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On the presence of Late Pleistocene wapiti, *Cervus canadensis* Erxleben, 1777 (Cervidae, Mammalia) in the Palaeolithic site Climăuți II (Moldova)

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Abstract

This article reports antler remains from the Late Paleolithic site of Climăuți II (Republic of Moldova) confirming the presence of wapiti *Cervus canadensis* in the Late Pleistocene of Western Eurasia. The occurrence of wapiti in the East Carpathian area by 20 ky BP coincides with the local extinction of *Megaloceros giganteus*, *Crocota spelaea*, and *Ursus spelaeus*, and substitution of local forest reindeer with grazing tundra-steppe *Rangifer tarandus constantini*. We here provide an overview of paleontological data and opinions on the presence of *Cervus canadensis* in Europe, a discussion on the taxonomic status and systematic position of the extinct deer *Cervus elaphus palmidactyloceros*, and propose a dispersal model for wapiti in Europe during the Late Pleistocene.

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Introduction

The debates on presence of wapiti-like deer in Europe have a long history since Owen (1846) described poorly represented fossil remains of an unusually large elaphine deer that rivalled the giant deer *Megaloceros giganteus* in size. Under the term “elaphine deer” we here understand the Eurasian and North American deer of the genus *Cervus* (red deer and wapiti) that were traditionally ascribed to the single species *Cervus*

elaphus (Flerov, 1952; Sokolov, 1959), but have complicated phylogenetic relationships according to the modern genetic data (Kuwayama and Ozawa, 2000). Therefore, our understanding of the “elaphine deer” group is more restricted than the definition proposed by Lydekker (1898), who also includes Thorold’s deer *Przewalskum albirostris* in his elaphine group.

Owen (1846) reported and figured an extremely large basal antler portion from the Late Pleistocene deposits of Kent’s Cavern (England) that recalled European red deer morphology but with large dimensions approaching those of the largest modern North American wapiti antlers. The antler fragment bears two basal tines (brow and bez) as in modern red deer; the circumference of the beam, according to Owen (1846), measures 381 mm (15 inches) between the brow and the bez tines. The circumference above the burr attains 375 mm, thus greatly exceeding the analogous measurements of modern European red deer *Cervus elaphus* L., which range between 220 and 230 mm (Friant, 1957). Owen (1846) defined this unusual deer antler from Kent’s Cavern as a representative of the “round-antlered section of Cervine genus” and designated it as a type specimen for a new species within the new subgenus *Strongyloceros* (together with *Cervus elaphus*, *Cervus strongyloceros*, and *Cervus canadensis*): *Cervus (Strongyloceros) spelaeus*. This proposed subgenus *Strongyloceros* thus created the tautonym *Cervus (Strongyloceros) strongyloceros* Schreber, 1836 for the type species of the subgenus. Owen (1846) assumed a close relationship of this new species from Kent’s Cavern with North American wapiti *Cervus strongyloceros* Schreber, 1836 and *Cervus canadensis* Brisson, 1756, with a remark that the deer from Kent’s Cavern may differ in having a longer distance between the brow and bez tines. The remains



Figure 2. The distal fragment of the left antler of *Cervus canadensis* from Climăuți II CLM-II-381: A, lateral view; B, upper view; C, view from the broken proximal side.

ulna Nr. 5.22, which was regarded by Friant (1957: Pl. IV, fig. 8) as evidence for the complete fusion of radius and ulna in the Kent's Cavern giant stag, actually belongs to a horse (Lister, 1987). Lister (1987), however, confirmed that the osteological remains of the cave stag from Kent's Cavern are much larger than those of any living European red deer and equal in size to modern American and Siberian wapiti. Lister (1987) also indicated stockier limb bones of the wapiti-like deer from Kent's Cavern ("too short for their breadth": *ibidem*), which approach the proportions of westernmost living wapiti *C. canadensis songaricus* (*C. elaphus songaricus* according to Lister, 1987).

Finally, the analysis of mitochondrial DNA of elaphine deer remains from Kent's Cavern revealed that they belong to European red deer *Cervus elaphus* (Meiri *et al.*, 2013), therefore the question on the presence of wapiti in the fauna from Kent's Cavern remains open. According to Lister (personal communication) the presence of wapiti in the fauna of Kent's Cavern is disproven, since the bones with *Cervus elaphus* mtDNA are large. The diagnostic distal antlers parts are missing in the European palaeontological record, representing

the main obstacle for the confirmation of wapiti (*Cervus canadensis*) in Western Eurasia (Friant, 1957).

The present communication proposes a description of antler fragments from the Palaeolithic site of Climăuți II (Dniester valley, Șoldanești Discript, Republic of Moldova) that undoubtedly attest the presence of wapiti remains in this Late Pleistocene human settlement.

