Late Pliocene cervids from Węże 2 in southern Poland

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The deer association composed of *'Cervus'* cf. *cusanus*, *'Cervus' pardinensis*, *Croizetoceros ramosus*, cf. *Arvenoceros ardei* indicates the late Pliocene age (zone MN 16) of the locality Węże 2. Outside Poland the species are known from France, Spain, Moldavia, and Ukraine. The composition of fauna indicates a woodland character of the habitat, with some open areas and vicinity of a water reservoir. The characters of dentition and wear of the crowns of teeth of the deer from Węże 2 suggest food containing both tree and bush leaves, and grasses.

Key words: Cervidae, Pliocene, Węże 2, Poland, morphology, palaeoecology, biostratigraphy.

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Introduction

The Pliocene and beginning of Pleistocene in Eurasia were characterized by large climatic changes. At boundary of the Early and Late Pliocene the climate cooled down. In result, thermophilous forms receded and were replaced by species associated with temperate climate (Bonifay 1990; Guérin 1990; Vislobokova 1990). The area of conifer-dominated forests increased, whereas in the south of Eurasia savannah was replaced by boreal steppes, and in the north woodland tundra appeared (Vislobokova 1990). The rate of species differentiation increased, distribution areas of many plant and animal species were disrupted and changed. These biogeographic changes have their expression also in the distribution of Pliocene deers.

The cervid faunas of the Early Pliocene included mainly forms associated with warm climate. Muntjacs *Paracervulus* and *Metacervulus*, and roe deer *Procapreolus* had survived since the Miocene; primitive Cervinae

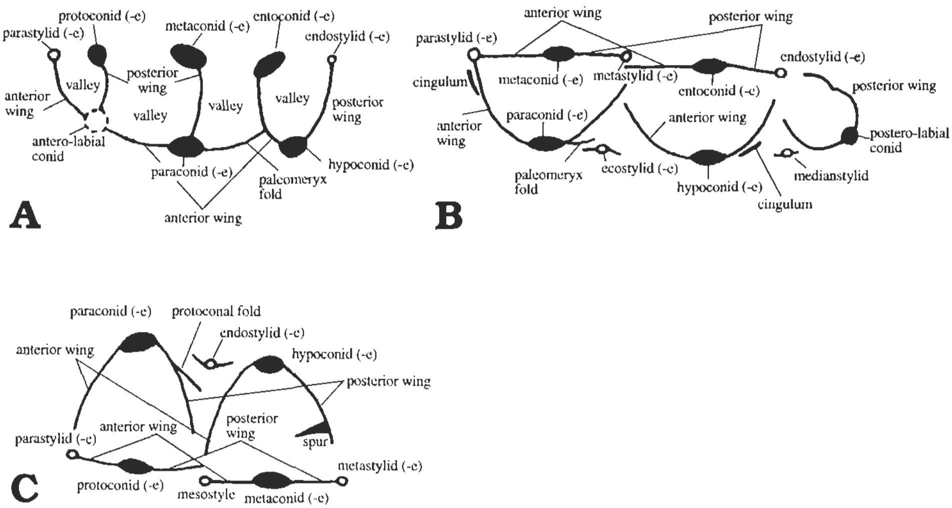

Fig. 1. Morphological elements of the cervid teeth, modified from Obergfell (1957) and Heintz (1970). A. Lower premolar teeth (-id). B. Lower molar teeth (-id). C. Upper molar teeth (-e).

Cervavitus, Pliocervus, and at the end of the Early Pliocene (Mammal Neogene zone MN 15 of Mein 1990) *Croizetoceros* and *Cervus* s.l. appeared (Vislobokova 1990).

Heintz (1970) described an array of deer associations from the Late Pliocene and Early Pleistocene of France. He traced their evolution and mutual relationships. For zone MN 16 these were: *'Cervus' (Procapreolus) cusanus* Croizet & Jobert 1828, *Croizetoceros ramosus* (Croizet & Jobert 1828), *'Cervus' pardinensis* Croizet & Jobert1828, *'Cervus' perieri* Croizet & Jobert 1828, and *Arvenoceros ardei* (Croizet & Jobert 1828). In zone MN 17 and the Early Biharian *Croizetoceros ramosus, 'Cervus' philisi* Schaub 1941, that originated from *'Cervus' pardinensis* and *Eucladoceros senezensis* Depéret 1910 occurred. At the end of the Villafranchian most of those forms became extinct, only *'Cervus' perolensis* Azzaroli 1952, a descendant of *'Cervus' philisi* and *Eucladoceros tetraceros* Dawkins 1878 remained. At the beginning of the Middle Pleistocene those species became extinct and got replaced by taxa characteristic of the Quaternary (Bonifay 1990; Vislobokova 1990).

In Poland the fauna of the Early Pliocene zone MN 15 was represented by the cervid association described by Czyżewska (1968) and composed of *Procapreolus wenzensis* Czyżewska 1968, *Cervus warthae* Czyżewska 1968, and *Muntiacus polonicus* Czyżewska 1968. *Croizetoceros ramosus* and *Eucladoceros* sp. are known from the Late Pliocene zone MN 16 in Rębielice Królewskie 1A (Czyżewska 1972, 1989). In Węże 2 remains of *Croizetoceros ramosus, 'Cervus' pardinensis, 'Cervus' cusanus*, and *Arvenoceros ardei*, whose description is the subject of this paper, were found (Czyżewska 1989; Kowalski 1990).

