAHLKE H. D. 1990, 1997, 2001; KAHLKE R. D. 1994; LISTER & PIJLEN 1990; MÄUSER 1990; PFEIFFER 1999a; SHER 1987; VISLOBOKOVA 1986, 1990), is still insufficiently studied and controversial. Within the subfamily *Alcinae* JERDON, 1874 three main genera have been distinguished: *Alces* GRAY 1821; *Cervalces* SCOTT 1885; *Libralces* AZZAROLI 1952. In addition, two further genera have been described from the area of the former USSR (Ciscaucasia): *Tamanalces* VERESHCHAGIN 1957 and *Pseudalces* FLEROV 1962, and have a questionable status and relevance to fossil elk (AZZAROLI 1979, 1981, 1985, 1994; FLEROV & SHEVRYEVA 1963; HEINTZ & POPLIN 1981; KAHLKE H. D. 1990; VISLOBOKOVA 1986, 1990). There are differences of opinion among authors on the generic affiliation of the described specimens, and consequently on different directions of elk evolution. Arguments also exist about whether Eurasian elk should be regarded as one genus *Alces* (HEINTZ & POPLIN, KAHLKE, LISTER, MÄUSER, PFEIFFER) or, as postulated by Azzaroli and other authors, as two genera: *Cervalces* and *Alces*. VISLOBOKOVA mentions all the genera listed above.

*C. gallicus* is regarded as the oldest species of "typical elk" (2-1.2 M years; LISTER 1993a, 1996). The biometrical analysis of remains of this species indicates that it was a large form, though smaller than younger Pleistocene elk, with long stem antlers (more than 500 mm long), wave-like and with a small blade, and long spines on the margin. The sizes and proportions of particular limb bones were similar to those of recent elk, except the metacarpal bones which were longer. In recent years some authors (BREDÁ 2001; BREDÁ & MARCHETTI 2005; KAHLKE H. D. 2001) have postulated a shorter time span of the occurrence for the species (2.55-1.8 M years).

*C. carnutorum* originates from the boundary of the Lower and Middle Pleistocene. It is a form first described based on few remains (fragments of maxillae and frontal bones with antler bases) by HEINTZ & POPLIN (1981). Recently, GUÉRIN et al. (2003) in their revision of the Saint-Prest locality have described further remains of the species. Outside France, it has been found in Untermassfeld (KAHLKE H. D. 1997, 2001) where the dating and the fauna indicate an age of ca. 1.1 M years, and is therefore younger than Żabia Cave. In their revision of Eurasian Alceini BREDÁ & MARCHETTI (2005) extended the distribution area of the species to Italy, the British Isles, Hungary, Russia, and Germany including some remains determined as *C. latifrons* were referred to *C. carnutorum*. The form was larger than *C. gallicus* and according to HEINTZ & POPLIN (1981); CZYŻEWSKA (1987) and KAHLKE H. D. (1990, 1997, 2001); BREDÁ & MARCHETTI (2005) was an intermediate link between *C. gallicus* and *C. latifrons*. The small number of the remains makes some authors deny the specific identity of *C. carnutorum* (AZZAROLI 1994; SHER 1987; VISLOBOKOVA 1990).