The site of Climăuți II (Fig. 1) was discovered in 1989 and represents a Palaeolithic site, exceptional in Moldova, of specialized mammoth hunters with remains of a dwelling made of mammoth skulls, tusks, and scapulae (Borziac *et al.*, 2007). The majority of the fossil animal remains comes from the upper layer dated to $20\,350 \pm 230$ y. BP (David and Obada, 1996). The osteological material unearthed from the upper layer of the Climăuți site includes 1323 mammal bone fragments, the majority of which (83%) belongs to *Mammuthus primigenius* (19 individuals). The fragments of large cervid antlers ascribed to *Cervus elaphus* by Borziac *et al.* (2007) were also retrieved from the upper layer. These antler fragments bear tool marks and are the only remains representing this cervid at the site, strongly

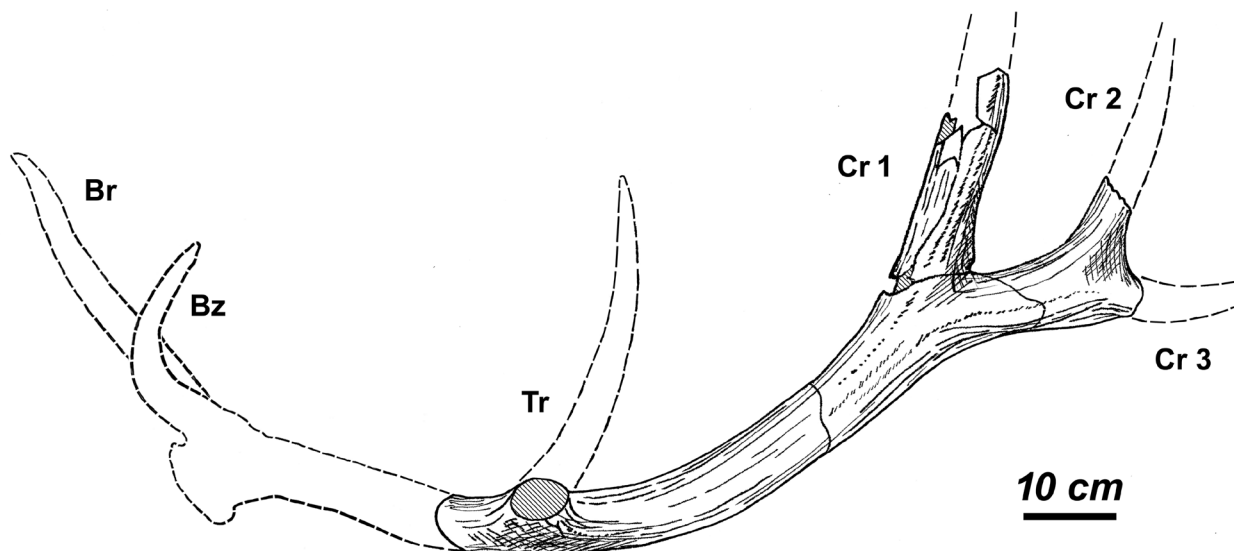


Figure 3. The reconstruction of the wapiti antler CLM-II-381 showing the missing proximal portion and the tines (dashed line): Br, brow (first basal) tine; Bz, bez (second basal) tine; Tz, trez (middle) tine; Cr, crown tine.

suggesting that the antler remains have been brought by the ancient humans to the site, possibly as raw material for product manufacture. The exceptionally large size of the antler fragments, in comparison to those of modern red deer, allowed Borziac *et al.* (2007) to conclude that the elaphine deer from Climăuți II had “des conditions excellentes de vie”. Besides the remarkably large size, the antlers possess some important diagnostic characteristics at the distal portion that permit us to attest to the presence of a new peculiar faunal element in the Climăuți II site: wapiti (*Cervus canadensis*).

Material and research methods

The antler remains from Climăuți II are stored at the Paleontological Museum of the Institute of Zoology of the Academy of Sciences of Moldova. The material is represented by a distal portion of the left antler (CLM-II-381) and a fragment of the left antler from the area of the middle (trez) tine bifurcation (CLM-II-382). Both specimens bear traces of human activity: specimen CLM-II-381 is cut below the middle tine (Fig. 2, C), while specimen CLM-II-382 bears multiple cut marks and impact pits on the medial side (Fig. 4, C).

The systematic description is focused on the morphology of the distal crown, taxonomically meaningful for systematic classification of the genus *Cervus* at the species and subspecies level (Heptner and Zalkin, 1947; Flerov, 1952; Geist, 1998). The

abbreviations used in the text are: DLM, lateromedial diameter; DAP, anteroposterior diameter; L, length, D, breadth; M, mean value; *min*, minimum; *max*, maximum.