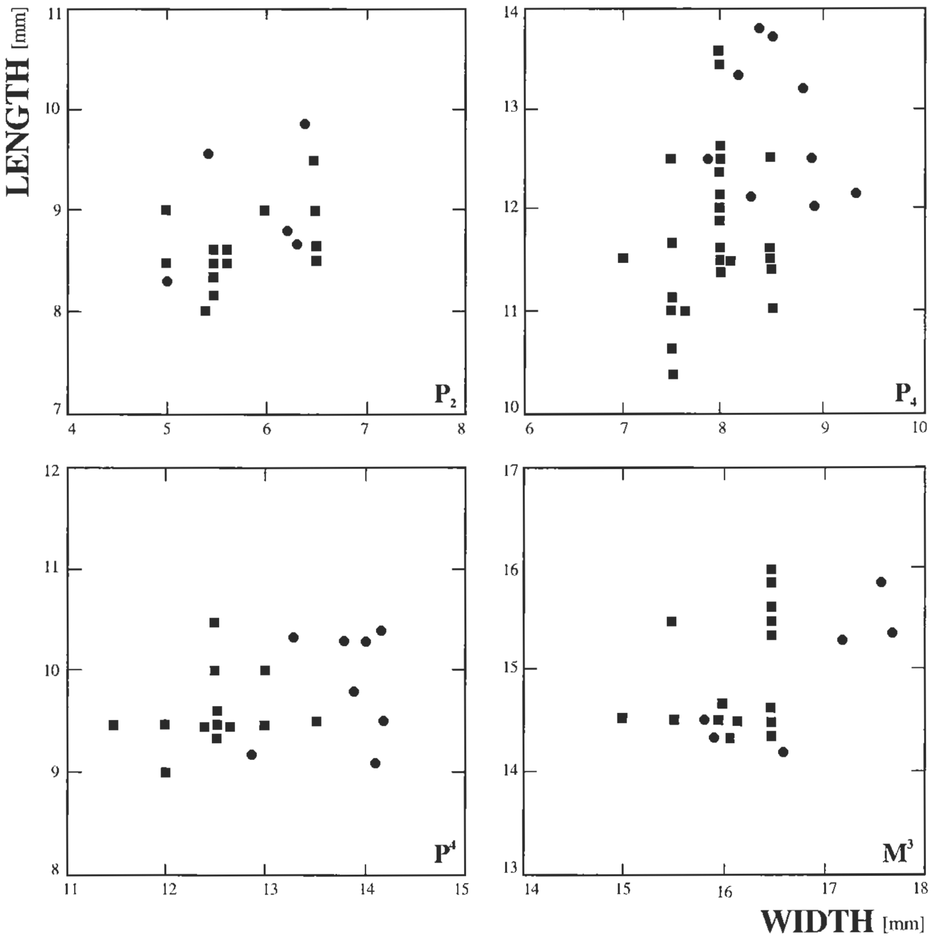

Fig. 2. Comparison of teeth dimensions in *Croizetoceros ramosus* (Croizet & Jobert 1828) from Węże 2 (dots) and Les Etouaires (squares; after Heintz 1970: figs 83, 90, 92).

All the teeth described come from the collection of the Institute of Palaeobiology of the Polish Academy of Sciences in Warsaw (abbreviated ZPAL). The material comprises over 80 entire and a few fragments of deer teeth. In the collection there are no larger parts of the skeleton and antlers. The nomenclature of deer cheek teeth was taken from Obergfell (1957) and Heintz (1970; Fig. 1).

Locality

The locality Węże 2 was discovered by Sulimski (1962) in the neighborhood of Działoszyn, on the NW slope of the hill Zelce. The name Węże 2 distinguishes it from the higher situated Węże 1 that contains also a rich fauna of Pliocene vertebrates (Samsonowicz 1934; Kowalski 1989). Excavations carried out in 1958–1961 provided material comprising remains of amphibians, reptiles (Młynarski *et al.* 1984; Młynarski & Szyndlar 1989) and mammals. A preliminary list of mammal species was given by Sulimski (1962), and in Kowalski (1989).

Age of the fauna

The deer association from the locality Węże 2 confirms its late Pliocene age (zone MN 16) (Sulimski 1962; Korotkevich 1964, 1970, 1988; Heintz 1970, 1974; Głazek *et al.* 1976; Głazek & Szynkiewicz 1987; Młynarski *et al.* 1984; Kowalski 1989; Guérin 1990; Vislobokova 1990). This is indicated by the presence of *Croizetoceros ramosus*, *'Cervus' pardinensis*, and also *Cervus* cf. *cusanus* and cf. *Arvenoceros ardei*, known from Late Pliocene localities in France (Heintz 1970, 1974; Guérin 1990, Vislobokova 1990). *'Cervus' cusanus* occurred also in the Early Pliocene of Ukraine and Moldavia (Korotkevich 1964, 1970, 1988; Vislobokova 1990). Głazek & Szynkiewicz (1987) estimated the age of Węże 2 as somewhat older (zone MN 15), based on the presence of such species as *Mimomys gracilis* (Kretzoi 1959) and *Mimomys* cf. *stehlini* Kormos 1931. However Sulimski (1962), Młynarski *et al.* (1984), Nadachowski *et al.* (1989), and Kowalski (1990) are of opinion that Węże 2 are contemporary with Rębielice Królewskie 1–2 (zones MN 16). The lack of *Eucladoceros*, recorded by Czyżewska (1972) from Rębielice Królewskie 1A, and known from younger (zone MN 17) localities Roccaneyra and Pardines from France (Heintz 1970; Mein 1990), in Węże 2 is consistent with the Late Pliocene age of the locality.

Taxonomy

Family Cervidae Gray 1821

Genus *Cervus* Linne 1758 *sensu lato*

'Cervus' cf. *cusanus* Croizet & Jobert 1828

Fig. 6F, G.

Material. — M_2 (ZPAL WII 7) of an adult individual.

Measurements. — Tooth length 13.0 mm, breadth 8.9 mm.

Description. — On the inner side of protoconid there is an enamel ridge which is a remnant of paleomeryx fold. All conid cusps are worn down, valleys open, metaconid and entoconid wings not connected (Fig. 6F, G).