CZYŻEWSKA (1987, 1989) identified the elk from Żabia Cave as *Libralces (Cervalces) gallicus* based on few remains. Additional materials obtained during further excavations allowed me to revise the material from Żabia Cave. In an earlier paper (STEFANIAK 2001) I classified the elk from that cave as *C. gallicus*, and at the same time stated that in view of its scarcity in the fossil record the species status of *C. carnutorum* was doubtful and could be a subspecies of *gallicus*. Based on available material I confirmed the evolutionary trend in elk consisting in gradual size increase from *C. gallicus* to *C. latifrons*. The comparison of teeth and limb bone sizes of the elk from Żabia Cave with fossil and recent elk indicates that the form was slightly larger than *C. gallicus* from the Upper Pliocene of France, but smaller than *C. carnutorum* from Untermassfeld, and similar to *C. carnutorum* from Saint-Prest. This is compatible with data in the literature postulating a size increase in elk from *C. gallicus* to *C. latifrons*. However, as noted by BREDÁ & MARCHETTI (2005), in view of the wide individual variation, as well as the small number and fragmentary character of elk fossil record, the question of morphological differences between the above-mentioned species remains open. In their opinion at this stage of studies the term chronospecies should be used. The question of the number of ancestral elk species and species identification criteria of elk fossils from Eurasian localities require further studies. Accepting the opinion of the Italian authors, I classify the elk from Żabia Cave as *C. carnutorum*.

The elk species *C. latifrons* is widespread in the Holarctic, and is described from the Middle Pleistocene deposits of the Cromer Forest-Bed Formation on the east coast of England. It reached its widest distribution in the Middle Pleistocene (0.9-0.125 M years). Its presence was also noted in Poland in Kozi Grzbiet. It was the largest elk and it was characterised by a very broad size variation in size and a long span of occurrence, from Middle to Upper Pleistocene. Its antler stem reached a length of 500 mm, was straight or bent slightly upwards and the blades were large, fan-like, with long spines. The thickness of the frontal bones was up to 40 mm. A smaller form (with an antler stem between 250 and 350 mm long), known from the Upper Pleistocene, which, according to some authors, became extinct during the Warta [Warthe] glaciation or during the last interglacial, is often referred to as subspecies *C. latifrons postremus* VANGENHEIM et FLEROV 1965 (AZZAROLI 1994; KAHLKE H. D. 1977, 1990), or, according to SHER (1987) and BOESKOROV (2002) as a separate species *C. postremus*. According to PFEIFFER (1999a) and BREDÁ & MARCHETTI (2005) the large form of *C. latifrons* survived in Europe until the Eem interglacial.

*C. latifrons* was the first elk species to cross Beringia; it occurred in North America from the Middle Pleistocene. It is known from over 80 localities in Eurasia and North America. There is no elk fossil record from Spain probably due to climatic factors (such as the warmer and drier climate) and the lack of suitable habitats. *C. latifrons postremus* crossed the Bering Strait in the Middle Pleistocene and was described from about a dozen localities in North America (BUBENIK 1986; CHURCHER & PINSOFF 1987; GUTHRIE 1995; KAHLKE H. D. 1990; SHER 1971, 1986).

*C. latifrons* from Eurasia occurred during periods of both milder and more severe climate. It was represented by many different forms and sizes. Generally, the larger forms were associated with steppe and cold steppe environments, and the smaller forms, which developed many characters typical of *A. alces*, were associated with taiga, mixed forests and interglacial conditions (CHURCHER & PINSOFF 1987; KAHLKE H. D. 1990; KAHLKE R. D. 1994). In the Holarctic *C. latifrons* became extinct at the end of Pleistocene.

According to HEINTZ & POPLIN (1981) recent *A. alces* originated in the Upper Pleistocene from *C. latifrons postremus*.

According to KAHLKE H. D. (1990) and VÖRÖS (1985) the intermediate form between *C. latifrons* and *Alces alces* was the Middle Pleistocene *A. brevirostris* KRETZOI, 1969, appearing in the Mindel - Riss (Elster-Saale) (Holstein) interglacial or in the early phase of Riss (Saale) glacial, i.e. from ca. 440 to 280-290 thousand years BP. Its antlers resembled those of recent elk. The antler stem was very short, like in *A. alces*. Its premaxillar bones were very short. Unfortunately, nothing is known of their possible contact with nasal bones. From the limb bone size data in the fossil and recent elk presented here, it can be estimated that *A. brevirostris* was the size of recent elk. The species

had smaller limb bones compared to *C. latifrons* and larger ones compared to *C. gallicus*. This conforms to the trend during the evolution of *Alcinae*, which is characterized by a gradual decrease in size from *C. latifrons* to *A. alces*. The size of the vertebrae in *A. brevirostris* indicates a rather short neck, with long thoracic and lumbar sections (KAHLKE H. D. 1990; VÖRÖS 1985).