Systematic Description

Family Cervidae Goldfuss, 1820
Subfamily Cervinae Goldfuss, 1820
Genus *Cervus* Linnaeus, 1758
Cervus canadensis Erxleben, 1777

Synonymy

1836: *Cervus canadensis* Brisson: SCHREBER, p. 990, tab. 246A.
1836: *Cervus strongyloceros* Schreber, p. 1074, tabs. 247F-G.
1846: *Cervus (Strongyloceros) spelaeus* Owen, p. 469, fig. 193.
1846: *Cervus (Strongyloceros) canadensis* Brisson: OWEN, p. 469.
1846: *Cervus (Strongyloceros) strongyloceros* Schreber: OWEN, p. 469.
1853: *Cervus intermedius* de Serres: POMEL, p. 104.
1883: *Cervus (canadensis?)* Brisson: BELGRAND, p.24, pl. 22, fig. 1.
1888: *Strongyloceros spelaeus* Owen: DE RANCE, p. 11.
1952: *Strongyloceros spelaeus* Owen: FRIANT, p. 1398.
2010: *Cervus elaphus spelaeus* Owen: VAN DER MADE, p. 434.

Taxonomic remarks

Schreber (1836) granted the authorship of the species *Cervus canadensis* to Brisson (1756). Nonetheless,

Brisson's "Regnum Animale" is regarded today as unavailable for zoological taxonomy, since Brisson (1756) did not apply binominal zoological nomenclature in his species descriptions. Also, according to the Article 3.2 of the International Code of Zoological Nomenclature, no name published before 1758 enters zoological nomenclature. Although a number of important generic names are currently accepted as from Brisson (Gentry, 1994), none of his specific names are accepted as available. Regarding the case of *Cervus canadensis* in particular, we add that "Cervus Canadensis" as mentioned by Brisson (1756) is directly quoted from Ray (1693: p. 84) who used it together with "Cervus Europaeus" as an indication of the geographic provenance of the common deer *Cervus*, not as a binominal term. Therefore, these quotations should not be regarded as available species designations.

Thus, Erxleben (1777) was the first who introduced the binominal species name *Cervus canadensis* for the Canadian stag or wapiti. Schreber (1836) proposed a new species name for a large form of North American deer *Cervus strongyloceros* accompanied by a brief description and figures representing a pelage color of a female and a shed antler. In the same work, Schreber (1836) published a description of "Cervus canadensis Brisson" supplemented with a figure of a stag with fantastic undulated antlers, suggesting that the author was poorly acquainted with this species.

Severtzoff (1873, 1876) was the first who noticed the striking resemblance between Siberian "*Cervus maral*" (not to be confused with *Cervus elaphus maral* Ogilby currently given to the Caspian red deer) and North American *Cervus canadensis*, indicating that the only difference between those two cervid forms is that Canadian deer lack the seasonal change in pelage color (based on an observation of only two captive individuals).

Lydekker (1898) regarded wapiti as a valid species *Cervus canadensis* and introduced a new subspecies name *C. canadensis asiaticus* for Asian wapiti which apparently represents a modification of *Cervus maral asiatica* as quoted from Severtzoff (1873). According to Allen (1930), Severtzoff (1873) used the term *asiatica* in a group sense, not as a technical name, and therefore it should be rejected, while the name *C. canadensis asiaticus* should then derive from Lydekker (1898).

Heptner and Zalkin (1947: 69) consider that populations of Siberian wapiti in natural conditions are genetically isolated from Western and Central Asian red deer (i.e. European forms of *Cervus elaphus* and the Asian subspecies *C. elaphus yarkandensis*,

C. elaphus hanglu, *C. elaphus affinis*, and *C. elaphus bactrianus*), stressing, however, that the areas of distribution of Asian wapiti and red deer forms never overlap, therefore most probably we are dealing with subspecies of the same species. The easy hybridization between wapiti and red deer is also regarded by Heptner and Zalkin (1947) as an argument for including various geographical elaphine forms as subspecies in the single species *Cervus elaphus*.

Flerov (1952: 175) included Asian wapiti in the subspecies *C. elaphus canadensis* together with North American wapiti. Sokolov (1959) rejected Flerov's (1952) viewpoint and suggested that the remarkable similarity in pelage coloring and antler shape of *Cervus elaphus sibiricus* Severtzov and *Cervus elaphus canadensis* Erxleben should be regarded as an evolutionary parallelism and preferred to keep them as distinct subspecies of *Cervus elaphus* Linnaeus.

Schonewald (1994), however, concluded that the differences in behavior (male vocalization), differences in sexual dimorphism, and semi-lethal (less viable) hybridization, support a species rank of *Cervus canadensis*.