Remarks. — The size of tooth M_2, which is within the variability range of such teeth in *'Cervus' cusanus* from Etouaires (Heintz 1970) and the presence of a vestigial paleomeryx fold seem to justify this species identification. Remains of that species found hitherto in Europe are very fragmentary and its generic position is disputable. Korotkevich (1964,

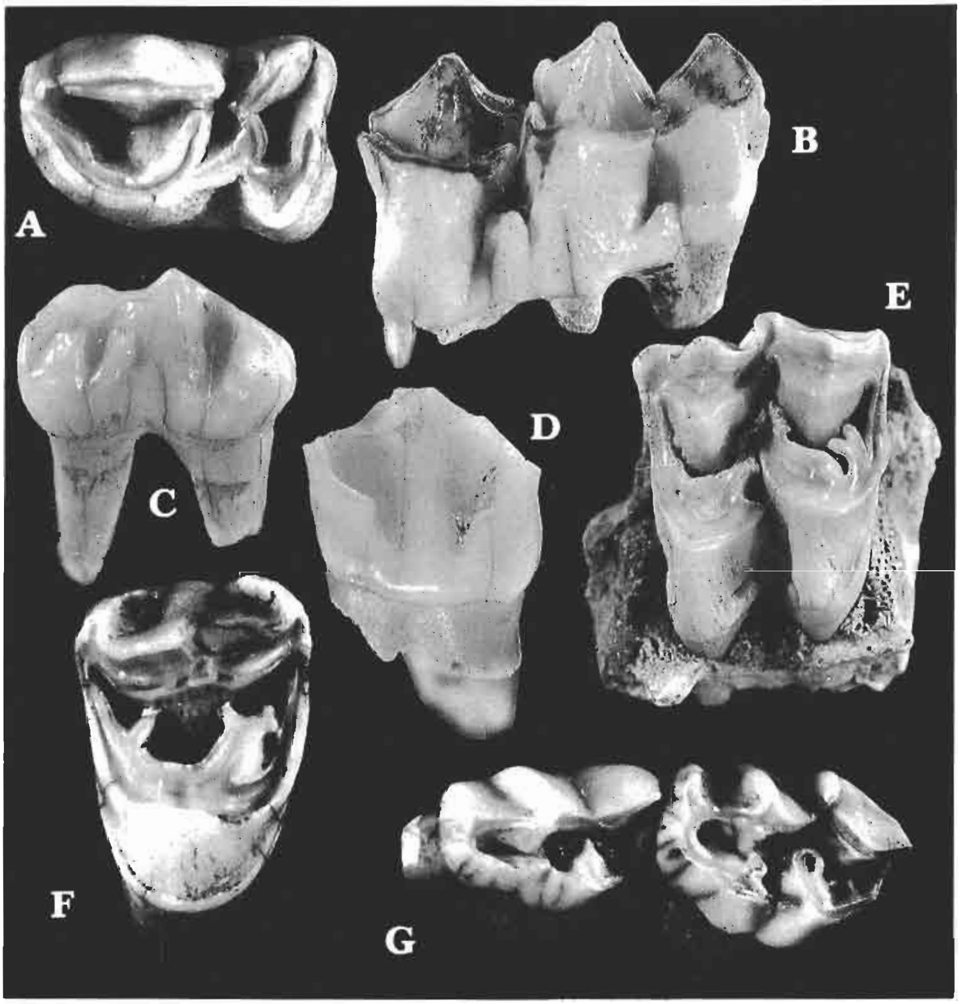

Fig. 3. *Croizetoceros ramosus* (Croizet & Jobert 1828), Late Pliocene, Węże 2, Poland. A. Left P_4 ZPAL WII 13 in lingual view; × 2. B. Right DP_4 ZPAL WII 33 in buccal view; × 4. C. Left P_2 ZPAL WII 28 in lingual view; × 4. D. Left P^4 ZPAL WII 53 in buccal view; × 3.5. E. Left M^2 ZPAL WII 58 in occlusal view; × 2.5. F. Left P^4 ZPAL WII 53 in lingual view; × 3.5. G. Fragment of maxilla with DP^2–DP^3 ZPAL WII 35 in lingual view; × 3.5.

1970, 1988) and Vislobokova (1990) regarded it member of the genus *Procapreolus*. No complete leg bones of *'Cervus' cusanus* are known, and it is not clear if their fragments were plesiometacarpal or telemetacarpal; this makes it impossible to answer the question of its generic afiliation.

Occurrence. — Pliocene of Moldavia and southern Ukraine (zone MN 14 – MN 15), in France Etouaires, probably Vialette (zone MN 16), in Poland Węże 2 (zone MN 16).

'Cervus' pardinensis Croizet & Jobert 1828

Fig. 6A–E.

Material. — 1 P_2: ZPAL WII 30, 2 P_3: ZPAL WII 20, 21, 2 P_4: ZPAL WII 19, 23, 1 M_3: ZPAL WII 2, 1 DP_2: ZPAL WII 29, 1 I_1: ZPAL WII 88, 1 P^3: ZPAL WII 43, 3 P^4: ZPAL WII 41, 44, 52, 1 M^2: ZPAL WII 60, 1 $\underline{M}$: ZPAL WII 118.
Measurements. —

Teeth	N	length		width		width/length × 100	
		observed range	mean	observed range	mean	observed range	mean
I_1	1	9.4	–	9.2	–		
P_2	1	10.6	–	6.8	–	64.1	–
P_3	2	11.1–11.8	11.4	7.9–8.8	8.3	68.1–72.8	70.9
P_4	2	12.9–13.3	13.1	8.0–8.7	8.3	68.2–72.8	70.9
M_3	1	23.7	–	11.1	–	46.6	–
DP_2	1	9.8	–	6.2	–	63.3	–
P^3	1	10.9	–	11.6	–	106.4	–
P^4	3	10.2–11.4	10.6	13.5–14.2	13.8	125.3–142.1	132.5
M^2	1	17.4	–	19.2	–	110.3	–

Description. — P_2 has not developed paraconid cusp, crown is strongly worn and valleys are closed. P_3 are poorly molarized, with well developed paraconid, valleys 1 and 4 are shallow. The metaconid has a short wing directed towards the entoconid cusp. P_4 are poorly molarized, with well developed paraconid, the entoconid cusp is not connected with the anterior wing of hypoconid. M_3 is a large tooth with a thick cingulum, small stylids and conid cusps. I_1 has a shape of an asymmetrical widened spade (Fig. 6A). DP_2 is a milk tooth, smaller than permanent teeth, worn in the posterior part of the crown.