AZZAROLI (1981, 1985); CHURCHER & PINSOFF (1987); KAHLKE H. D. (1990); KAHLKE R. D. (1994); VISLOBOKOVA (1986, 1990) think that *A. alces*, as a separate species, probably came into existence at the end of the Middle Pleistocene in Eurasia or even, according to AZZAROLI, in Europe.

BREDA & MARCHETTI (2005) left open the question of the origin of recent elk. Like BOESKOROV (2002), they suggest that the late form of *C. latifrons*, especially that from western Europe, could not be the ancestor of recent elk. According to BREDA & MARCHETTI (2005), like many other mammal species, *A. alces* probably originated in Asia.

The oldest occurrence of *Alces alces* in Poland was that from the Lower Paleolithic locality of Trzebnica 2, dated to the border between the Middle and Upper Pleistocene (PAKIET et al. 1993), where a single fragment of scapula was found. A single P<sup>2</sup> and two P<sup>4</sup> teeth of *A. alces* or *C. latifrons* were found in the Middle Pleistocene deposits in Jaskinia na Biśniku, dated to the Odra glaciation [Drenthe], Lubawski interglacial [Kärlich], Wartha glaciation (WISZNIOWSKA et al. 2001).

Based on the present analysis of the remains of *C. carnutorum* from Żabia Cave it can be said that ancestral elk probably had a more varied diet than recent elk. The manner in which they foraged and chewed their food was similar to that in other *Cervidae*. This is believed to be the case due to factors such as the structure of the incisors and the different angle formed by the mandible ramus and shaft.

As indicated by palaeobotanical data, during the "Otwork glaciation" [Eburon] (horizons 12 and 15 in the Żabia Cave) in Poland vegetation was of boreal in character, with a dominance of birch and large proportion of herbaceous plants. In the coolest phases steppe and forest-steppe prevailed. On the other hand the interglacial period ("Celestynów" [Waal]) (top of the deposit) was characterized by an increased proportion of thermophilous species and a decreased proportion of herbaceous vegetation. Deciduous forests with a high proportion of oak dominated, and marshy forests occurred in wetter places (STUCHLIK 1985; SZYMKIEWICZ 1992). It was the latter conditions which favoured the occurrence of *C. carnutorum* in the Lower Pleistocene in Poland.

Most authors mentioned above believe that members of the genus *Cervalces* inhabited open ground, with steppe or cold steppe, as indicated by their large size and antler structure. Their wide distribution in glacial localities of Eurasia and North America, including the area of Beringia, and the composition of the accompanying fauna are also considered evidence of their preference for open habitats. It is possible that *Cervalces latifrons* was less strictly attached to wetlands than recent *Alces alces*, which is also indicated by the limb bone structure (PFEIFFER 1999b). Elk of the genus *Cervalces* lived in river valleys, near water bodies which were present also in open, steppe areas (BREDA et al. 2004). Remains of these *Alcinae* have been preserved in interglacial localities which may suggest a wide range of occurrence.

As pointed out by BUBENIK (1986), the rapid expansion of elk into the east of Eurasia, their spread to the North American continent and subsequent colonisation of North America may have been facilitated by river systems and the adaptation of fossil elk to life in such environments. According to BUBENIK (1986), CHURCHER & PINSOFF (1987) and KAHLKE H. D. (1990) two forms of *C. latifrons* may have occurred in the Middle Pleistocene. One, living in open areas, was dominant during periods of more severe cold climate, the other, adapted to life in boreal forests, became more widespread during periods of warming and retreated to refugia in southern Europe in colder periods.

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