Geist (1998) regards wapiti as an eastern radiation of red deer that moved into dry, cold, continental regions and adapted to a grazing lifestyle in open landscapes. Although Geist (1998) continues to regard wapiti as a group of subspecies within *Cervus elaphus*, he confirms an effective reproductive isolation under natural conditions between Asian wapiti and the red deer subspecies *C. elaphus yarkandensis*. Although hybrids between wapiti and European red deer are obtained in captivity, Geist (1998) reports a poor health condition of such hybrids that likely would cause a low survival rate under natural conditions. Geist (1998) also reports ethological, physiological, and biological differences between wapiti and European red deer: the character of rutting call, courtship postures, differences in annual biological cycles, etc.

The species rank of *Cervus canadensis* is supported by recent genetic studies. Kuwayama and Ozawa (2000) revealed a closer phylogenetic relationship of Asian and North American wapiti with sika deer (*Cervus nippon*) than with Western (European) red deer (*Cervus elaphus*) inferred from mitochondrial DNA sequences. The mitochondrial DNA analysis carried out by Pitra *et al.* (2004) and Ludt *et al.* (2004) confirmed the monophyletic character of both Western red deer group and Eastern wapiti group and a closer association of wapiti with *Cervus nippon* and *Przewalskium albirostris*. Taking into consideration

Table 1. *Cervus canadensis* from Climăuți II: measurements of the antler CLM-II-381.

Measurements	mm
Distance between the trez and first crown tines	410.0
DLM of the antler beam between the trez tine and the crown	52.1
DAP of the antler beam between the trez tine and the crown	55.5
D max of the trez tine	43.7
D min of the trez tine	42.3
D max of the beam below the trez tine	74.7
D min of the beam below the trez tine	55.0
Circumference of the beam below the trez tine	211.0

the evidence on reproductive isolation of wapiti and Western red deer populations under natural conditions (Heptner and Zalkin, 1947; Geist, 1998), the physiological, ethological, and ecological differences reported by Geist (1998), confirming that Western red deer and wapiti occupy different ecological niches, and the genetic data opposing Western red deer to wapiti and sika deer, we regard wapiti as a valid species, *Cervus canadensis*, that is clearly distinct from red deer *Cervus elaphus*.

Wapiti remains from Climăuți II

The specimen CLM-II-381 represents a distal portion of left antler with basal part of middle (trez) tine and partially preserved crown tines (Figs. 2, 3). The antler surface bears weak longitudinal ribs and furrows and is covered with fine pearling, which is weak compared to that seen in European *Cervus elaphus*. The middle tine springs off sideward and forms an angle of 80° with the beam. The crown shape represents a comb-like

morphological pattern typical for *Cervus canadensis*: the antler crown consists of three tines that are situated almost in the same plane (more or less parasagittal with respect to the animal's main body axis). The first crown tine is the strongest and apparently the longest as well, as is typical for *Cervus canadensis*. The two distal tines are somewhat inwardly curved (towards the sagittal plane). The antler beam is cylindrical between the middle tine and the distal crown (Table 1); however, the antler becomes somewhat flattened in the area of bifurcations. The cross-section of the middle tine is circular, while the crown tines are significantly medio-laterally compressed.

The circumference of the antler beam between the bez and trez tines of specimen CLM-II-381 (Tab. 2) is just slightly below the mean value of antler circumference above the bez tine of the sample of modern *C. canadensis* from North America reported by Lydekker (1898) and is slightly larger than the maximal value of the sample of antlers of modern *C. canadensis* from Alaska reported by Boeskorov (2005). It should be noted that the sample described by Lydekker (1898) includes exceptionally large hunter trophies. The antler from Climăuți II corresponds to the most robust antlers of *C. canadensis cherskii* from the Late Pleistocene of Eastern Siberia (Tab. 2). The length of the beam segment between the trez tine and the first crown tine is absolutely and relatively significantly longer in the antler from Climăuți II than in the holotype of *C. canadensis cherskii* (ca. 147 mm; measured from Fig. 2d in Boeskorov, 2005) with respect to the circumference of the beam segment between the bez and trez tines, which attains 190 mm in the holotype of *C. canadensis cherskii*. The relative length of distal beam segment is regarded by Boeskorov (2005) as one of the diagnostic characters of his subspecies. The distance between the trez tine and the first crown tine in the antler from Climăuți is also much longer than the analogous measurement in *C. canadensis fossilis*

Table 2. Circumference of the antler beam (mm) between the middle (trez) tine and the crown in fossil and modern *Cervus canadensis*.

Specimen / sample	Geographical provenance	Beam circumference (max – M – min)	Number of specimens	Data source
CLM-II-381	Moldova	176.0	1	This study
CLM-II-382	Moldova	206.0	1	This study
<i>C. canadensis cherskii</i>	Eastern Siberia	165.0 – 186.7 – 210.0	6	Boeskorov (2005)
<i>C. canadensis</i>	North America	174.6 – 218.1 – 228.6	19	Lydekker (1898)
<i>C. canadensis</i>	Alaska	168.0 – 187.5 – 210.0	10	Boeskorov (2005)



Figure 4. The fragment of the left antler of *Cervus canadensis* from Climăuți II CLM-II-382 with basal portion of the broken middle tine: A, lateral side; B, upper side; C, middle side with cut marks.