The labial side of the upper premolars P^3 is bent so that the labial and lingual margins are not parallel. Paracone is strongly displaced towards the parastyle, on the lingual side there is a shallow groove separating the protocone and the hypocone. P^4 resembles P^3, but is shorter and broader (Fig. 6B, C). The lingual wall is strongly tilted towards the labial wall. In tooth ZPAL WII 52 the parastyle at the base of crown has a shape of a protruding collar. The protocone and hypocone are separated by a groove. The parastyle in tooth ZPAL WII 52 is poorly marked; between the protocone wing and the labial side there is a crevice, due to which the valley opens to the outside. Upper molars M^2 are characteristic in that they have a specially pronounced cingulum in the shape of a collar surrounding the conids of the lingual side; between the wall of the tooth and the collar of cingulum there is a deep groove (Fig. 8E). The tooth ZPAL WII 60 has a partly damaged cingulum (Fig. 6E). Specimen ZPAL WII 118 has only a posterior part of the crown preserved (Fig. 6D).

Remarks. — Two upper molars found in Węże 2 have cingulum characteristic of *'Cervus' pardinensis* (Heintz 1970). The size and structure of molar teeth resemble both those of *'Cervus' pardinensis* and of the related *'Cervus' philisi*. The incisive is classified on the basis of its size, being larger than I_1 in *Croizetoceros ramosus*, and smaller than I_1 in cf. *Arvenoceros*

ardei. On the enamel of teeth of *'Cervus' pardinensis* from Węże 2 there are scratches resembling those found on the teeth of *Croizetoceros ramosus*.
Occurrence. — Upper Pliocene localities Etouaires and Vialette in France (zone MN 16) and Węże 2 in Poland (zone MN 16).

Genus *Croizetoceros* Heintz 1970

Croizetoceros ramosus (Croizet & Jobert 1828)

Figs 3–5.

Material. — 1 fragment of mandible of an adult individual ZPAL WII 110, 2 fragments of upper jaw of adult individuals: ZPAL WII 45, 67, 1 fragment of jaw of a juvenile individual ZPAL WII 35, 5 P_2: ZPAL WII 25–28, 31, 2 P_3: ZPAL WII 12, 105, 8 P_4: ZPAL WII 12–18, 101, 2 M_1: ZPAL WII 8, 11, 4 M_2: ZPAL WII 6, 9, 10, 102, 3 M_3: ZPAL WII 1, 3, 4, 109, 1 DP_2: ZPAL WII 24, 1 DP_3: ZPAL WII 34, 3 DP_4: ZPAL WII 32–33, 107, 7 I_1: ZPAL WII 111–117, 1 P^2: ZPAL WII 47, 2 P^3: ZPAL WII 48–49, 6 P^4: ZPAL WII 50, 53–56, 100, 2 M^1: ZPAL WII 38, 61, 2 M^2: ZPAL WII 58–59, 6 M^3: ZPAL WII 57, 62–66, 5 DP^4: ZPAL WII 37, 39, 40–42.

Measurements. — (Abbreviations: V — variance, D — standard deviation).

Teeth	N	length				width				index of teeth width/length × 100		
		observed range	mean	V	D	D	mean	V	D	observed range	mean	D
I_1	7	5.3–8.0	7.23									
P_2	5	8.3–9.8	9.04	0.4030	0.6346	5.0–6.4	5.86	0.3880	0.6228	56.25–72.4	64.91	6.7675
P_3	3	12.1–13.0	12.63	0.2233	0.4725	7.0–7.7	7.46	0.1633	0.4041	57.9–59.37	58.83	0.8113
P_4	9	12.0–13.8	12.8	0.5025	0.7088	7.9–9.3	8.57	0.1864	0.4323	56.8–74.16	65.83	5.8692
M_1	3	14.1–14.4	14.3	0.3000	0.1732	8.9–9.8	9.3	0.2100	0.4582	65.2–74.49	70.37	4.7331
M_2	4	13.9–15.4	14.8	0.4066	0.6377	10.0–11.1	10.65	0.2566	0.5066	66.6–75.54	72.01	4.0094
M_3	4	18.8–19.9	19.1	0.2866	0.5354	9.1–10.0	9.5	0.1400	0.3741	47.23–53.19	49.83	2.6194
DP_2	1	7.4	–	–	–	4.1	–	–	–	55.4	–	–
DP_3	1	10.3	–	–	–	5.5	–	–	–	53.39	–	–
DP_4	3	14.5–16.6	15.53	1.1033	1.0503	7.5–8.0	7.33	0.0633	0.2516	48.0–53.1	50	2.7221
P^2	2	10.2–11.1	10.65	0.4050	0.6363	10.6–10.7	10.65	0.0050	0.0707	96.49–101.86	99.17	3.7971
P^3	4	10.3–10.7	10.45	0.0300	0.1732	11.1–12.4	11.72	0.3891	0.6238	106.89–119.23	111.96	5.5005
P^4	8	9.1–10.5	9.88	0.3183	0.5642	12.9–14.2	13.8	0.2171	0.4659	129.12–154.94	142.35	9.3747
M^1	2	13.5–14.9	14.2	0.9800	0.9899	15.2–16.3	15.75	0.6050	0.7778	109.39–112.59	110.99	2.2627
M^2	2	14.0–15.5	14.75	1.1250	1.0606	16–18	17	2	1.4142	114.28–116.71	115.49	1.7182
M^3	6	14.2–15.9	14.93	0.4826	0.6947	15.8–17.7	16.81	0.6576	0.8109	108.96–118.88	113.79	3.7874
DP^2	1	11.1	–	–	–	7.4	–	–	–	66.66	–	–
DP^3	1	11.7	–	–	–	9.5	–	–	–	76.92	–	–
DP^4	5	12.2–13.0	12.58	0.0870	0.2949	12.5–13.6	13	0.2466	0.4966	101.55–108.87	106.23	3.2188

Description. — The structure of the anterior part of the crown of P_2 varies. A well developed paraconid is observed and two wings of anterolabial conid separated by a shallow valley (ZPAL WII 27) or a paraconid with fused wings of anterolabial conid (Fig. 3C), or only a single anterior wing of anterolabial conid. P_3 is poorly molarized; its large metaconid is displaced posterad, due to which valley 3 is fairly narrow and with wear progressing it closes. All P_4 are molarized to a considerable degree (Fig. 3A). The wall extending from the paraconid to the metaconid closes valley 2 almost entirely. A total closure of that valley and valley 4 takes place with the wear of the tooth. The stylids and conid cusps on the lingual side of M_1 reach half height of the crown, and their thickness amounts to 1–2 mm. On the labial side there is a well developed ectostylid whose tip has undergone a wear. Anteriorly situated cingulum is strongly developed. The size of M_2 somewhat exceeds that of M_1, whereas the ectostylid is poorly developed. On the anterior wing of protoconid of M_3 there is a thick cingulum. A small ectoconid reaches one fourth of the crown height. Only in ZPAL WII 4 there is a small metastylid. The parastylid and medianstylid are well developed. The second and third lobes of the crown are connected by the posterior wing of hypoconid in the lower part of the crown, or by the posterior wing of entoconid. On the inner surface of the posterior wing of entoconid and on the third lobe spurs may occur. The first incisor has a form of an assymetrical and rather broad spade which edge contacting the crown of I_2 is concave. All the I_1 are poorly worn. Crown height 6.2–8.8. mm, mean 7.48 mm. The tri-lobate crown of the DP_4 resembles in shape that of the molars. The stylids and conid cusps on the labial side reach two thirds of the crown height (Fig. 3B). On the lingual surface of the crown of P^2 there is a small groove separating the crown in two parts. As a result of displacement of the metacone cusp towards the parastyle the labial surface of the tooth is asymmetrical. Paracone of P^3 is as in P^2 displaced towards the bigger parastyle, which increases the asymmetrical appearance of the labial wall of the tooth. The presence of metacone is marked as a small convexity on the labial surface of the crown. The paracone of P^4 is only slightly displaced towards the parastyle, due to which the surface of the crown on both sides of the paracone is symmetrical. The hypocone and protocone are separated by a groove. Cingulum on the lingual side is distinctly marked. On teeth ZPAL WII 53 and 56 spurs are present on both the hypocone and the metacone (Fig. 3F). The stylids and paracone cusp are connected at the base of the crown. Paramedian edges of the parastyle and paracone, broadened in the lower part of the crown of teeth ZPAL WII 55 and 56, form a flange (Fig. 3D).

The M^1 is smaller than the other molars. The parastyle, paracone and metacone have a shape of thick cusps united at the base of the crown. The thick anterior cingulum is larger than the cingulum situated in the posterior part between the lobes. The spur and protocone fold are poorly developed. The spur and protocone fold in M^2 are larger than in M^1. The spur is forked in its posterior part. On the posterior wing of protocone and anterior wing of hypocone there are small spurs. At the base of hypocone of tooth ZPAL WII 58 there are small enamel protuberances (Fig. 3E).

The posterior part of M^3 crown is smaller and displaced relative to the anterior part. Only in the tooth ZPALWII 63 the endostyle was observed. The tooth, besides the large spur on the anterior wing of protocone has a forked spur on the posterior wing of hypocone. The DP^2–DP^3 are embedded

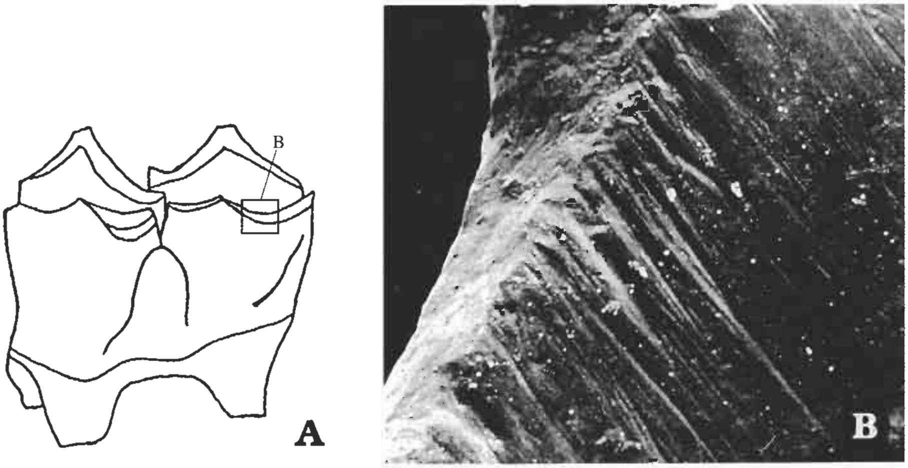

Fig. 4. *Croizetoceros ramosus* (Croizet & Jobert 1828), Late Pliocene, Węże 2, Poland; enamel surface with scratches (B; × 55) at the edge of M_2 ZPAL WII 9 (A; diagrammatic).

in a small fragment of the upper jaw (Fig. 3G). DP^2 resembles premolars, but is narrower. On the lingual side there is a small groove separating the protocone and hypocone. DP^3 is similar to permanent molars, anterior lobe having larger than the posterior. There is a groove separating two tubercles of the lingual side. The anterior wing of hypocone is branched, on the posterior wing there is a small spur. DP^4 is similar to M^3, but much smaller and with lower crown.