Zdansky, 1925 (255 mm) from the Pleistocene of China (Zdansky, 1925: Pl. XV, fig. 1). However, the antler of Chinese wapiti has a longer crown part.

The second specimen CLM-II-382 represents a portion of the beam (ca. 37 cm in length) from the area of the trez tine bifurcation and belongs to a somewhat larger antler (Fig. 4): DLM and DAP of the beam above the middle tine bifurcation are 64.3 mm and 64.5 mm respectively. The beam circumference above the middle tine places this specimen among the most robust wapiti antlers (Tab. 2). Therefore, the antlers from Climăuți II are as robust and large as the larger antlers of modern North American *Cervus canadensis* and exceed the largest specimens of fossil wapiti from Eastern Siberia in robusticity.

Discussion

The modern distribution of Asian *C. canadensis* ranges from Tian-Shan and Altai to the Far East and includes mountainous areas and lowland boreal forests (Flerov, 1952; Sokolov, 1959). Three subspecies of Asian wapiti are recognized by Flerov (1952): the most

advanced and largest *C. canadensis canadensis* (= *C. canadensis sibirica*) with large, six-pointed antlers that occupies mountain biotopes and that is practically indistinguishable from North American wapiti; the smaller southern form *C. canadensis alashanicus* with an advanced pattern of rump patch and antlers of typical wapiti form but somewhat smaller; and the lowland-forest dweller *C. canadensis xanthopygus* with primitive (or pedomorphic) characters of body color and social organs, including smaller antlers with a short, poorly developed distal portion and a poorly distinguished rump patch (Heptner and Zalkin, 1947; Flerov, 1952; Sokolov, 1959; Geist, 1998). The northern border of the area of distribution of modern Asian wapiti lies in Central Yakutia; however, the palaeontological record indicates a much broader Late Pleistocene area of distribution reaching the far Northeast Asia (Boeskorov, 2005). *Cervus canadensis cherskii* from the Late Pleistocene of Eastern Siberia, is slightly smaller than modern North American *C. canadensis canadensis*, but its antlers are relatively larger (Boeskorov, 2005). Boeskorov (2005) also reports the relatively long distance between bez and trez tines as a distinguishing taxonomic character of

Late Pleistocene Siberian wapiti. Nonetheless, the peculiar antler proportions in Late Pleistocene wapiti seem to be caused by the shortened distal portion of the antler that approaches *C. canadensis cherskii* to modern *C. canadensis xanthopygus*, thus suggesting the primitive condition of the short distal part of antlers in these wapitis. The relatively broad metapodials of *C. canadensis cherskii* represent a remarkable affinity with the robust metapodials of the cave stag from Kent's Cavern reported by Lister (1987).

The finding of wapiti antlers in the Paleolithic site of Climăuți II confirms the dispersal into Western Eurasia of wapiti, coinciding in Moldova with a local faunal turnover shortly before 20 ky BP: the local extinction of *Megaloceros giganteus*, *Crocota spelaea*, and *Ursus spelaeus*, as well as the substitution of local forest reindeer (*Rangifer tarandus* ssp.) with Siberian grazing tundra-steppe subspecies *Rangifer tarandus constantini* (Croitor, 2018). The poor preservation of the wapiti remains at Climăuți II (represented so far only by two humanly-imported specimens) may be explained by the cultural tradition of mammoth-specialized hunters at Climăuți (Borziac *et al.*, 2007). Although we have only one individual, the relatively longer distal portion of antler from Climăuți II may suggest that we are dealing here with a quite advanced form of wapiti, more advanced than *C. canadensis xanthopygus* and *C. canadensis cherskii*, however, this conclusion should be taken with caution. The presence of wapiti in South-Eastern Europe was earlier attested by the analysis of mtDNA sequences from Late Pleistocene remains of elaphine deer from the Emine-Bair-Khosar Cave in Crimea, Ukraine (Stankovic *et al.*, 2011). According to these authors, two Crimean specimens dated back to $33,100 \pm 400$ BP and $42,000 \pm 1200$ BP belong to a wapiti closely related to the modern southern form *C. canadensis songaricus* (synonymized with *C. canadensis canadensis* by Flerov, 1952, or with *C. canadensis sibirica* by Sokolov, 1959). Stankovic *et al.* (2011) regard the arrival of wapiti in Crimea as a part of invasion of cold-loving forms into Eastern Europe at the end of the Würm II/Würm III Interstadial period. According to Stankovic *et al.* (2011), the modern Altai environmental conditions, where Asian wapiti survived, represent the recent analogue of the environment of the full-glacial period of Central Europe. The exceptionally large postcranial and dental remains of an elaphine deer (larger than elaphine remains from Kent's cavern) were reported from the Peștera cu Oase site, Romania (Parfitt and