Remarks. — The structure of teeth of *Croizetoceros ramosus* from Węże 2 does not differ from that described earlier by Heintz (1970) in the forms from the localities in France and Spain. The variability ranges of the size of particular teeth and the breadth/length index do not depart from the ranges given by Heintz (1970) who had at his disposal a larger number of teeth of *Croizetoceros ramosus* from various localities of different age and geographic position. The length and breadth of teeth P_2, P_4, P^4 and M^3 from Węże 2 and Etouaires are presented in Fig. 2. The size of P_4 from Węże 2 is larger than those from Etouaires, whereas the remaining teeth are within the upper variability range of the size given by Heintz (1970). It can be thus supposed that in Węże 2 a large form of the species occurred, with teeth size close to that of the population from Etouaires (Heintz 1970).

On the enamel of teeth of Croizetoceros ramosus from Węże 2 scratches were found. They have a form of grooves of gently concave bottom (Fig. 4). The scratches result probably from grinding the enamel by grains with blunt edges (e.g. smooth-edged sand grains) during feeding. As a result of mandible forward and lateral movements scratches appeared on the wings of anterior conids, and during backward movements posterior wings were scratched. On many teeth of *Croizetoceros ramosus* anterior wings of conids are more worn than posterior wings, which indicates a stronger pressure of jaws during the forward and lateral movement of the mandible.

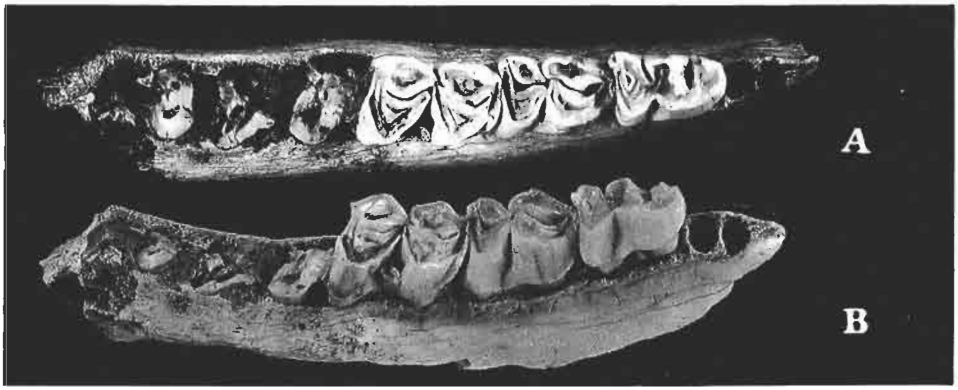

Fig. 5. *Croizetoceros ramosus* (Croizet & Jobert 1828), Late Pliocene, Węże 2, Poland. Fragmentary right mandible ZPAL WII 110 in oblique buccal and occlusal views; ca natural size.

Occurrence. — *Croizetoceros ramosus* occurred abundantly in the Pliocene and Pleistocene (zones MN 16 to MQ 1) of France and Spain (Heintz 1970), in the Pliocene of Ukraine and Moldavia (Korotkevich 1988; Vislobokova 1990), in Poland in Węże 2 (zone MN 16) and Rębielice Królewskie 1A (zone MN 16).

Genus *Arvenoceros* Heintz 1970

cf. *Arvenoceros ardei* (Croizet & Jobert 1828)

Fig. 6F, G.

Material. — I_1: ZPAL WII 74, M^3: ZPAL WII 70.

Description. — The incisor I_1 size exceeds that of I_1 of other species of deer from Węże 2. It has a shape of a broad, asymmetrical spade whose concave margin contacts with I_2 (Fig. 6F). Crown length is 13.0 mm, crown height 14.5 mm.

Posterior lobe of the M^3 has no traces of wear. The shape of metastyle and metacone cusps is characteristic, not found in other deer species, since they are of equal thickness, somewhat bent towards the posterior margin of the tooth (Fig. 6G). On the posterior wing of hypocone there is a spur; on the anterior there are small thickenings of enamel reaching two thirds crown height.

Remarks. — Two teeth described above, I_1 and M^3, because of their large size are distinct from the rest of the described material. In the Late Pliocene only two species of deer of similar size occurred (Heintz 1970). These were *Arvenoceros ardei* and *'Cervus' perieri*. The morphology of the posterior lobe of M^3 of the specimen found in Węże 2, and especially the form of its labial wall, indicate *Arvenoceros ardei*. However, as in the case of *'Cervus'* cf. *cusanus* the scarcity of material does not allow certain identification. All the finds of *Arvenoceros ardei* are very fragmentary. According to Vislobokova (1981) the species is the ancestor of the lineage of giant deer leading to the *Megaceros*.