Lister, 2013). The mitochondrial DNA extracted from the Romanian sample indicate clearly that the Romanian elaphine deer falls within the “wapitoid” clade (Parfitt and Lister, 2013; Meiri *et al.*, in press)

The confirmed presence of wapiti in Europe is important for our understanding of the poorly known elaphine deer with palmated antlers from the Late Pleistocene and Early Holocene of Italy. *Cervus elaphus palmydactyloceros* De Stefano, 1911 is a peculiar and still poorly understood large-sized form of elaphine deer with distal portions of the antlers extending into palmations. The distal antler part consists of a flattened beam with several tines situated in the parasagittal plane (with the exception of the specimen in Tab. XIV, fig. 1 in De Stefano, 1911, where a crown tine is split into a transversally-oriented fork), unlike the multiaxial crown as typical for European red deer. De Stefano (1911) clearly distinguished this large-sized elaphine deer with palmated antlers from *C. elaphus maral* Ogilby, which he also reported from Italy. De Stefano (1911), however, rejected the idea that *C. elaphus palmidactyloceros* could be related to *Cervus canadensis*. The elaphine deer remains with palmated antlers come from the Late Pleistocene and the cold phase of the Younger Dryas in Italy (De Stefano, 1911; Abbazzi, 1995). The body size of De Stefano's deer is very large: the condylobasal skull length, as measured from the photo published by Abbazzi (1995), is ca. 430 mm and falls within the range of variation of modern Siberian *C. canadensis canadensis* (411-444 mm) reported by Flerov (1952). *C. elaphus palmidactyloceros* is characterized by remarkable distal palmations of its antlers with the palmation tines situated more or less in the same plane as in wapiti. Abbazzi (1995) casted doubts on the validity of *C. elaphus palmidactyloceros*, suggesting that the palmated distal portion of antler rather represents an individual variation of European red deer, noticing that some of the specimens ascribed by De Stefano (1911) to *C. elaphus palmidactyloceros* are not palmated. Abbazzi (1995) also quotes some examples of occasional development of palmation under certain conditions in some individuals of wapiti, which she regards as a subspecies of *Cervus elaphus*. Indeed, unlike European red deer, wapiti *Cervus canadensis* generally grows more flattened antlers that occasionally may develop palmations. The “palmated” variants of antlers are found in some individuals of modern Asian wapiti (Heptner and Zalkin, 1946: 25), as well as in North American wapiti (Nelson, 1902: fig. 3). Actually, the variability of palmation in the Italian

sample does not exclude the validity of the taxon *C. elaphus palmidactyloceros*, characterized by a large body size and frequent development of distal antler palmations, while the examples of the occasional development of palmated antlers in red deer quoted by Abbazzi (1995) in fact concern *Cervus canadensis*. Therefore, we suggest that the large elaphine deer with palmated antlers from the Italian Peninsula is a local form of wapiti, *Cervus canadensis palmidactyloceros* De Stefano, 1911. Apparently, *C. canadensis palmidactyloceros* entered the Italian Peninsula during the Last Glacial Maximum and became extinct after the cold phase of Younger Dryas.

Conclusions

The distal part of the large elaphine deer antler from Climăuți II provides important diagnostic characters confirming the presence of wapiti (*Cervus canadensis*) in Western Eurasia during the last glaciation. The wapiti antler from Climăuți II is characterized by a relatively long beam segment between the middle (trez) tine and the first crown tine, regarded here as an advanced character opposite to the short distal antler part of modern *C. canadensis xanthopygus* from the Far East and the Late Pleistocene *C. canadensis cherskii* from Eastern Siberia. The comb-like crown of the antler from Climăuți II is composed of three tines situated in almost the same parasagittal plane. The dispersal of wapiti into the East Carpathian area may have been caused by climate changes that triggered the local extinction of *Megaloceros giganteus*, *Crocota spelaea*, and *Ursus spelaeus*, and the substitution of local forest reindeer with Siberian grazing tundra-steppe subspecies *Rangifer tarandus constantini*. The Late Pleistocene wapiti reached the far North-West of Europe, where it was described as *Strongyloceros spelaeus* Owen, 1846 (a junior synonym of *Cervus canadensis* Erxleben, 1777) and even dispersed into the Italian Peninsula, where it survived until the cold phase of Younger Dryas as an endemic glacial holdover, *C. canadensis palmidactyloceros* De Stefano, 1911.