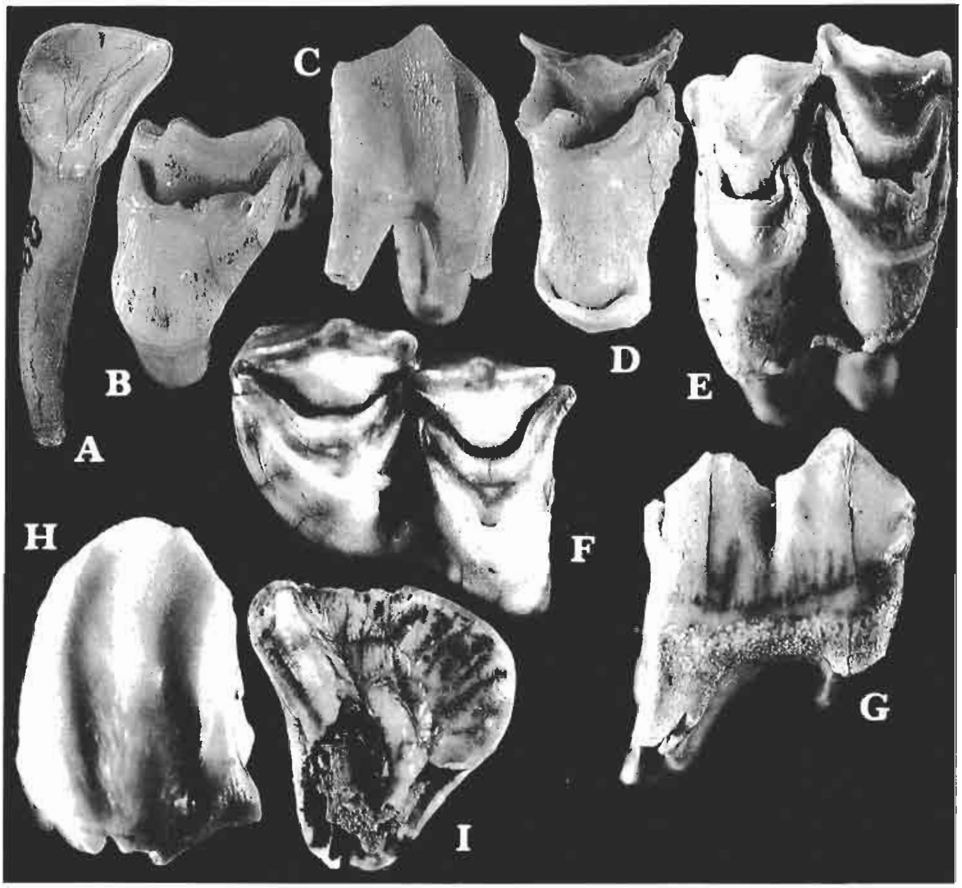

Fig. 6. ❑A–E. *'Cervus' pardinensis* Croizet & Jobert 1828, Late Pliocene, Węże 2, Poland. A. Right I_1 ZPAL WII 88 in upper view; × 3. B. Left P^4 ZPAL WII 44 in lingual view; × 2.5. C. Left P^4 ZPAL WII 44 in buccal view; × 2.5. D. Right fragmentary upper molar ZPAL WII 118 in occlusal view, note characteristic collar of cinqulum; × 2.5. E. Right M^2 ZPAL WII 60 in occlusal view; × 3. ❑F–G. *'Cervus'* cf. *cusanus* Croizet & Jobert 1828, same locality. F. Right M_2 ZPAL WII 7 in occlusal view; × 3.3. G. Right M_2 ZPAL WII 7 in lingual view; × 3. ❑H–I. cf. *Arvenoceros ardei* (Croizet & Jobert 1828), same locality. I. Left fragment I_1 ZPAL WII 74 in upper view; × 3. H. Left fragment M^3 ZPAL WII 70 in buccal view; × 2.2.

Palaeoecology

Incisor I_1 from Węże 2 belonging to *Croizetoceros ramosus, 'Cervus' pardinensis* and cf. *Arvenoceros ardei* have a similar, spade-like, asymmetrical shape which suggests a similar mode of feeding. According to Flerov (1962) such a shape is characteristic of Ruminantia feeding on mixed vegetation, comprising both tree and bush leaves, and grasses. Among the Cervidae the elk, feeding mainly on twigs and bark, has a different structure of I_1 (spade-like but with symmetrical crown).

According to Heintz (1970) small forms (*'Cervus' cusanus, Croizetoceros ramosus*) fed on the forest undergrowth and in open areas, most of their diet consisting of grasses, herbs and leaves of lower tree branches and bushes. However, *'Cervus' pardinensis* and *Arvenoceros ardei* could have fed on leaves from upper parts of trees and bushes, inaccessible to smaller deer species.

The fact that the fauna from Węże 2 is dominated by the Cervidae, inhabiting mostly forests, at the expense of the Bovidae and Equidae — ungulates of open habitats (Kurtén 1963; Heintz 1970), which are absent from this locality — would indicate a woodland character of the habitat. This is confirmed by the presence of numerous squirrels (Sulimski 1962, 1964). However, the remains of Lagomorpha (especially pikas) and rodents of open areas, such as spalacids (Sulimski 1962), indicate some open areas between dense forests (limestone hills higher than today). Moreover, fish vertebrae (Sulimski 1962), remains of amphibians, mud turtle, grass snake, *Mioproteus vezei* Estes (Młynarski *et al.* 1984), as well as desman, evidence the presence of a water body nearby, and an extensive karst system.

Conclusions

The deer found in Węże 2 were earlier described from the Late Pliocene of Etouaires and Villaroya. *Cervus cusanus* and *Croizetoceros ramosus* were also recorded from the Pliocene of Ukraine and Moldavia. The association of the Cervidae of such a composition has not been found before in Poland. The measurements of teeth of the deer from Węże 2 and their structure do not differ from those of forms found in French and Spanish localities. The species found in the locality indicate a forest habitat, with some open areas and a water body.

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References

Bonifay, M.F. 1990. Relations between paleoclimatology and Plio-Pleistocene biostratigraphic data in west European countries. In: E.H. Lindsay, V. Fahlbusch, & P. Mein (eds) *European Neogene Mammal Chronology*, 475–485. NATO ASI Series A, vol. 180. Plenum Press, New York.

Czyżewska, T. 1968. Deers from Węże and their relationship with Pliocene and Recent Eurasiatic Cervidae. *Acta Palaeontologica Polonica* **13**, 537–603.

Czyżewska, T. 1972. Remains of Cervidae (Mammalia) from Rębielice Królewskie in Poland. *Acta Zoologica Cracoviensia* **25**, 261–270.

Czyżewska, T. 1989. Parzystokopytne – Artiodactyla. In: K. Kowalski (ed.) Historia i ewolucja lądowej fauny Polski. *Folia Quaternaria* **59–60**, 209–217.

Flerov, K.K. (Флеров, К.К.) 1962. Об основных направлениях экологической эволюции жвачных (Ruminantia). *Палеонтологический журнал* **4**, 31–40.