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References

- Abbazzi L. 1995. Occurrence of palmated *Cervus elaphus* from Italian Late Pleistocene localities. *Atti della Accademia Nazionale dei Lincei, Scienze Fisiche e Naturali, Serie IX*, 6(3): 189-206.
- Ahlén I. 1965. Studies on the red deer, *Cervus elaphus* L., in Scandinavia. 1. History of distribution. *Swedish Wildlife*, 3: 1-88.
- Allen GM. 1930. Pigs and deer from the Asiatic expeditions. *American Museum Novitates*, 430: 1-19.
- Belgrand E. 1883. *La Seine : I. Le bassin parisien aux âges antéhistoriques*. Paris: Imprimerie Nationale.
- Boeskorov GG. 2005. Taxonomic position of the Red Deer *Cervus elaphus* L. (Cervidae, Artiodactyla, Mammalia) from the Neopleistocene of Northeastern Asia. *Paleontological Journal*, 5 : 73-84.
- Borziac I, Chirica V, David A. 2007. *L'Aurignacien moyen et tardif de l'espace carpatique-dnestreen. Le gisement Climăuți II*. Iași: Institut d'Archeologie, Edition PIM.
- Brisson MJ. 1756. *Regnum Animale in classes IX distributum, sive synopsis methodica sistens generalem animalium distributionem in classes IX, & duarum primarum classium, quadrupedum scilicet & cetaceorum, particularem divisionem in ordines, sectiones, genera & species*. Parisiis: Bauche.
- Croitor R. 2018. Paleobiology as a clue to Paleolithic taphonomy: the case of reindeer hunting in Moldova. *Quaternaire* 29(1): 81-86.
- Croitor R, Stefaniak K, Pawłowska K, Ridush B, Wojtal P, Stach M. 2014. Giant deer *Megaloceros giganteus* Blumenbach, 1799 (Cervidae, Mammalia) from Palaeolithic of Eastern Europe. *Quaternary International*, 326-327: 91-104.
- David A, Obadă Th. 1996. Fauna de mamifere din săpăturile stațiunii paleolitice Climăuți II. *Buletinul Academiei de Științe Republicii Moldova, Științe biologice și chimice*, 1: 42-48.
- De Stefano G. 1911. I mammiferi preistorici dell'Imolese. *Palaeontographia Italica*, 17: 49-139.
- Erxleben ICP. 1777. *Systema regni animalis per classes, ordines, genera, species, varietates: cum synonymia et historia animalium: Classis I. Mammalia*. Lipsiae: Impensis Weygandianis.
- Heptner VG, Zalkin VI. 1947. Deer of the USSR (Systematics and Zoogeography). *Transactions on Study of Fauna and Flora of the USSR, the Moscow Society of Naturalists*, 10(25): 1-176 (in Russian).
- Higham T, Compton T, Stringer C, Jacobi R, Shapiro B, Trinkaus E, Chandler B, Gröning F, Collins C, Hillson S, O'Higgins P. 2011. The earliest evidence for anatomically modern humans in northwestern Europe. *Nature*, 479 (7374): 521-524.
- Flerov KK. 1952. *Musk deer and deer. The Fauna of USSR. Mammals, 1(2)*. Moscow-Leningrad: Publishing House of Academy of Sciences (in Russian).
- Friant M. 1952. Le *Strongyloceros spelaeus* Owen (Cerf géant des Cavernes). *Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences*, 234 : 1398-1400.
- Friant M. 1957. Le *Strongyloceros spelaeus* Owen de Kent's Hole (Angleterre). *Annales de la Société Géologique du Nord*, 77 : 57-74.
- Geist V. 1998. *Deer of the World: Their Evolution, Behavior and*

- Ecology*. Mechanicsburg: Stackpole Books.
- Gentry A. 1994. Case 2928. *Regnum Animale...*, Ed. 2 (M. J. Brisson, 1762): proposed rejection with the conservation of the mammalian generic names *Philander* (Marsupialia), *Pteropus* (Chiroptera), *Glis*, *Cuniculus* and *Hydrochoerus* (Rodentia), *Meles*, *Lutra* and *Hyaena* (Carnivora), *Tapirus* (Perissodactyla), *Tragulus* and *Giraffa* (Artiodactyla). *Bulletin of Zoological Nomenclature*, 51(2): 135-146.
- Gervais P. 1861. Notes sur différentes espèces de vertébrés fossiles observés pour la plupart dans le midi de la France. *Annales des Sciences Naturelles, Quatrième Série, Zoologie*, 16 : 286-302.
- Gervais P. 1872. Rapport sur les découvertes faites dans la Grotte de Loubeau, pres Melle. *Archives des Missions Scientifiques et Littéraires*, 7 : 531-536.
- Kuwayama R, Ozawa T. 2000. Phylogenetic relationships among European Red Deer, Wapiti, and Sika Deer inferred from mitochondrial DNA sequences. *Molecular Phylogenetics and Evolution*, 15(1): 115-123.
- Lister AM. 1987. Giant deer and giant red deer from Kent's Cavern, and the status of *Strongyloceros spelaeus* Owen. *Transactions and Proceedings of the Torquay Natural History Society*, 19: 189-198.
- Lister AM. 1994. The evolution of the giant deer, *Megaloceros giganteus* (Blumenbach). *Zoological Journal of the Linnaean Society*, 112: 65-100.
- Ludt CJ, Schroeder W, Rottmann O, Kuehn R. 2004. Mitochondrial DNA phylogeography of red deer (*Cervus elaphus*). *Molecular Phylogenetics and Evolution*, 31(3): 1064-1083.
- Lydekker R. 1898. *Deer of All lands: A History of the Family Cervidae Living and Extinct*. London: Rowland Ward, Ltd..
- Lydekker R. 1915. *Catalogue of the Ungulate Mammals in the British Museum (Natural History). Vol. IV. Artiodactyla, Families Cervidae (Deer), Tragulidae (Chevrotains), Camelidae (Camels and Llamas), Suidae (Pigs and Peccaries), and Hippopotamidae (Hippopotamuses)*. London: Trustees of the British Museum.
- Meiri M, Lister AM, Higham TF, Stewart JR, Straus LG, Obermaier H, Gonzalez Morales MR, Marín-Arroyo AB, Barnes I. 2013. Late-glacial recolonization and phylogeography of European red deer (*Cervus elaphus* L.). *Molecular Ecology*, 22 (18): 4711-4722.
- Meiri M, Barnes I, Kosintsev P, Meiri S, Conroy K, Lister AM. In press. Subspecies dynamics in space and time: a study of the red deer complex using ancient and modern DNA and morphology. *Journal of Biogeography*, DOI: 10.1111/jbi.13124
- Nelson EW. 1902. A new species of elk from Arizona. *Bulletin of American Museum of Natural History*, 16: 1-12.
- Owen R. 1846. *A History of British Fossil Mammals, and Birds*. London: John van Voorst.
- Parfitt SA, Lister AM. 2013. The Ungulates from the Peștera cu Oase. In: Trinkaus E, Constantin S, Zilhao J, eds. *Life and Death at the Peștera cu Oase: A Setting for Modern Human Emergence in Europe*. Oxford: Oxford University Press, 189-203
- Pitra C, Fickel J, Meijaard E, Groves C. 2004. Evolution and phylogeny of old world deer. *Molecular Phylogenetics and Evolution*, 33(3): 880-895.
- Pomel, M. 1853. Catalogue méthodique et descriptif des vertébrés fossiles découverts dans le bassin hydrographique de la Loire. Paris : chez J.-B. Baillière.
- Rance CE. De 1888. Notes on the Vale of Clwyd Caves. *Proceedings of the Yorkshire Geological and Polytechnic Society*, 11(1): 1-20.
- Ray J. 1693. *Synopsis Methodica Animalium Quadrupedum et Serpentina Generis*. London: Impensis S. Smith & B. Walford.
- Severtzoff NA. 1873. Altitudinal and latitudinal distribution of Turkestan animals. *Proceedings of the Imperial Society of Naturalists, Anthropologists, and Ethnographers*, 8(2): 1-157 (in Russian).
- Severtzoff NA. 1876. The Mammals of Turkestan. *The Annals and Magazine of Natural History, including Zoology, Botany, and Geology*, 18(4): 377-388.
- Schonewald C. 1994. *Cervus canadensis* and *C. elaphus*: North American subspecies and evaluation of clinal extremes. *Acta Theriologica*, 39(4): 431-452.
- Schreber JCD. Von 1836. *Der Säugetiere in Abbildungen nach der Natur. Abteilung 5*. Erlangen: Wolfgang Walther.
- Sokolov II. 1959. *Hoofed Animals (Orders Perissodactyla and Artiodactyla). Fauna of the USSR. Mammals, 1 (3)*. Moscow-Leningrad: Publishing House of Academy of Sciences.
- Stankovic A, Doan K, Mackiewicz P, Ridush B, Baca M, Gromadka R, Socha P, Weglenski P, Nadachowski A, Stefaniak K. 2011. First ancient DNA sequences of the Late Pleistocene red deer (*Cervus elaphus*) from the Crimea, Ukraine. *Quaternary International*, 245(2): 262-267.
- van der Made J. 2010. The rhinos from the Middle Pleistocene of Neumark-Nord (Saxony-Anhalt). *Veröffentlichungen des Landesamtes für Archeologie*, 62: 432-527.
- Zdansky O. 1925. Fossile Hirsche Chinas. *Palaeontologia Sinica*, Series C, 2(3): 1-90.

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