Głazek, J., Sulimski, A., Wysoczański-Minkowicz, T. 1976. On the stratigraphic position of Węże 1 locality (Middle Poland). In: V. Panos (ed.) *Procedings of the 6th International Congress of Speleology*, 427–434. Academia, Praha.

Głazek, J., Szynkiewicz, A. 1987. Stratygrafia mlodotrzeciorzędowych i staroczwartorzędowych osadów krasowych oraz ich znaczenie paleogeograficzne. In: A. Jahn *et al.* (eds) *Problemy mlodszego neogenu i eoplejstocenu w Polsce*, 113–129. Ossolineum. Wrocław. Warszawa.

Guérin, C. 1990. Biozones or mammal units? Methods and limits in biochronology. In: E.H. Lindsay, V. Fahlbusch, P. Mein (eds) *European Neogene Mammal Chronology*, 119–130. NATO ASI Series A, vol. 180. Plenum Press, New York.

Heintz. E. 1970. Les Cervidés villafranchiens de France et d'Espagne. *Mémoires du Muséum National d'Histoire Naturelle, n.s. C,* **1–2**, .

Heintz, E. 1974. Les populations de Croizetoceros ramosus (Cervidae, Mammalia) dans le temps et dans l'espace. *Bulletin de la Sociéte Géologique de France 7e ser.* **16**, 411–417.

Korotkevich, E.L. (Короткевич, Е.) 1964. Нові знахідки пліоценової козулі роду *Procapreolus* на півдні СРСР. *Доклады Академии Наук УССР* **3**, 382–395.

Korotkevich, E.L. (Короткевич, Е.) 1970. *Поздненеогеновые олени Северного Причерноморья.* 175 с. Наукова Думка, Киев.

Korotkevich, E.L. (Короткевич, Е.) 1988. *История формирования гиппарионовой фауны Восточной Европы.* 164 с. Наукова Думка, Киев.

Kowalski, K. (ed) 1989. Historia i ewolucja lądowej fauny Polski. *Folia Quaternaria* **59–60**, 278.

Kowalski, K. 1990. Stratigraphy of Neogene mammals of Poland. In: E.H. Lindsay, V. Fahlbusch, P. Mein (eds) *European Neogene Mammal Chronology*, 119–130. NATO ASI Series A, vol. 180. Plenum Press, New York.

Kurtén, B. 1963. Villafranchial faunal evolution. *Societas Scientarum Fennica, Commentationes Biologicae* **26**, 1–18.

Mein, P. 1990. Updating of MN Zones. In: E.H. Lindsay, V. Fahlbusch, & P. Mein (eds) *European Neogene Mammal Chronology*, 73–90. NATO ASI Series A, vol. 180. Plenum Press, New York.

Mlynarski, M., Szyndlar, Z., Estes, R., & Sanchíz, B. 1984. Amphibians and reptiles from the Pliocene locality of Węże II near Dzialoszyn (Poland). *Acta Palaeontologica Polonica* **29**, 209–226.

Mlynarski, M., Szyndlar, Z. 1989. Plazy i gady — Amphibia et Reptilia. In: K. Kowalski (ed.) Historia i ewolucja lądowej fauny Polski. *Folia Quaternaria* **59–60**, 68–88.

Nadachowski, A., Pawlowski, J., Stworzewicz, E. 1989. Charakterystyka stanowisk i ich korelacja stratygraficzna. In: K. Kowalski (ed.) Historia i ewolucja lądowej fauny Polski. *Folia Quaternaria* **59–60**, 5–19.

Obergfell, F.A. 1957. Vergleichende Untersuchungen an Dentitionen und Dentale altburdigaler Cerviden von Wintershof-West in Bayern und recenter Cerviden (eine phylogenetische Studie). *Palaeontographica* **109A**, 71–166.

Samsonowicz, J. 1934. Zjawiska krasowe i trzeciorzędowa brekcja kostna w Wężach pod Działoszynem. *Zabytki Przyrody Nieożywionej* **3**, 151–162.
Sulimski, A. 1962. O nowym znalezisku kopalnej fauny kręgowców w okolicy Dzialoszyna. *Przegląd Geologiczny* **10**, 219–223.
Sulimski, A. 1964. Pliocene Lagomorpha and Rodentia from Węże I (Poland). *Acta Palaeontologica Polonica* **9**, 149–261.
Vislobokova, I.A. (Вислобокова, И.А.) 1981. К вопросу о ранней эволюции мегацерии. *Палеонтологический журнал* **4**, 105–117.
Vislobokova, I.A. (Вислобокова, И.А.) 1990. Ископаемые олени Евразии. *Труды Палеонтологического Института* **240**, 208.

Streszczenie

Niniejsza praca zawiera opis szczątków kopalnych Cervidae pochodzących z górnoplioceńskiego (zona MN16) stanowiska Węże 2. W materiale, zawierającym głównie zęby, oznaczono następujące gatunki jeleni: *„Cervus”* cf. *cusanus*, *Croizetoceros ramosus*, *„Cervus” pardinensis*, cf. *Arvernoceros ardei*. Gatunki te poza terenem Polski znane są z szeregu górnoplioceńskich stanowisk z obszaru Francji, Hiszpanii, Mołdawii i Ukrainy.

Zespół jeleni o takim składzie gatunkowym nie był znany wcześniej z górnego pliocenu Polski. Budowa zębów, charakter starcia ich koron, opisanych gatunków jeleni sugeruje dla opisanych gatunków jeleni pokarm roślinny, który zawierał zarówno liście drzew, krzewów, jak i trawy.

Cervidae oraz skład fauny towarzyszącej wskazują na leśny charakter środowiska otaczającego stanowisko Węże 2. Obecne były także obszary pozbawione zwartej roślinności, w pobliżu znajdować się musiał duży zbiornik wodny, połączony z rozległym systemem krasowym.